



Trabecular structure of the proximal and distal ulna in extant primates

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Abstract

Trabecular bone (re)models in response to localized mechanical loading, potentially enabling inferences about the positional behavior of extinct taxa. However, the trabecular architecture of the ulna remains understudied in extant primates, particularly regarding whether it reflects habitual joint posture and loading. Across a broad sample of anthropoid primates, including apes, atelids, and cercopithecoids, we quantified the relative bone volume fraction (rBV/TV) of trabeculae in the proximal and distal ulna and applied a two-block partial least squares analysis between rBV/TV and locomotor frequencies to explore the relationship between trabecular bone and



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locomotor behavior. In the distal ulna, high rBV/TV values at the tip of the styloid process in non-hominoids are consistent with its known role in load transmission through the ulnocarpal articulation. In hominoids, the absence of direct articulation with the carpus offloads internal stresses, weakening the functional signal in the trabeculae, which is consistent with the lack of covariation between rBV/TV and the quantified locomotor behaviors. In contrast, proximal ulnar trabecular structure covaries with the frequency of quadrupedalism and captures clearer functional signals; arboreal monkeys display mediolateral stress patterns consistent with mobile, semipronated elbow use, whereas terrestrial monkeys show compressive patterns linked to semiflexed, pronated elbow use. *Symphalangus* show dense trabecular reinforcement around the triceps insertion related to forelimb overhead reaching, while hominid trabecular patterns appear related to more versatile locomotor behaviors, with *Gorilla* and *Pongo* showing evidence of extended-elbow loading. Overall, our results indicate that the proximal ulna more accurately reflects loadings related to locomotor behavior than the distal ulna, providing a valuable framework for inferring locomotor behaviors in fossil primates.

Keywords Monkeys · Hominoids · Locomotor behavior · Functional morphology · Elbow · Wrist

Introduction

Previous studies have thoroughly examined the external morphology of the ulna in primates from a functional perspective, particularly in relation to locomotor behaviors. Diaphyseal features, such as ulnar curvature, provide valuable functional information with more curved ulnae generally characterizing taxa that engage more frequently in arboreal locomotion and climbing, whereas straighter ulnae are more typical of predominantly terrestrial taxa (Milne & Granatosky, 2021). In addition, the external shape of the proximal and distal epiphyses correlates with ranges of joint mobility and stability at the elbow and the wrist, respectively (Lewis, 1965, 1969; Lewis *et al.*, 1970; O'Connor, 1975; Cartmill & Milton, 1977; Rose, 1983, 1993a, 1997; Nakatsukasa *et al.*, 1996; Drapeau, 2004; Rein *et al.*, 2015). Indeed, ulnar morphological variation across primates—such as olecranon length (Harrison, 1982), trochlear notch shape (Rose, 1988, 1993b; Nakatsukasa *et al.*, 1996; Richmond *et al.*, 1998; Drapeau, 2008), coronoid orientation (Conroy, 1976; Rose, 1997), ulnar head expansion (Lewis, 1965, 1969; Lewis *et al.*, 1970; Sarmiento, 1985, 1988), styloid process length, and ulnocarpal articulation (Lewis, 1965, 1969; O'Connor, 1975; Cartmill & Milton, 1977; Sarmiento, 1985, 1988; Sarmiento *et al.*, 2002; Orr *et al.*, 2024)—reflects the functional requirements of particular locomotor behaviors. For example, the proximal ulna of great apes combines a short olecranon for enhanced elbow extension and a broad trochlear notch with a median keel to resist mediolateral forces incurred during arboreal locomotor behaviors given their large body size (Rose, 1983, 1988, 1993a, b; Sarmiento, 1985; Nakatsukasa *et al.*, 1996; Drapeau *et al.*, 2005). Non-hominoid primates show features providing joint stability during

flexed postures typically used during quadrupedalism (Rose, 1983, 1988, 1993a, b), such as a long olecranon, an anteriorly directed coronoid process, and a strongly concave radial notch. The proximal ulna of hylobatids represents a specialized condition marked by a combination of features that reduce joint stress, including a moderately developed keel and laterally oriented trochlea (Sarmiento, 1985; Takahashi, 1990; Hunt, 1991; Isler, 2005; Zihlman *et al.*, 2011), and soft tissue characteristics, such as robust collateral ligaments (Michilsens *et al.*, 2009), which may be related to the use of specialized suspensory behaviors, including ricochet brachiation.

Distal ulnar morphology also reflects differences in mobility and stabilization strategies of the wrist. In hominoids, the distal ulna shows a reduced or absent direct ulnocarpal contact and a greater reliance on soft tissue structures to stabilize the joint without compromising mobility, consistent with the demands of suspensory and other arboreal behaviors in which a wide range of pronosupination movements is required (O'Connor, 1975; Cartmill & Milton, 1977; Sarmiento, 1988). In contrast, quadrupedal non-hominoid anthropoids show a close-packed ulnocarpal articulation that increases joint stability, particularly during in weight-bearing locomotor modes, such as quadrupedalism (Lewis, 1965, 1969; Lewis *et al.*, 1970; O'Connor, 1975; Cartmill & Milton, 1977; Sarmiento, 1985, 1988; Sarmiento *et al.*, 2002).

Many studies use functionally relevant traits of ulnar external morphology identified in extant primates to make paleobiological inferences about fossil primates (Lewis, 1972; Rose, 1983, 1993a, 1997; Harrison, 1989; Nakatsukasa *et al.*, 1996; Drapeau, 2004; Alba *et al.*, 2012; Dayer & Nakatsukasa, 2015; Rein *et al.*, 2015; Nishimura *et al.*, 2022; Pina & Nakatsukasa, 2024; Raventós-Izard *et al.*, 2025). However, while external morphology can provide insight into joint function, epiphysis shape is more genetically determined than more plastic aspects of bone structure (e.g., diaphyseal cortical thickness, trabecular structure) and thus does not necessarily reflect the full extent of actual use during life (Lanyon, 1980; Ruff *et al.*, 2013). Instead, internal bone microarchitecture and, especially, trabecular bone structure may be (re)modeled throughout life in response to the direction, magnitude and frequency of mechanical loading, providing complementary information about function during life (Jacobs, 2000; Rubin *et al.*, 2002; Pontzer *et al.*, 2006; Ryan & Walker, 2010; Barak *et al.*, 2011, Barak, 2020; Ryan & Shaw, 2012; Kivell *et al.*, 2016a). In other words, while external ulnar morphology provides valuable insight into an animal's locomotor and postural adaptations (the potential niche), integrating trabecular bone analysis may offer a more comprehensive understanding of how these joints were actually used (the realized niche). For a thorough discussion of the terminology used to describe the processes leading to trabecular plasticity, see Barak (2020).

Trabecular Bone Structure

Although trabecular bone develops from a genetically influenced developmental blueprint, throughout life it is (re)modeled in response to localized mechanical loading during habitual behaviors through the addition and resorption of bone tissue, modifying the shape and structure of trabecular struts to reduce strain and prevent fractures (Biewener *et al.*, 1996; Rodan, 1997; Mittra *et al.*, 2005; Pontzer *et al.*,

2006; Ruff *et al.*, 2006; Barak *et al.*, 2011; Harrison *et al.*, 2011; Sinclair *et al.*, 2013). Other factors, such as genetics, age, sex, hormones, and body size, can also influence trabecular bone structure (Turner *et al.*, 2000; Loewen *et al.*, 2001; Khosla *et al.*, 2006; Ryan & Shaw, 2012, 2013; Paternoster *et al.*, 2013; Ryan *et al.*, 2017; Tsegai *et al.*, 2018; Alfieri *et al.*, 2025). In this context, variation between groups (e.g., sex differences, species differences) in trabecular architecture may reflect not only local mechanical loading during an individual's ontogeny, but also other biological factors—including genetic ones—which might potentially lead to phylogenetic effects (i.e., phylogenetic constraints and/or embedded phylogenetic signal). These influences are generally expressed systemically, affecting the trabecular bone throughout the skeleton rather than producing localized patterns within individual joints. Unfortunately, the extent to which trabecular organization is inherited (and, hence, subject to natural selection) or is (re)modeled as a result of external bone morphology irrespective of loadings remains poorly understood (but see Pietrobelli *et al.*, 2026). Nevertheless, the relationship between trabecular organization and behavioral differences has been well documented experimentally (Barak *et al.*, 2011; Pontzer *et al.*, 2006) and across several skeletal elements (Ryan & Shaw, 2012; Tsegai *et al.*, 2013; Saers *et al.*, 2019).

Many previous studies on primate trabecular bone architecture have focused on the lower limbs (Su *et al.*, 2013; Saers *et al.*, 2016; Tsegai *et al.*, 2017; Sylvester & Terhune, 2017; Georgiou *et al.*, 2018, 2019, 2020; Cazenave *et al.*, 2019; Lukova *et al.*, 2024, 2025). In contrast, comparatively fewer studies have assessed the internal bone structure of the primate forelimb, with most of previous work concentrating on the hand (Marchi, 2005; Bird *et al.*, 2021, 2022; Dunmore *et al.*, 2019, 2020; Syeda *et al.*, 2023, 2024). For example, metacarpal cortical bone cross-sectional properties can distinguish habitual locomotor behaviors among extant great apes (Marchi, 2005; Patel *et al.*, 2020). Likewise, analyses of trabecular bone in the metacarpals have produced results consistent with interspecific differences in observed patterns of finger and thumb use (Tsegai *et al.*, 2013; Stephens *et al.*, 2016; Dunmore *et al.*, 2019, 2020, 2024). Investigation of internal cortical bone structure of proximal and intermediate manual phalanges in hominoids indicate variation consistent with differences in locomotor and manipulative behaviors (Doden, 1993; Matarazzo, 2015; Syeda *et al.*, 2023, 2024). Moreover, the carpals' functional morphology of trabecular bone suggests that internal bone structure in the capitate, scaphoid, lunate, and triquetrum shows functional responses and can reflect differences in locomotor modes in extant hominoids (Bird *et al.*, 2021, 2022; Schilling *et al.*, 2014). Beyond the hand, recently Farrell *et al.* (2025) investigated trabecular bone with the primate clavicle.

Regarding the long bones of the forelimb, research has focused primarily on the humerus (Ruff & Jones, 1981; Fajardo & Müller, 2001; Ryan & Shaw, 2012, 2013; Shaw & Ryan, 2012; Mather *et al.*, 2013; Scherf *et al.*, 2013; Kivell *et al.*, 2018; Arias-Martorell *et al.*, 2021), with the radius and ulna remaining comparatively understudied (but see Chirchir, 2015, 2019; Turcotte *et al.*, 2026). In the proximal humerus, multiple studies have explored potential functional signals in trabecular bone structure, although results have been mixed (Fajardo & Müller, 2001; Ryan & Shaw, 2012, 2013; Shaw & Ryan, 2012; Scherf *et al.*, 2013). Traditional trabecular bone analyses have primarily relied on extracting one or a few localized

three-dimensional cubic volumes of interest (VOIs) positioned manually within an epiphysis (Fajardo & Müller, 2001; Ryan & Ketcham, 2002a, b; Maga *et al.*, 2006). However, this method has notable limitations (Maga *et al.*, 2006; Lazenby *et al.*, 2011), particularly regarding VOI placement, because the results may vary depending on the location of the VOI (Kivell *et al.*, 2018). More recently, analyses considering the entire epiphysis have shown greater potential for distinguishing functional signals of joint loading across extant primates (Kivell *et al.*, 2018; Bird *et al.*, 2021; Arias-Martorell *et al.*, 2021; Lukova *et al.*, 2024, 2025; Alfieri *et al.*, 2025). The main strength of this approach is that it compares the relative spatial distribution of trabecular properties throughout the epiphysis rather than their raw values, thereby reducing the influence of systemic differences in trabecular architecture and allowing comparisons to focus on regional patterns that are more closely related to local mechanical loading (Bachmann *et al.*, 2022). Using this approach, Arias-Martorell *et al.* (2021) revealed consistent interspecific differences in trabecular distribution in the distal humerus related to habitual flexed- versus extended-elbow postures during locomotion among African apes. Given the shared loading environment between the humerus and proximal ulna at the elbow joint and between the carpals and distal ulna at the wrist, trabecular bone distribution within both the proximal and distal ulnar epiphyses may also reflect variation in positional behaviors among extant primates. However, although aspects of ulnar trabecular structure have been examined in several extant primates (Chirchir, 2015, 2019; Turcotte *et al.*, 2026), no in-depth study has investigated the variation in three-dimensional trabecular structure of the ulna across a broad comparative sample of anthropoids to determine whether it reflects habitual joint posture and locomotor loading. Such an analysis might ultimately provide critical insights into the positional behaviors of extinct species.

Locomotor Behavior and Joint Loadings

Primates show varied locomotor repertoires that influence how mechanical load is distributed at the elbow and wrist and are therefore expected to result in differences in trabecular structure. We summarize current knowledge on the biomechanical distinctions in elbow and wrist postures and loading patterns between quadrupedal non-hominoid anthropoids and hominoids.

Alouatta, *Ateles*, *Papio*, and *Macaca* (howler monkeys, spider monkeys, baboons, and macaques, respectively) most frequently engage in pronograde quadrupedalism, which occur in arboreal settings in *Alouatta* and *Ateles*, primarily on the ground in *Papio*, and in both settings among *Macaca* species (*M. sylvana*, *M. fascicularis*, and *M. mulatta*) included in our sample (Fleagle & Mittermeier, 1980; Cant, 1986, 1988; Schmidt, 2011; Galán-Acedo *et al.*, 2019; Estrada & Marshall, 2024). In both arboreal and terrestrial quadrupedalism, the elbow typically remains semiflexed (Rose, 1983, 1988, 1993a, b; Sarmiento, 1985; Nakatsukasa *et al.*, 1996; Drapeau *et al.*, 2005). In addition, *Ateles* also employs forelimb-dominated suspension assisted by its prehensile tail, using the elbow in more extended postures (Cant, 1986; Drapeau, 2004; Schmidt, 2011) and being subject to both compressive and tensile forces—in contrast

to *Alouatta*, *Papio*, and *Macaca*, where the elbow primarily sustains compressive loads (Schmidt, 2011; Vanhooff *et al.*, 2024). At the wrist, arboreal quadrupeds adopt a more supinated posture and use more extended wrist postures (primarily palmigrady) than terrestrial quadrupeds (Lemelin & Schmitt, 1998; Schmitt, 1994). Accordingly, the mainly terrestrial *Papio* most often employs digitigrady, a hand posture associated with limited ulnar deviation and wrist extension. *Macaca*, although digitigrade on the ground, may be palmigrade on arboreal substrates (Jones, 1967; Rawlins, 1993; Hayama *et al.*, 1994; Lemelin & Schmitt, 1998; Patel, 2009; Orr, 2017), thus showing an intermediate wrist mobility (Vanhoof *et al.*, 2023).

Symphalangus (siamangs) are brachiators, a form of suspensory locomotion associated with extended elbow postures (Swartz *et al.*, 1989; Hunt, 1991). In addition to brachiation, they also engage in vertical climbing and leaping, as part of a broader locomotor repertoire shared with other hylobatids (Fleagle, 1976). *Symphalangus* shows high wrist mobility in all directions, including a high range of ulnar deviation and pronation-supination movements despite having a relatively long ulnar styloid process (Vanhoof *et al.*, 2023; Raventós-Izard *et al.*, 2025).

Pongo (orangutans), the most arboreal of great apes, relies on forelimb suspensory behaviors and clambering with extended elbows under tensile loads, while also frequently climbing with flexed elbows (Cant, 1987; Hunt *et al.*, 1996; Thorpe *et al.*, 2009). Although quite rarely, *Pongo* also performs pronograde quadrupedal locomotion, during which they load their hands compressively with extended wrists (MacKinnon, 1974; Tuttle & Cortwright, 1988; Thorpe & Crompton, 2006; Orr, 2017). Generally, their hands display a wide range of ulnar deviation across all substrates (Tuttle, 1967). Therefore, *Pongo* exhibits a remarkable degree of joint flexibility (Isler, 2005; Payne *et al.*, 2006; Thorpe & Crompton, 2006; Thorpe *et al.*, 2009).

African apes engage most frequently in knuckle-walking on the ground, although arboreal activity varies substantially between *Gorilla* (gorillas) and *Pan* (chimpanzees and bonobos) and also with habitat, age, and body size (Remis, 1994; Doran, 1996, 1997; Hunt *et al.*, 1996; Isler, 2005; Drummond-Clarke *et al.*, 2024, 2025; Robbins *et al.*, 2025). *Pan* displays a versatile locomotor repertoire—frequently incorporating vertical climbing, suspension, and, more rarely, bipedalism and leaping (Hunt, 1991; Doran, 1993, 1997; D’Août *et al.*, 2004; Pontzer *et al.*, 2009; Crompton *et al.*, 2010)—whereas *Gorilla* relies more heavily on terrestrial knuckle-walking, with lower frequencies of vertical climbing and other arboreal behaviors (Remis, 1994; Doran, 1996, 1997). The wrist in African apes is limited in extension and is most often loaded in compression during knuckle walking (Jenkins & Fleagle, 1975; Kivell & Schmitt, 2009; Orr, 2005, 2017; Tuttle, 1967; Vanhoof *et al.*, 2021, 2024). Both *Pan* and *Gorilla* show ulnar deviation during climbing and in the initial phases of knuckle-walking (Tuttle, 1967; Jenkins & Fleagle, 1975; Sarmiento, 1988; Neufuss *et al.*, 2017; Thompson, 2020). Notably, *Pan* occasionally adopts supinated palmigrady on narrow arboreal supports (Hunt, 2016), indicating a broader range of pronation-supination despite limited extension (Vanhoof *et al.*, 2023).

Aim, Hypothesis, and Predictions

We compared the internal trabecular architecture distribution throughout the proximal and distal ulna of apes with that of both arboreal and terrestrial quadrupedal anthropoids, as well as semi-suspensory monkeys, which differ in their locomotor behaviors and habitual elbow and wrist postures. We test the hypothesis that trabecular bone in the ulnar epiphyses reflects differences in habitual elbow and wrist postures in relation to the main locomotor behaviors of the taxa studied. Published evidence supports this hypothesis, indicating that trabecular architecture is responsive to local mechanical loading and can (re)model throughout life in accordance with functional demands (Biewener *et al.*, 1996; Rodan, 1997; Mittra *et al.*, 2005; Pontzer *et al.*, 2006; Ruff *et al.*, 2006; Barak *et al.*, 2011; Harrison *et al.*, 2011; Sinclair *et al.*, 2013). Following automatic segmentation of bone tissue, we quantified and statistically compared the distribution of trabecular bone volume fraction (i.e., the ratio of bone volume to total volume [BV/TV]) across the entire epiphyses using canonical holistic morphometric analysis (cHMA) (Bachmann *et al.*, 2022). This method integrates statistical deformation modeling and holistic morphometric analysis to address interspecific differences in shape biases and ensure geometric homology (Steiner *et al.*, 2021; Bachmann *et al.*, 2022). We standardized all raw BV/TV values to account for taxon-specific differences (e.g., systemic differences) in overall trabecular bone density and thus compare relative BV/TV (rBV/TV) to facilitate investigation of between-species differences in trabecular bone density. Finally, to assess patterns of covariation between proximal and distal ulnar trabecular structure and locomotor mode percentages, we also performed a two-block partial least squares (2B-PLS) analysis (Rohlf & Corti, 2000). We evaluate the hypothesis through specific qualitative and quantitative predictions based on the hypothesis and the known locomotor behaviors of taxa (Fig. 1).

Our first prediction (P1) is that terrestrial and arboreal quadrupedal non-hominoid anthropoids will share trabecular patterns in the proximal and/or distal ulna related to quadrupedalism. In these taxa, quadrupedalism involves the use of flexed elbow postures—although not fully flexed—due to their limited range of elbow extension, which we predict will be reflected in the proximal ulna. We predict that wrist trabecular patterns will vary among taxa in ways that reflect differences in habitual hand posture and substrate use (reviewed above), while still reflecting the use of a generally pronated hand.

Our second prediction (P2) is that *Ateles* may additionally show similarities to *Symphalangus* and/or *Pongo* due to its varied positional repertoire, which includes quadrupedalism but also climbing and tail-assisted brachiation with an extended elbow.

Our third prediction (P3) is that *Symphalangus* will display a trabecular pattern reflecting suspensory behaviors, which entail high joint mobility. Therefore, the trabecular pattern will be homogenous, without clearly localized areas of enhanced trabecular reinforcement on the articular surfaces.

Our fourth prediction (P4) is that *Pongo* will be similar to *Symphalangus* in showing a more homogenous distribution of trabecular bone, as its varied locomotor

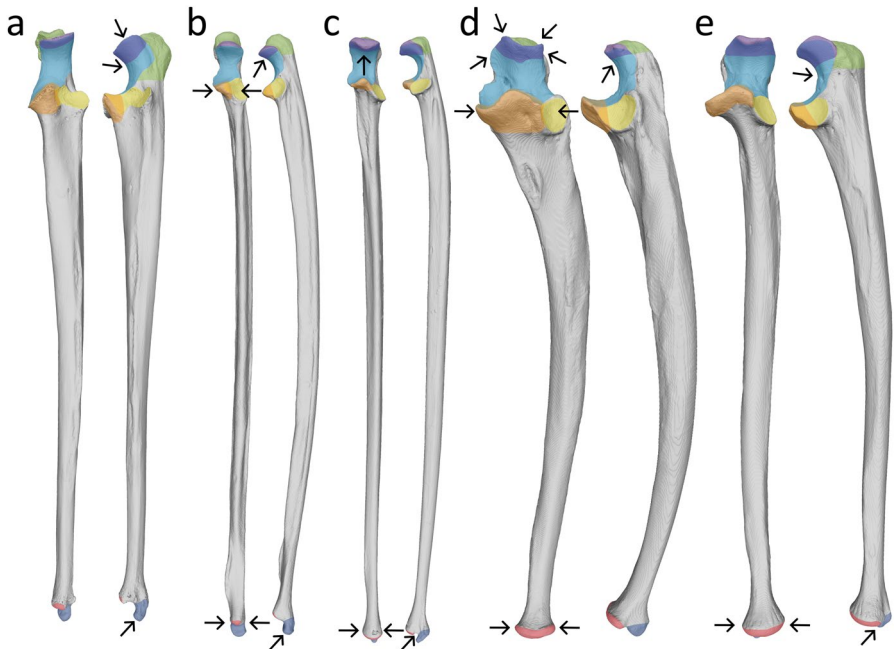


Fig. 1 Left ulnae of (a) *Papio hamadryas* (ZMB 65265), (b) *Ateles sp.* (ZMB 44979), (c) *Symphalangus syndactylus* (ZMB 38573), (d) *Pongo pygmaeus* (ZMB 19090801), and (e) *Pan troglodytes* (MPITC 11778) in anterior and lateral views. The black arrows indicate the expected points of loading according to predictions P1–P5, corresponding to specimens (a)–(e), respectively (see main text for further details). The anatomical areas of the ulna are marked as follows: olecranon (green), olecranon beak (purple), trochlear notch (cyan), coronoid process (orange), radial notch (yellow), ulnar head (red), and styloid process (blue).

repertoire may not produce localized regions of preferential trabecular reinforcement within the joint.

Finally, our last prediction (P5) is that African apes will display trabecular patterns in the proximal and distal ulna related to their primary use of quadrupedalism (knuckle-walking), and thus might be similar to those of quadrupedal non-hominoid anthropoids, despite also displaying suspensory and climbing behaviors.

Methods

Study Sample and Scanning

We studied trabecular bone in 41 proximal ulnae and 35 distal ulnae pertaining to eight genera of extant platyrrhines, cercopithecoids, and hominoids (Table 1). The ulnae are curated at the following institutions: the Max Planck Institute for Evolutionary Anthropology (MPI-EVA; Leipzig, Germany); the Powell-Cotton Museum (Birchington, UK); the Senckenberg Natural History Museum (Frankfurt, Germany);

Table 1 Details of the sample, including the number of specimens per sex, the number of specimens per side, the minimum and maximum log Volume, and housing institutions

	<i>n</i>	Sex (F/M/?)	Side (L/R)	log Volume (mm ³)		Institutions
				Min	Max	
Proximal (<i>n</i> = 41)						
<i>Alouatta</i>	5	0/1/4	4/1	3.21	3.43	SMF, ZMB, ZMS
<i>Ateles</i>	5	1/1/3	2/3	2.94	3.31	SMF, ZMB
<i>Papio</i>	5	0/1/4	3/2	3.71	4.01	SMF, ZMB
<i>Macaca</i>	6	0/0/6	6/0	2.38	3.76	SMF, ZMB
<i>Symphalangus</i>	5	2/0/3	3/2	3.22	3.67	SMF, ZMB
<i>Pongo</i>	6	1/0/5	3/3	4.04	4.29	SMF, ZMB, ZMS
<i>Gorilla</i>	5	4/1/0	3/2	4.04	4.78	GP, PCMER
<i>Pan</i>	4	1/0/3	3/1	4.11	4.29	MPIT, SMF
Distal (n=35)						
<i>Alouatta</i>	4	0/1/3	4/0	2.28	2.46	SMF, ZMB
<i>Ateles</i>	4	1/1/2	1/3	2.40	2.60	SMF, ZMB
<i>Papio</i>	5	0/1/4	2/3	2.85	3.18	SMF, ZMB
<i>Macaca</i>	4	0/0/4	4/0	2.18	2.81	SMF, ZMB
<i>Symphalangus</i>	5	2/0/3	3/2	2.67	2.83	SMF, ZMB
<i>Pongo</i>	7	1/0/6	4/3	3.38	3.74	SMF, ZMB, ZMS
<i>Gorilla</i>	3	2/0/2	2/1	3.48	3.88	PCMER
<i>Pan</i>	3	1/0/2	2/1	3.49	3.59	MPIT, SMF

M = male; F = female; ? = unknown sex; L = left; R = right; ZMB = Museum für Naturkunde-Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany; ZMS = Zoologische Staatssammlung München, Munich, Germany; MPI = Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; SMF = Senckenberg Society for Nature Research, Frankfurt, Germany; GP= Mountain Gorilla Skeletal Project, Dian Fossey Gorilla Fund International's Karisoke Research Centre, Rwanda; PCMER = Powell-Cotton Museum, Birmington, UK

the Museum für Naturkunde–Leibniz Institute for Evolution and Biodiversity (Berlin, Germany); the Zoologische Staatssammlung München (Munich, Germany); and the Mountain Gorilla Skeletal Project, Dian Fossey Gorilla Fund International's Karisoke Research Centre (Rwanda).

MicroCT Scanning

We scanned all ulnae via high-resolution micro-computed tomography (μCT) using three different high-resolution μCT scanners: a BIR ACTIS 225/300 or Diondo 1 μCT scanner housed in the Department of Human Origins of the MPI-EVA (Leipzig, Germany), a Nikon XT 225 ST μCT scanner, housed in the Cambridge Bioto-mography Centre, Department of Zoology of the University of Cambridge (Cambridge, UK), and a Nikon XTH 320 housed in the 3D Imaging Lab, Senckenberg Centre for Human Evolution and Palaeoenvironment (Tübingen, Germany). The

isotropic voxel size range for the sample is 21.9–99.9 μm , depending on individual size. The lowest resolution sample corresponds to three proximal ulnae of *Gorilla beringei*. Excluding these specimens of *Gorilla beringei*, voxel size ranges from 21.9 to 50.0 μm , with the majority of specimens scanned at ~ 40 μm or higher resolution. We performed a visual inspection of the trabeculae in the scans of the lower resolution sample (Online Resource 1: Figs. S1–S4), and we evaluated the distribution of *Gorilla* individuals in subsequent analyses in order to ascertain that the resulting pattern in lower resolution individuals displayed the same trabecular patterns as the higher resolution ones, ensuring no artifacts or loss of information due to resolution differences. Scan parameters were 100–160 kV and 100–140 μA , using a brass or copper filter of 0.2–0.5 mm. We reconstructed all scans from 16-bit TIFF image stacks.

Trabecular Bone Analysis

With Avizo 2019.1 (ThermoFisher, Waltham, MA), we first rotated each ulna into standard anatomical orientation and then cropped it at an anatomically defined homologous regions accounting for morphological variation across our sample. For the proximal ulna, the bone was cropped immediately distal to the radial notch, at the beginning of the ulnar neck—where the shaft begins. For the distal ulna, the bones were cropped at the beginning of the neck constriction (Online Resource 1: Fig. S5). We mirrored right-sided bones to the left side to enable methodological analyses and morphological comparisons. Following this, we segmented scans using the medical image analysis (MIA) clustering method to produce a binary segmentation of bone and non-bone material (Dunmore *et al.*, 2018). We then processed the image segmentations in Medtool v. 4.3 (Dr. Pahr Ingenieure, Vienna), following established protocols (Pahr & Zysset, 2009; Gross *et al.*, 2014). Medtool uses a ray-casting technique to assign scalar values to voxels by projecting a series of mathematical rays across the scan. These rays extend from the outer surface of the bone inward, continuing until a non-bone voxel is reached, allowing the software to classify voxels into trabecular bone, cortical bone, internal air, and background. Morphological filters are applied to fill small holes in the porous cortical shell, producing a smooth and continuous boundary between cortical and trabecular regions. This process results in masks for both the outer cortical layer and the internal trabecular structure.

Subsequently, we used canonical holistic morphometric analysis (cHMA) to quantitatively and statistically analyze BV/TV values, following published protocols (Bachmann *et al.*, 2022). We applied this analysis separately to the proximal and distal ulna. The cHMA method integrates statistical deformation modeling (SDM) with holistic morphometric analysis (HMA) to address interspecific differences in shape and ensure geometric homology across individuals. First, we aligned each ulna to a randomly selected reference using similarity transforms and then applied B-spline registration to generate a canonical bone representing the average internal and external morphology across the sample—one canonical mesh was generated for the proximal ulna and another for the distal ulna. We then morphed each individual

trabecular volume onto the canonical mesh and performed HMA in Medtool. We generated a 3D background grid with nodes spaced 2.5 mm apart was generated within each segmented trabecular volume, and a 5-mm diameter sampling sphere was centered on each node to measure BV/TV (Gross *et al.*, 2014; Tsegai *et al.*, 2013). We interpolated these BV/TV values onto the morphed canonical meshes since data for each individual were collected on the canonical mesh, the tetrahedra of this mesh are geometrically homologous among individuals and among taxa for each anatomical region.

To account for systemic differences across individuals and particularly among taxa (Chirchir *et al.*, 2015; Tsegai *et al.*, 2018; but see Ryan & Shaw, 2015), we calculated the relative BV/TV (rBV/TV) by dividing the BV/TV at each mesh cell by the mean BV/TV of the corresponding individual. The resulting rBV/TV distributions highlight regions of increased or decreased trabecular bone volume relative to the mean and can be compared across individuals and species that may differ in absolute BV/TV (Dunmore *et al.*, 2019; Sukhdeo *et al.*, 2020). Based on the experimentally-validated concept of bone functional plasticity (Pontzer *et al.*, 2006; Barak *et al.*, 2011; Sinclair *et al.*, 2013), we assume that regions with lower rBV/TV reflect lower mechanical stress while, conversely, areas of high rBV/TV reflect habitually higher mechanical loading. We visualized the final rBV/TV distributions using ParaView v. 5.13 (Kitware, Clifton Park, NY; Ahrens *et al.*, 2005).

Statistical Analyses

To examine trabecular bone distribution across taxa, we computed mean rBV/TV patterns by calculating the arithmetic mean individual rBV/TV values at corresponding homologous tetrahedra within each genus, and then projected these genus-level distributions onto a canonical mesh and visualized using ParaView. For the analysis of trabecular variation, principal component analysis (PCA), between-group principal component analysis (bgPCA), and canonical variate analysis (CVA) we conducted separate analyses for the distal and proximal ulna. We used PCA to explore the main patterns of trabecular variation without maximizing variance among a priori-defined groups. To further assess differences among major anthropoid clades, we performed bgPCA and CVA using a priori-defined clades (platyrrhines, cercopithecoids, hylobatids, and hominids). Whereas PCA maximizes total variance among individuals, both bgPCA and CVA maximize variation among groups. Specifically, bgPCA is based on a PCA of group means onto which individual specimens are subsequently projected, whereas CVA maximizes among-group variance relative to within-group variance. Because bgPCA may potentially overestimate group discrimination—particularly when the number of variables is high relative to sample size (Bookstein, 2019; Cardini *et al.*, 2019), as in our analysis—the robustness of the grouping structure was further evaluated following a cross-validation (leave-one-out classification) approach (Cardini & Polly, 2020). We performed the cross-validated bgPCA (cv-bgPCA) by sequentially excluding each specimen from the training dataset of the bgPCA, and projecting the omitted specimen into the resulting space. To rule out spurious group separation, we calculated Z scores and coefficients

of determination (R^2) using permutation tests. The Z score measures the extent to which the observed differences among groups exceeds that expected at random, whereas R^2 represents the proportion of total variance accounted by group membership. We used comparisons between raw data (i.e. rBV/TV dataset), bgPCA, and cv-bgPCA results, based on the Z scores and associated R^2 values to assess to what extent the definition of groups a priori inflated the differences among them, thereby ensuring that grouping structure is not spurious (i.e., a methodological artifact). Additionally, we extracted pairwise distances between genera from the CVA results, evaluating their significance using random permutation tests using the R package Morpho. We performed the PCA and bgPCA directly on the rBV/TV dataset for each anatomical region, whereas we based the CVA on the principal components obtained from the PCA of the rBV/TV dataset. We then performed the CVA using a reduced set of principal component (PC) scores to avoid overfitting and unstable discrimination. To determine the optimal subset of PCs, we screened the classification results and selected the minimum number of PCs that maximized the percentage of correct classification (Hastie *et al.*, 2009), given that the classification accuracy of the CVA only increases up to a certain point, and after a plateau it starts to decrease because PCs introduce more noise than signal. Based on this criterion, we retained five PCs for both the distal and proximal ulna, which accounted for a substantial proportion of variance and yielded correct classification percentages of 86% and 90%, respectively, using this optimal subset of PCs as input to perform the CVAs. We conducted the analyses in R v 4.4.2 (R Core Team, 2024), generating three-dimensional plots using the rgl package (R Core Team, 2017). To illustrate the morphological extremes along the PCA, the bgPCA and the CVA axes, we mapped the loadings representing three standard deviations of each principal component (PC) between-group principal component (bgPC) and canonical variate (CV) of interest onto the canonical mesh to highlight contrasting trabecular structures at both ends of each axis.

To assess whether size influences trabecular structure, we computed a bivariate linear regression of each PC and bgPC analyzed vs. total epiphyseal volume (i.e., a metric of the size of the epiphysis). We measured total epiphyseal volume for each individual as the solid volume of the distal ulna and the proximal ulna separately in Avizo. Accordingly, this metric represents the entire epiphyseal volume, including trabecular bone, cortical bone, and all internal void spaces between them.

Locomotor Frequency Analysis: Covariation Between Trabecular Structure and Locomotion

We compiled a locomotor dataset with locomotor percentages for all taxa in the sample using published sources, following previous work (Monclús-Gonzalo *et al.*, 2023, 2025a, b; Raventós-Izard *et al.*, 2025; Arias-Martorell *et al.*, 2026), for which we defined five locomotor categories based on standardized descriptions of locomotor behavior (Hunt *et al.*, 1996): quadrupedalism (Q), leaping (L), forelimb-dominated suspension (FDS), climbing (C), and clambering (CLA). Because we obtained locomotor data from multiple sources, not all behaviors quantified in the original studies were included. Therefore, we rounded the percentages of those species with

small amounts of locomotor modes not included in this study ensuring that they add up to 100% (Online Resource1: Table S1). Due to methodological limitations, we did not quantitatively include substrate preference (arboreality vs. terrestriality) into our locomotor variables but potential morphological differences related to substrate use are qualitatively evaluated and discussed.

We performed two two-block partial least squares (2B-PLS) analyses (Rohlf & Corti, 2000) to examine the covariation between both proximal and distal ulnar trabecular structure (separately), as measured by rBV/TV values, and locomotor percentages. We conducted the analyses using the function `two.b.pls` in the R package `geomorph` v.4.0.7 (Adams & Otárola-Castillo, 2013). Based on rBV/TV values, we computed a singular value decomposition of the covariance matrix between the two blocks, yielding two eigenvector matrices and a matrix of eigenvalues. We assessed the significance of each linear combination by resampling the original blocks of data. If the singular value is higher (>95%) than the singular values obtained from the permuted blocks, we considered the covariance between the pair of linear combinations significant (Rohlf & Corti, 2000).

Ethical Note

The samples used in this study correspond to primate skeletons curated in different research- and collections-based institutions and museums in Europe and Africa. All bones are carefully curated by specialists, and records regarding any additional data, such as place of origin, approximate age or date of inclusion in the collections are kept. Most specimens in skeletal collections of Natural Sciences museums were not ethically sourced, but both the curating institutions and the researchers involved in this study treated their remains with respect and with due recognition of the circumstances in which they were obtained.

Conflict of Interest The authors declare that they have no conflict of interest.

Data Availability The datasets generated during or analyzed during the current study, which are the inputs for the cHMA analysis (inner and outer masks per individual in the sample), the outputs of the cHMA analysis (VTK files and BV/TV individual values), and the script for running cHMA in R are available in the Zenodo repository: <https://doi.org/10.5281/zenodo.21237503>.

Results

Statistical Analyses

The PCA, bgPCA, and CVA analyses overall presented similar group distribution patterns and rBV/TV patterns (Online Resource 1: Figs. S6–S12). The Z-scores are similar for the raw data (proximal = 6.33; distal = 4.55), bgPCA (proximal = 7.95;

distal = 5.34), and cross-validated cv-bgPCA (proximal = 6.12; distal = 4.69). Similarly, R^2 increases from the raw data comparisons (proximal = 0.38; distal = 0.47) to both standard bgPCA (proximal = 0.64; distal = 0.58) and cv-bgPCA (proximal = 0.52; distal = 0.52), showing that the bgPCA (as expected) maximizes group discrimination but further indicating grouping structure is not spurious. Pairwise comparisons extracted from the CVA results showed greater discrimination between genera in the proximal ulna, whereas fewer pairwise differences were significant for the distal ulna (Online Resource 1: Table S5). The Electronic Supplementary Material includes the bgPCA and CVA results, which are consistent with the PCA.

Principal Component Analyses

Proximal Ulna

The PCA yielded 41 PCs (Online Resource 1: Table S2), of which the first three explain 47.88% of the total variance in rBV/TV values and which all three together are not significantly correlated with total epiphyseal volume [$R^2 = 0.0255$, $F(1, 39) = 0.01$, $p = 0.94$]. The PC1 accounts for 19.92% of the variance (Fig. 2) and is significantly correlated with total epiphyseal volume [$R^2 = 0.2291$, $F(1, 39) = 34.19$, $p < 0.01$; Online Resource 1: Table S3 and Fig. S13]. Although there is overlap, *Alouatta*, *Ateles*, *Symphalangus* and most *Pan* are positioned toward the negative end—associated with high rBV/TV values at the radial notch, coronoid process, the proximal part of the trochlear notch and triceps attachment site—whereas *Macaca* and *Papio* (with moderately positive scores), and *Pongo* and *Gorilla*—associated with high rBV/TV at the central-medial aspects of the trochlear notch—are positioned toward the positive end, particularly *Gorilla*. The PC2 explains 16.05% of the variance (Fig. 2) and is significantly correlated with total epiphyseal volume [$R^2 = 0.1407$, $F(1, 39) = 0.21$, $p = 0.01$; Online Resource 1: Table S3]. *Symphalangus* and *Alouatta* display positive scores, associated with high rBV/TV at the proximal aspect of the triceps attachment site and the radial notch. Cercopithecoids and, to a lesser extent, *Pongo* display scores around zero, in contrast to *Pan* and *Gorilla*, which display negative scores associated to high rBV/TV values at the olecranon beak, the proximolateral aspect of the trochlear notch and the central-medial aspect of the trochlear notch. The PC3 accounts for 11.9% of the variance (Fig. 2) and is not significantly correlated with total epiphyseal volume [$R^2 = 0.0160$, $F(1, 39) = 0.18$, $p = 0.21$; Online Resource 1: Table S3]. Platyrrhines display positive scores related to high rBV/TV values at the triceps attachment site and the coronoid process, whereas cercopithecoids and some hominoids (*Symphalangus* and *Pongo*) display negative scores related to high rBV/TV values at the proximal aspect of the trochlear notch. *Pan* and *Gorilla* are more widely spread, encompassing the entire PC3 range.

Distal Ulna

The PCA yielded 35 PCs (Online Resource 1: Table S2), of which the first three explain 71.18% of the total variance in rBV/TV values and which all three together

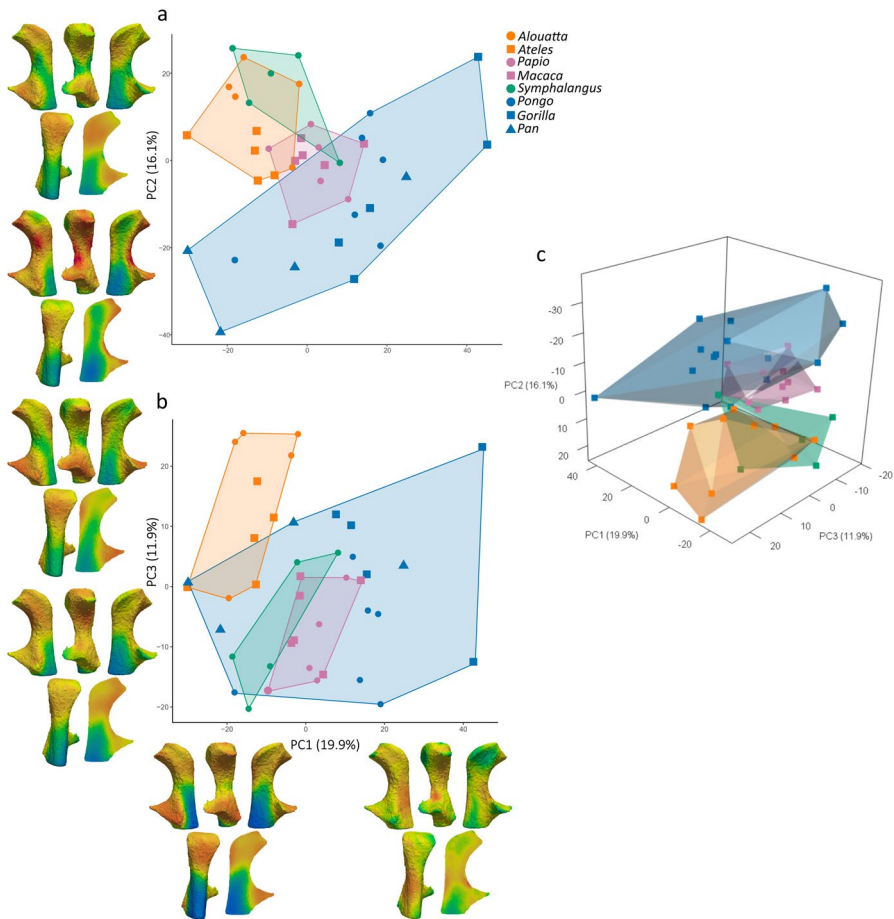


Fig. 2 Results of the principal component (PC) analysis of the proximal ulnae, as depicted by a bivariate plot of PC1 vs. PC2 (**a**), a bivariate plot of PC1 vs. PC3 (**b**) and a 3D plot of PC1 vs. PC2 vs. PC3. Group symbols and convex hulls (in semitransparency) are color-coded: orange = platyrrhines; pink = cercopithecines; green = hylobatids; blue = hominids. The three-dimensional models of the extreme rBV/TV values (in lateral, anterior, medial, and posterior views, and a cross section) for each PC are wrapped in the canonical mesh in the bivariate plots.

are significantly correlated with total epiphyseal volume [$R^2 = 0.1609$, $F(1, 33) = 7.52$, $p = 0.01$]. The PC1 accounts for 39.93% of the variance (Fig. 3) and is not significantly correlated with total epiphyseal volume [$R^2 = -0.0278$, $F(1, 33) = 0.14$, $p = 0.78$; Online Resource 1: Table S3]. *Ateles*, some *Macaca*, *Papio*, *Pongo*, *Pan* and *Gorilla* are positioned toward negative scores, related to high rBV/TV at the tip of the styloid process. In contrast, *Symphalangus*, *Alouatta* and some *Pongo* display positive scores, associated with low rBV/TV values throughout all of the distal ulnae. The PC2 accounts for 20.11% of the variance (Fig. 3) and is not significantly correlated with total epiphyseal volume [$R^2 = 0.0820$, $F(1, 33) = 20.45$, $p = 0.05$; Online Resource 1: Table S3]. Although there is overlap, cercopithecoids

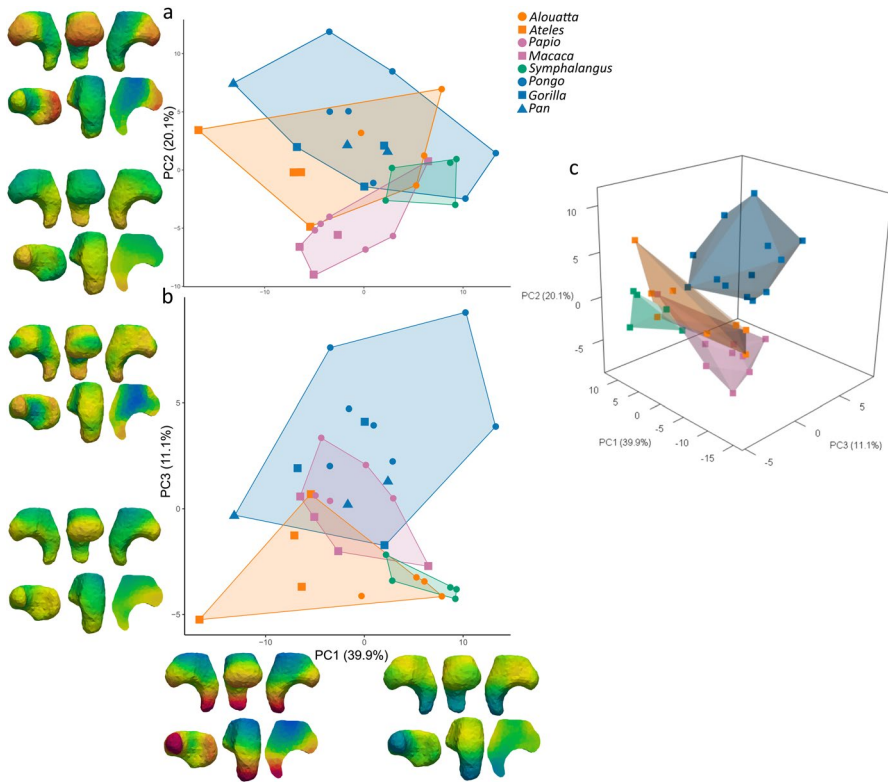


Fig. 3 Results of the principal component (PC) analysis of the distal ulnae, as depicted by a bivariate plot of PC1 vs. PC2 (**a**), a bivariate plot of PC1 vs. PC3 (**b**) and a 3D plot of PC1 vs. PC2 vs. PC3. Group symbols and convex hulls (in semitransparency) are color-coded: orange = platyrrhines; pink = cercopithecines; green = hylobatids; blue = hominids. The three-dimensional models of the extreme rBV/TV values (in lateral, anterior, medial, and posterior views, and a cross section) for each PC are wrapped in the canonical mesh in the bivariate plots.

are driven to the negative end due to their low rBV/TV values across all the distal ulna with relative moderate rBV/TV values at the tip of the styloid process. Platyrrhines, *Symphalangus*, and some hominoids generally display scores around zero and some hominoids show positive scores related to low rBV/TV at the central trabecular region of the distal ulnar epiphysis and high rBV/TV values around the ulnar head. The PC3 accounts for 11.14% of the variance (Fig. 3) and is significantly correlated with total epiphyseal volume [$R^2 = 0.5313$, $F(1, 33) = 2.17$, $p < 0.01$; Online Resource 1: Table S3 and Fig. S14]. Hominoids and, to a lesser extent, *Papio*, show positive scores related to low rBV/TV at the central trabecular region of the distal ulnar epiphysis. In contrast, platyrrhines, *Symphalangus* and *Macaca* are driven toward the negative end due to their moderately high rBV/TV values at the tip of the styloid process and the distal portion of the ulnar head.

Trabecular Bone Distribution Pattern

Proximal Ulna

Among great apes, we observed considerable variation in rBV/TV distribution patterns across the proximal ulna (Fig. 4 and Online Resource 1: Fig. S1–2). *Pan* shows on average high values at the olecranon beak, along the medial and lateral margins of the proximal trochlear notch, at the distoposterior aspect of the radial notch, and notably at the triceps brachii insertion site. *Gorilla* individuals present a sharply defined focal concentration of high values at the centromedial aspect of the trochlear notch, forming a discrete “hotspot” within the articular surface, with additional localized areas of high rBV/TV at the olecranon and coronoid processes. Some degree of intraspecific variation also occurs within each genus. Accordingly, a few *Pan* individuals also show high values at the center of the trochlear notch, resembling the pattern observed in *Gorilla*, while one *Gorilla* individual shows a pattern more similar to *Pan*, displaying high values at the olecranon beak.

Pongo resembles *Gorilla* in showing high values at the center of the trochlear notch, and like *Pan*, it displays elevated values at the proximal aspect of the trochlear notch and at the triceps insertion site. Additionally, *Pongo* shows high rBV/TV values in the posteroproximal region of the radial notch. Among hominoids, *Pongo* shows the greatest intraspecific variation, such that all individuals display relatively high values in the aforementioned regions but with highly variable rBV/TV values. Moreover, the two most divergent *Pongo* individuals also exhibit high values at the olecranon beak.

Symphalangus shows a broad region of high rBV/TV at the triceps insertion site and elevated values at the anterodistal portion of the radial notch. These characteristics are generally consistent among individuals, except for one specimen, which displays medium values at the triceps insertion site and high values at the radial notch.

Arboreal quadrupeds resemble *Symphalangus* in exhibiting elevated rBV/TV values at the triceps insertion site, although these values are lower than in the latter. They also show high values in the coronoid process and the radial notch. In particular, most *Ateles* individuals display high rBV/TV values across the entire proximal ulna, including the triceps insertion site, the olecranon beak, the most proximal portion of the trochlear notch, and the region opposite the trochlear notch, in the posterior aspect of the proximal ulna, as well as at the coronoid process. One *Alouatta* individual shares this pattern. Two *Ateles* individuals differ slightly by showing relatively lower values in the most proximal region of the proximal ulna (although still within the medium range) but have high values at the coronoid process, making them more similar to the remaining *Alouatta* individuals.

Among terrestrial quadrupeds, *Macaca* shows a pattern comparable to that of most *Ateles* individuals, displaying high values at the proximal aspect of the trochlear notch. However, in *Macaca* this region extends more anteriorly and does not extend posteriorly, as observed in some arboreal taxa. High values are also present at the coronoid process. Only one *Macaca* individual more closely resembles *Papio*, in which all individuals exhibit high values at the olecranon beak, at the distal region of the coronoid process, and at the most distoposterior aspect of the radial notch.

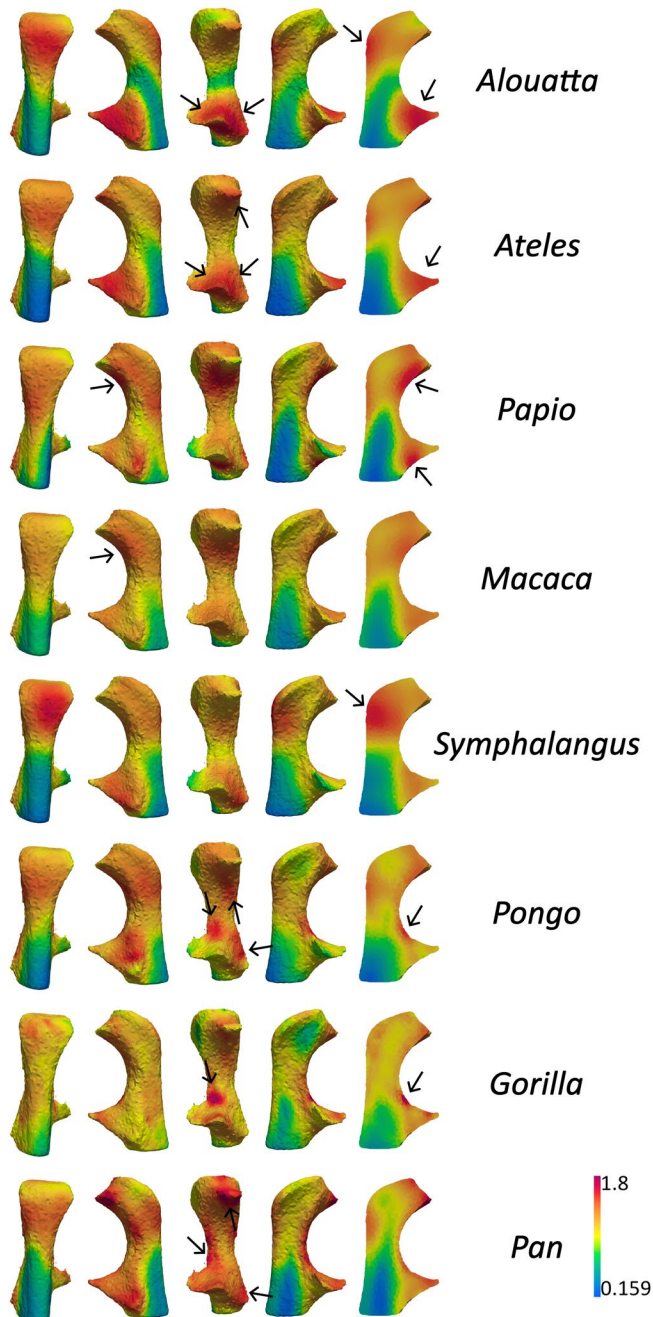


Fig. 4 Mean rBV/TV of every genus for the proximal ulna. The three-dimensional models of the mean rBV/TV values (in posterior, lateral, anterior, and medial views, and a cross section) are wrapped in the canonical mesh. The black arrows indicate the location of the highest mean rBV/TV value for each genus and are shown in the view where this region is most clearly visible, which may differ among genera

Distal Ulna

In general, great apes show a broadly similar rBV/TV distribution pattern across the distal ulna (Fig. 5 and Online Resource 1: Fig. S3–4). High rBV/TV values are consistently concentrated at the ulnar head and along the posterior and/or anterior aspects of the styloid process, whereas the central trabecular region of the distal ulnar epiphysis displays markedly lower values. Nevertheless, clear species-specific differences are evident. *Pongo* shows more pronounced high values at both the proximal and distal aspects of the ulnar head, together with relatively low rBV/TV values at the tip of the styloid process. *Gorilla* shows elevated values primarily at the anterior aspect of the styloid process and at the distal articular surface of the ulnar head. *Pan* shows the highest rBV/TV values among the great apes, predominantly localized at the distal aspect of the ulnar head and at the tip of the styloid process.

Intraspecific differences are most evident in *Pongo* and, to a lesser extent, in *Gorilla*. In *Pongo*, two individuals display relatively high values at the tip of the styloid process, whereas the most divergent individuals include one specimen with high values at the posteriorproximal region of the styloid process and another with elevated values at the proximal portion of the distal epiphysis. In *Gorilla*, one individual—besides exhibiting the general pattern described for the genus—also shows high values at the posteroproximal region of the styloid process, resembling the pattern observed in *Pongo*. By contrast, *Pan* shows little variation among the analyzed individuals in the distal ulna.

Symphalangus exhibits relatively low rBV/TV values across the distal ulna, with higher values at the fovea and the lowest values concentrated at the tip of the styloid process. Nevertheless, a small number of individuals display relatively high values at the styloid tip, although in these specimens the highest rBV/TV values are still located at the fovea or the ulnar head.

Among quadrupedal anthropoids, *Papio* and *Macaca* display elevated rBV/TV values at the tip of the styloid process. However, one *Macaca* individual—specifically the sole representative of *Macaca fascicularis*—shows a pattern more similar to *Alouatta*, in which all individuals generally exhibit lower values at the styloid tip but relatively high values at the ulnar head. All *Ateles* individuals display a mixed trabecular pattern between the two aforementioned quadrupedal anthropoids pattern, with high values at both the tip of the styloid process and the ulnar head, resembling the pattern observed in *Pan*.

Locomotor Frequency Analysis: 2-Block Partial Least Squares

Proximal Ulna

The first block of the 2B-PLS for the proximal ulna indicated a significant correlation between trabecular structure and locomotor behavior (PLS1: $r\text{-PLS} = 0.8666$, $p = 0.013$; Fig. 6 and Online Resource 1: Table S4). *Symphalangus* was located at the negative extreme, followed by *Pongo*, *Ateles*, and *Alouatta*, whereas *Papio anubis* (followed

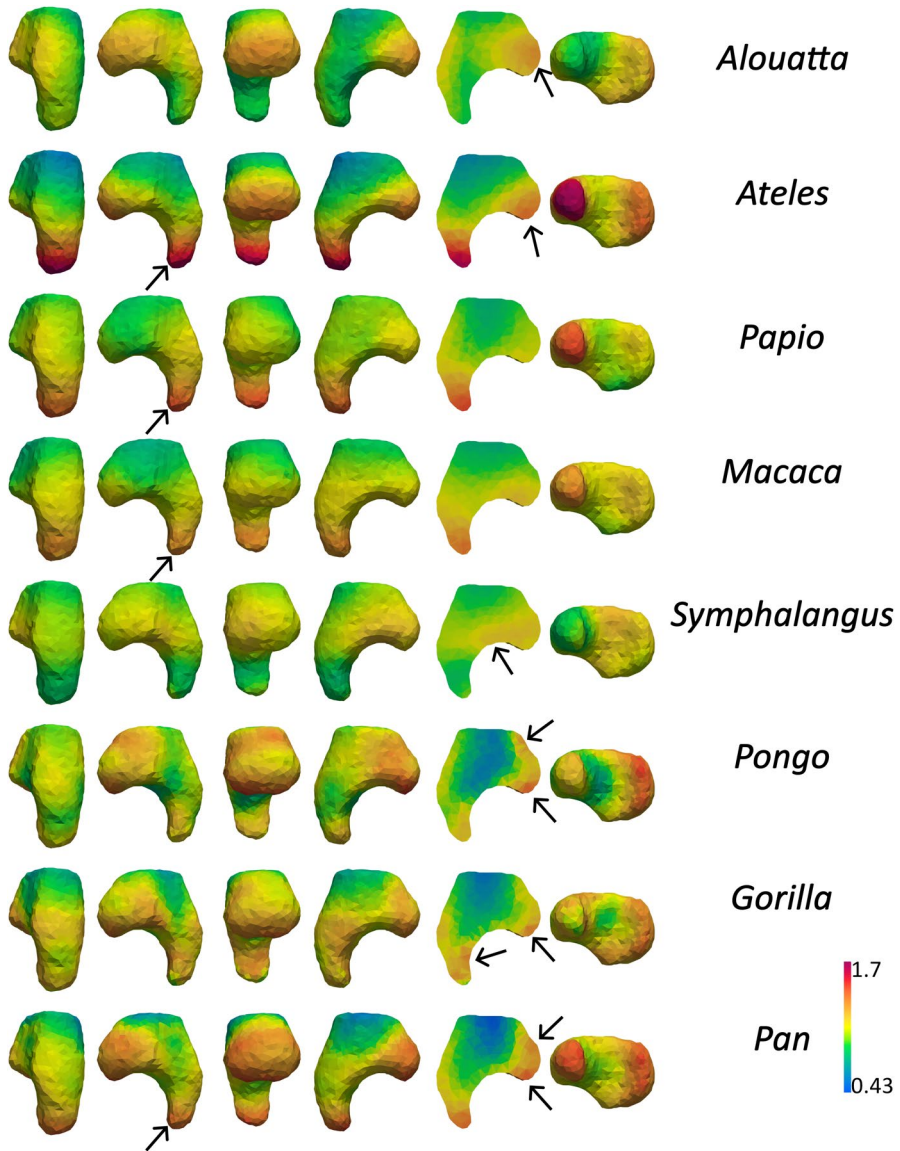


Fig. 5 Mean rBV/TV of every genus for the distal ulna. The three-dimensional models of the mean rBV/TV values (in posterior, lateral, anterior, medial, and distal views, and a parasagittal section) are wrapped in the canonical mesh. The black arrows indicate the location of the highest mean rBV/TV value for each genus and are shown in the view where this region is most clearly visible, which may differ among genera

by *Papio hamadryas*, *Papio ursinus* and *Gorilla*) occupied the positive extreme. Trabecular pattern differences included higher rBV/TV in the proximal portion of the trochlear notch, the central-medial aspect of the trochlear notch, posterolateral to the

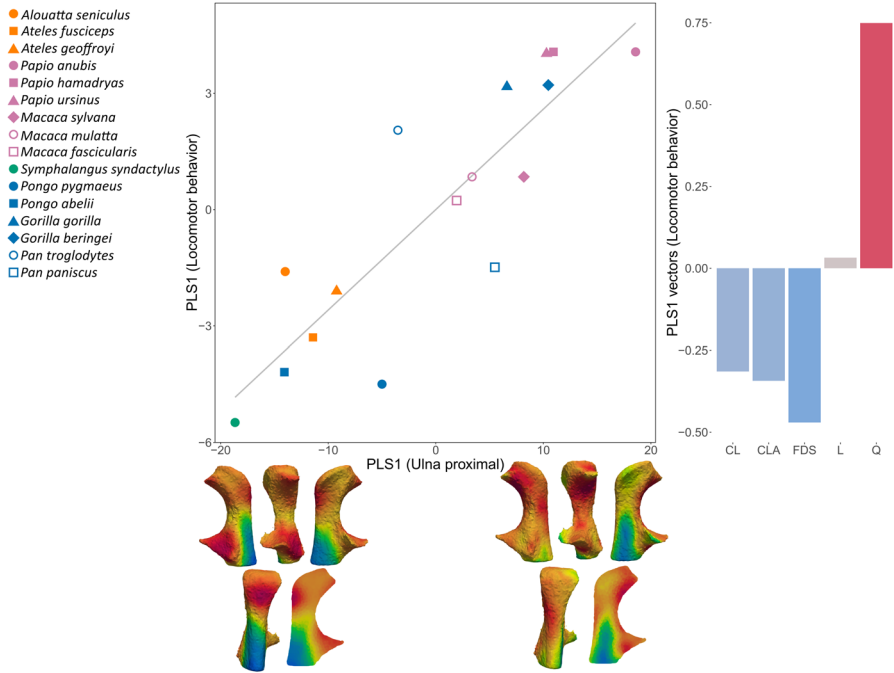


Fig. 6 Results of the two-block partial least squares (PLS) analysis between species mean rBV/TV and quantified locomotor data for the proximal ulna. The three-dimensional models of the minimum and maximum ulnar (in lateral and anterior views) are superimposed on the canonical mesh. Data points are color-coded by taxonomic groups: orange = platyrrhines; red = cercopithecines; green = hylobatids; blue = hominids. C = climbing; CL = clambering; FDS = forelimb-dominated suspension; L = leaping; Q = quadrupedalism

trochlear notch, and distal to the coronoid process at the positive end. Conversely, specimens at the negative end showed increased rBV/TV in the radial notch, at the triceps attachment, and at the olecranon beak. Positive PLS1 values corresponded to quadrupedalism, whereas negative values corresponded to FDS, CLA, and CL.

Distal Ulna

The first block of the 2B-PLS for the distal ulna revealed a nonsignificant correlation between distal ulnar trabecular pattern and locomotor behavior (PLS1: r -PLS = 0.6334, p = 0.2629; Fig. 7 and Online Resource 1: Table S4). *Pongo abelii* falls at the negative end of the PLS1 axis, whereas *Macaca sylvana*, *Macaca mulatta* and *Papio* fall at the positive extreme. Regarding differences in trabecular architecture along this axis, specimens at the positive end exhibited higher rBV/TV at the tip of the styloid process, whereas those at the negative end showed increased rBV/TV around the ulnar head and low rBV/TV values at the central trabecular region of the distal ulnar epiphysis. CLA and FDS corresponded to negative PLS1 values, while quadrupedalism corresponded to the positive end.

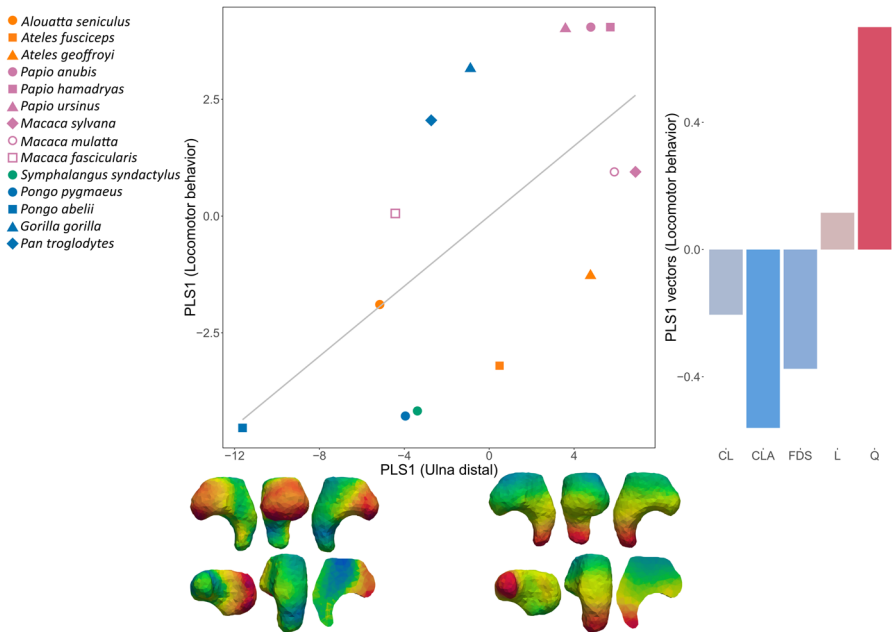


Fig. 7 Results of the two-block partial least squares (PLS) analysis between species mean rBV/TV and quantified locomotor data for the distal ulna. The three-dimensional models of the minimum and maximum ulnar (in lateral and anterior views) are superimposed on the canonical mesh. Data points are color-coded by taxonomic groups: orange = platyrrhines; red = cercopithecines; green = hylobatids; blue = hominids. C = climbing; CL = clambering; FDS = forelimb-dominated suspension; L = leaping; Q = quadrupedalism

Discussion

Our results show that the trabecular structure of the primate proximal ulna is correlated with its functional role in resisting stresses generated by locomotor behaviors, complementing the functional signal previously documented in external ulnar morphology. In primates, the external morphology of the proximal ulna reflects differences in locomotor behaviors among taxa, with features, such as the wide trochlear notch, and the presence of a median keel of great apes contrasting with the highly derived radial notch with an elongated coronoid process of cercopithecines (Rose, 1983, 1993a, 1997; Drapeau, 2008; Rein *et al.*, 2015; Nishimura *et al.*, 2022; Raventós-Izard *et al.*, 2025). Many of these structural features likely accommodate substantial mechanical loads related to locomotion. However, our results suggest that the trabecular structure of the proximal ulna, reflecting an ecophenotypic response to differential elbow joint use, appears to be potentially informative for inferring locomotor and postural behaviors in extinct taxa.

Comparative Trabecular Patterns Across Genera

In non-hominoid anthropoids, the distal ulnar external morphology and the associated soft tissue structures have been shown to be more plesiomorphic than in hominoids (Lewis, 1965, 1969; Lewis *et al.*, 1970; O'Connor, 1975; Cartmill & Milton, 1977) and appear to be associated with adaptations for locomotor behavior. These taxa typically exhibit a square radial articular facet that restricts the rotational range of the radius, so that the distal radioulnar joint acts as an incipient synovial articulation (Lewis, 1965, 1969; O'Connor, 1975). Furthermore, the styloid process is long and articulates with the pisiform and triquetrum, forming the ulnocarpal joint (Lewis, 1965, 1969; Lewis *et al.*, 1970; O'Connor, 1975; Cartmill & Milton, 1977). This configuration suggests that the distal ulna retains its primary functional role in transmitting forces from the wrist to the forearm via the styloid process, as also observed in high rBV/TV at the tip of the styloid process. Conversely, hominoid distal ulnae display external morphological features that facilitate greater joint mobility and a wider range of pronation–supination movements (but see Orr *et al.*, 2024), allowing for forelimb movements that are not restricted to the parasagittal plane. Such features include the expansion of the ulnar head—which forms a semilunar radioulnar articulation—and the reduction of the styloid process, enhancing wrist mobility without compromising joint stability against potential dislocations (Lewis, 1965, 1969; Lewis *et al.*, 1970; O'Connor, 1975; Cartmill & Milton, 1977). However, the absence of a significant correlation in the first PLS component and locomotor frequency in the 2B-PLS analysis supports the view that trabecular structure in the distal ulna exhibits limited discriminative power and does not appear to be strongly associated with locomotor behavior. One explanation might be that bones do not function in isolation; their interaction with soft tissues forms a complex system that responds collectively to biomechanical demands of locomotion (Molnar *et al.*, 2017). In hominoids, soft tissues have also undergone adaptive changes, contributing to passive stabilization and load absorption (Lewis, 1965, 1969; Lewis *et al.*, 1970). These modifications may allow external structures to assimilate most of the mechanical loads associated with positional behavior, thereby reducing stress transmission to the trabecular bone. This interpretation is consistent with our observation that hominoids exhibit higher rBV/TV values in the peripheral regions of the distal ulna, whereas the more internal trabecular areas display markedly lower values.

Furthermore, hominoids within our sample displayed differences in their trabecular patterning that may also reflect differences among genera in external morphology and soft tissues. In *Symphalangus*, the nonarticular triangular ligament, which inserts into the fovea—which lies between the ulnar head and the styloid process (Daver & Nakatsukasa, 2015)—appears to play a key role in reinforcing the distal radioulnar joint against dislocations (Lewis, 1965, 1969; Lewis *et al.*, 1970; Cartmill & Milton, 1977; Sarmiento, 1985, 1988; Sarmiento *et al.*, 2002), as confirmed by the fovea displaying the highest rBV/TV values. In *Pongo*, the moderate rBV/TV observed slightly anterior to the tip of the styloid process may indicate contact with the diverticulum, a soft tissue structure that prevents direct articulation between the styloid process and the carpal bones (Sarmiento, 1985, 1988; Sarmiento *et al.*, 2002). In *Gorilla*, the fusion of the meniscus and the triangular disk, combined with

the pronounced reduction of the styloid process, prevents the tip of the styloid from transmitting loadings from the forearm to the carpals, thereby showing no signs of compressive loading. Nevertheless, the anterior and posterior aspects of the styloid process in *Gorilla* exhibit increased rBV/TV, which is where the fused articular triangular disk and semilunar meniscus attach (Lewis, 1965, 1969; Lewis *et al.*, 1970; Sarmiento, 1985, 1988; Sarmiento *et al.*, 2002). In *Pan*, the condition differs slightly, as the triangular disk and semilunar meniscus are not fully fused, allowing partial contact between the styloid and the carpals (Lewis, 1965, 1969; Lewis *et al.*, 1970; Sarmiento, 1988). Consequently, the rBV/TV pattern reflects that compressive loadings still occur at the tip of the styloid process.

Trabecular Bone Structure and Locomotor Behavior

We predicted that quadrupedal non-hominoid anthropoids (*Ateles*, *Alouatta*, *Papio*, and *Macaca*) would show trabecular patterns related to their locomotor behavior, mostly incurring compressive loading at the joints in flexed (or not fully extended) positions of the elbow (P1). Our results are generally consistent with this prediction; specifically, the proximal ulna of the most terrestrial monkeys (*Papio* and *Macaca*) show the highest rBV/TV at the proximal trochlear notch, as a result of axial compressive forces achieved when the forearm is used with a degree of flexion and is pronated (Rose, 1988; Schmitt, 2003; Drapeau, 2004). There is no high rBV/TV on the medial or lateral aspects of the joint, which may reflect the absence of substantial mediolateral loading, consistent with elbow movements predominantly occurring on the parasagittal plane, as expected from a locomotor pattern adapted to a stable substrate with predictable loading vectors. Compared to *Papio* and *Macaca*, *Ateles* and *Alouatta* show high rBV/TV at the radial notch, which potentially reflects mediolateral loads during semipronated arboreal quadrupedalism (Rose, 1988; Youlatos, 2008). This might be related to their use of more irregular substrates where joint posture must constantly adapt body weight distribution relative to branch diameter (Daver *et al.*, 2012; Kikuchi *et al.*, 2012; Kivell, 2016b).

Interestingly, although we predicted *Ateles* to show greater similarities with *Symphalangus* or *Pongo* (P2), its trabecular pattern does not resemble that of the Asian apes and instead resembles that of *Pan*, thereby suggesting a strong functional response of the trabecular structure (given that *Ateles* and *Pan* are distantly related). At the elbow, however, *Ateles* has a distinct slight signal of high rBV/TV at the posterior ulnar aspect roughly corresponding to the triceps brachii insertion, which is also found (more pronounced) in *Alouatta*. This may be interpreted as a relatively stronger involvement of elbow extension in *Alouatta* than in *Ateles* and potentially linked in the former to arm overhead reaching movements during locomotor behaviors such as climbing or clambering (Michilsens *et al.*, 2009). We cannot rule out a similar explanation for *Ateles*. Additionally, *Ateles* exhibits increased rBV/TV at the olecranon beak, which may reflect extensive and compressive contact—by virtue of the olecranon beak pulling on the humeral olecranon fossa—associated with elbow extension during suspensory positional behaviors. However, this signal is not as strong as in *Pan*, possibly due to the additional support provided by the prehensile

tail, which reduces the need for the forelimbs to bear the entire body weight during suspension (Schmitt *et al.*, 2005; Youlatos, 2008). We cannot exclude a flexed-elbow posture use, reflected in their trabecular pattern, in either *Ateles* or *Alouatta*, consistent with the habitual use of arboreal quadrupedalism.

At the wrist, terrestrial quadrupeds exhibit high rBV/TV values at the tip of the ulnar styloid process, reflecting the transmission of compressive forces from the carpus in extended wrist postures during quadrupedal locomotion. *Ateles* exhibits high rBV/TV values at the tip of the ulnar styloid process, which could indicate compressive loading associated with its habitual arboreal quadrupedalism. The overall distal ulnar pattern of *Ateles* resembles that of *Pan*, including elevated rBV/TV values around the ulnar head. This may indicate compressive loading, reflecting the demands of more variable forelimb use (including arboreal quadrupedalism and forelimb-dominated suspension) while maintaining an ulnocarpal articulation, which demands increased wrist mobility. In contrast, *Alouatta* does not exhibit high rBV/TV at the tip of the styloid process, which could reflect the influence of a crouched posture adopted during above-branch locomotion (Bezanson, 2009), where the elbows project laterally beyond the substrate in a flexed position. This configuration likely shifts load transmission toward a more radial region, resulting in higher rBV/TV at the ulnar head.

Contrary to our prediction that *Symphalangus* would show a trabecular structure related to suspensory behaviors (P3), our results show a distinct trabecular architecture at the proximal ulna. *Symphalangus* shows high rBV/TV in the posterior aspect of the proximal ulna, below the olecranon, broadly corresponding with the triceps brachii insertion observed in *Ateles* and *Alouatta*, but being markedly more pronounced than these platyrrhines, while contrasting with the trabecular structure observed in *Pan* and *Pongo*. The triceps brachii is the main elbow extensor muscle in *Symphalangus*, which show a reduced or absent anconeus muscle, the other elbow extensor found in most other primates (Michilsens *et al.*, 2009; de Diego *et al.*, 2022). The triceps is recruited during overhead reaching phases in climbing, whereas it is usually silent during suspension as gravity extends the elbow naturally (Tuttle & Basmajian, 1974; 1977, 1978). The high concentration of trabeculae at or near the triceps insertion site may thus reflect repeated loading associated with climbing/clambering behaviors, and generally during overhead reaching movements of the forelimb. Because Tuttle *et al.* (1983) reported triceps activity in *Pongo* during hoisting (or the pull-up phase) in climbing and arm-swinging, the hylobatid pattern could also be related to brachiation—either one or both behaviors. Indeed, hylobatid brachiation biomechanics emphasize elbow flexion control to avoid dislocation and forceful extension throughout the locomotor cycle (Swartz, 1989; Swartz *et al.*, 1989). Therefore, the strong signal in the triceps insertion area of *Symphalangus* may also reflect soft tissue loading associated with joint stabilization during brachiation (Michilsens *et al.*, 2009). Regarding the distal ulna, *Symphalangus* shows the longest styloid process among extant hominoids (Sarmiento, 1988); however, the absence of elevated rBV/TV values in this region indicates that there is no direct transmission of compressive forces between the carpus and the styloid process. This is consistent with their suspensory locomotor behavior, where noncompressive

forces (such as tensile stresses driven by body weight) dominate (Swartz *et al.*, 1989).

We predicted that *Pongo* would show a trabecular pattern related to a high degree joint flexibility (P4), consistent with its predominantly suspensory locomotor repertoire (Cant, 1987; Fleagle, 1976; Hunt *et al.*, 1996; Thorpe *et al.*, 2009). The results provide support for this prediction by showing multiple focal areas of elevated rBV/TV at the proximal epiphysis, which may suggest a loading regime of variable magnitude in multiple directions. Similar to *Gorilla*, *Pongo* shows a central concentration of rBV/TV within the trochlear notch—which previous studies interpreted as an extended elbow signal in the distal humerus of virtually the same sample (Arias-Martorell *et al.*, 2021)—while also showing increased rBV/TV at the radial notch and the proximolateral aspect of the trochlear notch, potentially reflecting mediolateral stresses associated with forearm pronation–supination. The pronounced signal in broadly the triceps attachment area, although less marked than in *Symphalangus*, is consistent in *Pongo* with the biomechanical demands overhead reaching (forelimb extension) associated with vertical climbing behaviors (Thorpe & Crompton, 2005, 2006; Thorpe *et al.*, 2009). Alternatively, although not mutually exclusive, and as mentioned above, Tuttle *et al.* (1983) also recorded triceps activity during the pull-up phase of climbing and clambering in *Pongo*, which may also contribute to the observed trabecular pattern (Tuttle *et al.*, 1983). Overall, the trabecular structure does not appear to be related with a specific locomotor behavior that results in a distinct trabecular pattern and may align with a diverse loading pattern in *Pongo*, not exclusively driven by forelimb suspension. At the wrist, *Pongo* shares with *Pan* a concentration of higher rBV/TV values surrounding the ulnar head, likely related to pronation–supination movements, which may indicate increased loading in the area. As in *Gorilla*, the styloid process does not appear to participate significantly in load transmission to the carpus, possibly due to its markedly reduced styloid process and the influence of surrounding soft tissues that may instead mediate force dissipation in this region.

We predicted that the ulna of African apes would show trabecular patterns resembling those of quadrupedal non-hominoid anthropoids due to their frequent use of knuckle-walking, thus incurring compressive loading in extended elbow and wrist postures (P5; Inouye, 1994; Hunt *et al.*, 1996; Zylstra, 1999; Isler, 2005; Finestone *et al.*, 2018; Thompson, 2020). Although a few *Gorilla* and *Pan* individuals display trabecular patterns similar to *Macaca* and *Papio*, most *Pan* show different trabecular patterns from *Gorilla*, despite both being generally treated as biomechanically similar due to their reliance on knuckle-walking (Finestone *et al.*, 2018).

At the proximal ulna, and in agreement with previous findings for the distal humerus (Arias-Martorell *et al.*, 2021), *Gorilla* exhibits high rBV/TV concentrated centrally within the trochlear notch, reflecting compressive forces during elbow extension postures. This signal, although present, is less pronounced in *Pan*. Conversely, *Pan* displays higher rBV/TV laterally and medially around the trochlear notch, suggesting resistance to mediolateral stresses, and at the proximal aspect of the notch, consistent with a (semi)flexed elbow posture—that is, not using the full extension of which hominoids are capable due to olecranon reduction (Rose, 1993a; Inouye, 1994; Zylstra, 1999; Finestone *et al.*, 2018). Additionally, *Pan* shows

enhanced rBV/TV at the olecranon beak, similarly to *Ateles*, also indicating resistance to compressive forces (between the olecranon beak and the olecranon fossa) resulting from tensile regimes at the forelimb that may be generated during climbing or arm-swinging. *Pan* also shows a stronger signal in the area broadly corresponding to the triceps attachment site than *Gorilla*, although less developed than in *Symphalangus*. In *Pan*, triceps activity is primarily associated with knuckle-walking, where it plays a critical role during both the swing and stance phase (Tuttle & Basmajian, 1974; Fleagle *et al.*, 1981; Tuttle *et al.*, 1983; Tuttle & Watts, 1985; Ciurana *et al.*, 2024). Accordingly, the trabecular signal in this area may reflect repeated loading generated by recruitment during the second phase of the swing, as the hand advances forward, and during stance, when the muscle contributes to elbow stabilization by maintaining extension the body passes over the limb (Tuttle *et al.*, 1983; Oishi *et al.*, 2009). Beyond knuckle-walking, the triceps is also moderately involved in overhead reaching behaviors in *Pan* (Tuttle *et al.*, 1983), which may additionally contribute to the observed trabecular pattern.

At the wrist, *Gorilla* presents high rBV/TV values primarily at the anterior aspect of the styloid process and the distal articular surface of the ulnar head. This pattern suggests that the styloid does not play a major mechanical role in transferring loads from the carpus. Thus, the surrounding soft tissues may stabilize the wrist and contribute to dissipating compressive forces. Additionally, the radiocarpal articulation may further redistribute loads; however, we would need to quantify the trabecular architecture of the distal radius to ascertain the force distribution in the African great ape wrist. Overall, both proximally and distally, the trabecular patterns of the ulna of *Gorilla* appear consistent with habitual quadrupedalism (knuckle-walking), thus reflecting the use of extended elbow postures under compressive loading.

In contrast, *Pan* exhibits the highest rBV/TV values among great apes, concentrated at the distal ulnar head and the tip of the styloid process. This pattern indicates that the styloid process contributes to transmitting compressive forces to the carpals, resembling the condition in quadrupedal anthropoids and consistent with *Pan* retaining some contact with the carpals. However, relatively high rBV/TV values around the ulnar head articular surface may be associated with functional demands related to pronation–supination. Thus, the trabecular architecture of both the proximal and distal ulna in *Pan* may instead reflect a more complex combination of pronation–supination movements and a more flexed elbow posture than in *Gorilla*. In contrast to the findings of Bird *et al.* (2022), where the BV/TV patterns of the scaphoid, lunate, and triquetrum are similar between *Pan* and *Gorilla*, the differences found here may reflect biomechanical variation in knuckle-walking between the two taxa, suggesting distinct mechanics for load transmission during this locomotor behavior (Arias-Martorell *et al.*, 2021).

Previous studies have shown greater variability in *Pan* elbow kinematics during knuckle-walking than in *Gorilla* (Finestone *et al.*, 2018; Thompson, 2020), which could explain the observed rBV/TV distribution. Alternatively, the observed patterns may not solely reflect habitual knuckle-walking but also mechanically-demanding arboreal behaviors that may induce trabecular (re)modeling (Umemura *et al.*, 2002; Arias-Martorell *et al.*, 2021). *Pan* typically engage in a higher degree of arboreality than *Gorilla*, involving positional behaviors such as climbing and suspension

(Drummond-Clarke *et al.*, 2022, 2024). Moreover, we found a strong similarity between the trabecular patterns of *Pan* and *Ateles*, which may reflect habitual quadrupedalism together with versatile arboreal behaviors. However, recent studies suggest that some *Gorilla* populations are more arboreal than previously thought (Robbins *et al.*, 2025). Our proximal ulna sample includes *Pan* from the Tai National Park, Ivory Coast—one of the most arboreal and acrobatic populations (Doran & Hunt, 1994)—western lowland (*Gorilla gorilla*) from Cameroon and mountain gorillas (*Gorilla beringei beringei*) from the Virunga Volcanoes National Park, Rwanda. The latter are by far the most terrestrial *Gorilla* and likely represent an ecological outlier among all *Gorilla* species (Robbins *et al.*, 2025). This highlights the importance of analyzing here the trabecular patterns of *Gorilla gorilla*, which shows intermediate arboreality between the *Pan* and the Virunga *Gorilla* (Robbins *et al.*, 2025; Remis, 1995). In the distal ulna sample, *G. b. beringei* could not be included, such that our analyses only included one *Gorilla* species (*Gorilla gorilla*). Therefore, given our restricted sample to the more arboreal *Gorilla*, if arboreal behaviors such as climbing were sufficiently demanding to induce trabecular remodeling, patterns similar to those observed in *Pan* should also appear in *Gorilla* other than those investigated here. Nevertheless, these interpretations remain tentative, as our conclusions are constrained by sample composition and the absence of data from other skeletal elements, such as the distal radius, which may play a critical role in load redistribution.

The differences between African apes revealed here tentatively support the view that knuckle-walking may not represent a biomechanically uniform locomotor mode. While this may have different interpretations from an evolutionary perspective, our results support the view that further research is required to clarify the extent of biomechanical differences in knuckle-walking between *Gorilla* and *Pan* and its evolutionary implications. These differences may have important consequences for understanding the biomechanical diversity of this locomotor mode and its potential role (if any) in the emergence of hominin bipedalism.

Limitations of the Study

Several potential limitations may have influenced our results: (1) Possible size-scaling effects; (2) The influence of other factors, including diet, hormonal status, and genetic background; (3) The limited availability and discrepancies among published data on the frequency of locomotor behaviors in extant primates; and (4) Sample size.

To test the possible allometric signal in the PCA results of the trabecular rBV/TV distribution, we regressed each PC scores onto the total epiphyseal volume (Online Resource 1: Table S3). Previous studies investigated the relationship between total epiphyseal volume and absolute BV/TV values (Lukova *et al.*, 2024), whereas our analyses investigate whether size correlates with the distribution patterns of rBV/TV captured by the PC scores. Current evidence on size-scaling patterns of trabecular bone structure remains inconsistent, although body mass is a relevant factor known

to influence trabecular bone structure (Swartz *et al.*, 1998; Currey, 2003; Doube *et al.*, 2011; Barak *et al.*, 2013a; Ryan & Shaw, 2013; Saers *et al.*, 2019). While variation in body size has been shown to influence some trabecular parameters, such as trabecular thickness, spacing, connectivity, and number, the variable explored in this work—BV/TV—generally shows no significant correlation with body mass (Barak *et al.*, 2013b; Cotter *et al.*, 2009; Doube *et al.*, 2011; Ryan & Shaw, 2013). However, studies including a broader taxonomic sample (including non-hominoid primates) have reported correlations with humeral size proxies, specifically the geometric mean of epiphyseal dimensions (Kivell *et al.*, 2018) and the log-transformed average humeral head diameter (Arias-Martorell *et al.*, 2021). Our results reveal relatively weak correlation between epiphyseal size and both the proximal and distal ulnar trabecular patterns. Nonetheless, our results also indicate that factors other than size (particularly, locomotion in proximal ulna) determine most aspects of the trabecular pattern.

Other factors not considered here (such as hormones, sex, and genetics) may also contribute to the trabecular patterns observed. These factors are generally expected to act systemically, affecting the overall properties of trabecular bone throughout the skeleton rather than producing localized changes within a joint. Because our analyses focus on the relative spatial distribution of trabecular rBV/TV rather than absolute trabecular values, they are expected to be less sensitive to such systemic influences. The potential influence of phylogeny is more difficult to disentangle. Although relatively little is known about the extent to which trabecular architecture itself exhibits phylogenetic signal (but see Alfieri *et al.*, 2025), phylogeny may influence trabecular distribution indirectly through its effect on external skeletal morphology. Variation in trabecular structure might show phylogenetic structure because locomotor adaptations in skeletal external morphology have an influence on the loading regimes to which trabecular structure is subjected (Pietrobelli *et al.*, 2026) and/or because closely related taxa tend to display similar locomotor repertoires. Disentangling these various components of trabecular structure is still a work in progress, yet there is no question that focusing on trabecular structure is the most promising approach to discriminate how animals actually move (realized locomotor niche) as opposed to what they are adapted as a result of their evolutionary history (potential locomotor niche). Furthermore, some specimens show regions of compact cortical bone, where no trabecular bone is found, as seen in the median keel of the proximal ulna of hominoids (Online Resource 1: Fig. S16)—which is a key passive stabilization feature (Sarmiento, 1985; Rose, 1988, 1993b; Nakatsukasa *et al.*, 1996; Richmond *et al.*, 1998; Drapeau, 2008; Alba *et al.*, 2012). Therefore, future research should also investigate size-scaling effects based on larger samples, as well as to apply phylogenetic comparative methods—outside the scope of the present study—to determine if there is phylogenetic signal embedded in the variation of cortical bone thickness and/or trabecular structure, even if interpreting its biological and evolutionary bases might not be straightforward.

The use of locomotor frequency data compiled from the literature entails inherent limitations, as published behavioral data may vary substantially across studies, not only due to intraspecific differences related to habitat, sex, and ontogeny, but also owing methodological differences (including the definition of locomotor modes). To

mitigate these biases, we compiled locomotor data from the minimum possible number of references and standardized according to the locomotor categories defined by Hunt *et al.* (1996). This approach provides the most consistent framework currently available for quantitative analyses of locomotor behavior across species. Consequently, while keeping these considerations in mind, the results of the present study might provide a foundation for reconstructing joint posture and locomotor patterns in extinct species.

Conclusions

This study shows that ulnar trabecular bone structure captures functionally meaningful information related to joint use and the mechanical stresses generated by locomotor behaviors, reinforcing the view that trabecular architecture is highly responsive to habitual biomechanical demands and is (re)modeled accordingly (Biewener *et al.*, 1996; Lieberman, 1997; Pontzer *et al.*, 2006; Ruff *et al.*, 2006; Barak *et al.*, 2011; Kivell, 2016a). However, the functional signal varies between proximal and distal ulnar epiphyses and among primate clades, with a clear association between trabecular pattern and locomotor behavior at the proximal ulna, but a weaker and more variable signal at the distal ulna, particularly in hominoids. Overall, these results highlight the complex interaction between external shape, soft tissue and trabecular bone structure, emphasizing that trabecular bone does not record locomotor behavior uniformly across skeletal regions or taxa.

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Declarations

Inclusion and Diversity Statement The author team includes researchers of different genders and career stages, with women represented among both the first and senior authors. We are committed to promoting inclusion and diversity in scientific research.

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