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Trabecular bone response variation in the hominoid clavicle

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Previous studies have identified substantial variations in trabecular bone structure at regions of soft tissue attachment (entheses) and joint surfaces. However, the different effects of tensile and compressive forces on trabecular microarchitecture have remained largely unexplored. This study turns attention to such forces within the clavicle, a bone subjected to both compressive and tensile loading, to compare trabecular microstructure in these distinct loading environments. Using micro-CT scans of adult hominoid clavicles of several distinct genera, we measured trabecular thickness (Tb.Th), trabecular separation (Tb.Sp), and trabecular number (Tb.N) across the entire element. Our findings reveal nuanced differences in trabecular bone structure between entheses and subarticular surfaces. Entheses achieve higher density by increasing trabecular separation and trabecular thickness, while subarticular surfaces achieve it through higher trabecular number, and decreased trabecular thickness and trabecular separation. Notably, the joint region exhibited a higher trabecular number and lower trabecular separation, indicative of response to compressive forces. Conversely, at muscular entheses, a decrease in trabecular number alongside increased trabecular thickness, countered by higher trabecular separation, suggested a contrasting structural arrangement. These discernible variations likely correlate with diverse adaptations in muscle placements on the clavicle, significantly influencing the nuanced biomechanics and distinctive locomotor behaviours observed across primate species (Crane et al., 2019).

INTRODUCTION

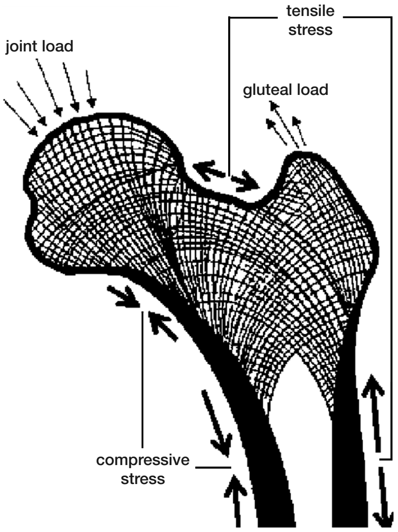
Trabecular bone, an essential component of the skeletal system, plays a pivotal role in resisting mechanical forces and maintaining skeletal integrity (Kivell et al., 2016, see **Figure 1**). Previous investigations into trabecular bone structure have demonstrated obvious variations at regions of soft tissue attachment (Biewener et al., 1996), known as entheses, and at joint surfaces (Barak et al., 2011; Crane et al., 2019). While certain aspects of external bone shape can be influenced by factors like the boundaries of muscle attachments or joint articulations, their reliability in inferring behaviour has been a subject of debate among researchers. Despite some studies suggesting a potential correlation between bone shape and behaviour, scepticism persists regarding the accuracy of using these skeletal markers to infer locomotive regime (Kivell, 2016). More recently, examining trabecular bone (spongy material that occupies the epiphysis and metaphysis of most bones) alongside external morphology has emerged as a critical piece of the paleoanthropological investigation into the evolution of locomotive behaviour.

To delve deeper into this complex terrain, it is crucial to consider the broader context of trabecular bone structure. For instance, an increased bone volume fraction (BV/TV) has been a focal point in trabecular bone research due to its relevance in understanding bone strength and resistance to mechanical stress (Mori et al., 1997; Georgiou et al., 2019); however, achieving increased BV/TV (calculated bone volume/total volume per voxel) involves intricate combinations of various trabecular parameters, such as trabecular thickness, number, and separation. This study aims to explore the nuanced mechanisms behind increases in trabecular bone density, specifically the role of these parameters furthering our understanding of the functional significance of internal bone structure. Specifically, on the measurement of three critical trabecular parameters: trabecular thickness, trabecular separation, and trabecular number across the clavicle. Understanding parameters of morphology contributes directly to the understanding of the specimens studied (humans, chimpanzees, gorillas) and indirectly can be informative of morphological behaviour across the hominin clade (Tsegai et al., 2013; Voisin, 2006).

Generally regarded as a “neglected bone” (Voisin, 2006, p. 944), the clavicle serves as a critical component of the shoulder girdle, and as such reflects the forces applied in locomotion. Muscular groups relevant to the clavicle’s function include the pectoralis major, vital for arm flexion initiation, especially in humans (Gagey, 1985), and the deltoid, whose primary function is in arm abduction in obligate bipedal genera. For other apes, clavicular shape and curvature may allude to the necessity of powerful arm elevation (Voisin, 2006), but the trabecular structure underlying the enthesis[1] may provide more insight into their use. For tree dwellers, a more extensive response from the deltoid may reflect in the microstructure due to brachiation[2]; for knuckle walkers, this would be unnecessary. In examining trabecular behaviour in these entheses, recent studies suggest that the properties of trabecular bone under multiaxial loading could depend more on individual struts than the overall structure, a factor potentially relevant to understanding the clavicle’s adaptive responses (Januddi et al., 2020; Pontzer et al., 2006). Furthermore, the ability of trabecular bone to rapidly remodel throughout life

Figure 1

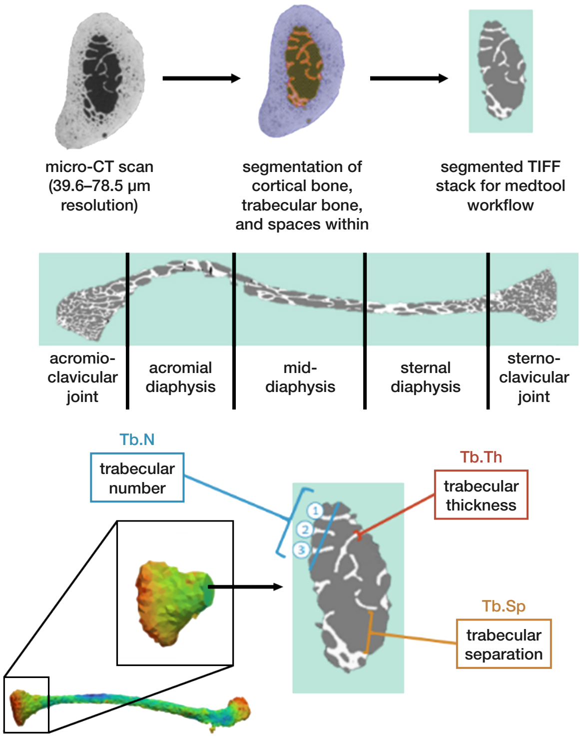
Cross-sectional view of a femur, delineating its internal composition



Note. This femur exhibits two fundamental components: cortical bone, constituting the outer shell, and trabecular bone, situated in the inner region. The cortical layer, displayed as a dense, continuous structure, encompasses the femur's outer surface, adept at bearing and distributing compressive forces efficiently. In contrast, the inner region showcases the trabecular bone, featuring a lattice-like pattern. This porous structure within the femur provides flexibility and resilience, crucial for adapting to varying mechanical demands. Notably, the figure highlights the responses of trabecular bone to different mechanical stresses. Arrows denote the specialised adaptations of cortical and trabecular bone to distinct mechanical (tensile and compressive) stresses, portraying their synergistic role in maintaining the femur's structural integrity and functionality during weight-bearing activities.

Figure 2

Diagram of the process to obtain trabecular number, separation, and thickness from the segmented scans of each specimen



Note. The clavicle was divided into five sections (acromioclavicular joint, acromial diaphysis, mid-diaphysis, sternal diaphysis, and sternoclavicular joint), with each section analysed for the three parameters listed above. Generally defined as the number of trabeculae per unit length, trabecular number (Tb.N) is calculated as the inverse of the mean spacing between the midlines of the trabeculae. The metric of trabecular thickness (Tb.Th) is calculated in this work as the mean trabecular bone diameter derived from the segmented trabeculae. Trabecular separation (Tb.Sp) is defined as the primary diameter of the cavities containing bone marrow, calculated here as the mean spacing between the edges of segmented trabeculae.

offers valuable insights into an individual's behaviour and joint posture under predominant stress (Tsegai et al., 2013); however, relative to our understanding of external morphology, the mechanisms by which trabecular bone senses and responds to strains, particularly tension, remain elusive (Pontzer, 2006). Despite insights from tissue engineering studies which suggest that trabecular struts may be particularly responsive to such tensile strains (Crane et al., 2019), gaps remain in our understanding of the specific mechanisms governing the remodelling of trabecular bone and its precise structural relationship to bone strength (Goulet et al., 1994; Mori et al., 1997; Georgiou et al., 2019).

Comparing samples from gorillas, chimpanzees and humans is essential in understanding variation in trabecular bone adaptation throughout the hominoid lineage. This variation is related to differences in modes of locomotion: *Gorilla* sheds light on terrestrial knuckle-walking adaptations; *Homo* illustrates the stability of obligate bipeds; *Pan* demonstrates agility in arboreal and terrestrial settings (Tsegai et al., 2013). The predictive capacity of locomotor biomechanics in deducing the behavioural patterns and posture of last common ancestors among hominoids, hominines, and hominins can be supported in this study of the internal morphology of the clavicle. Common understanding (Larson, 1998) attributes physical characteristics of the these living genera's trunk and upper limbs with bipedality. These characteristics include a rigid lumbar spine, a wide and flattened rib cage integrating the spine ventrally, a correspondingly broad pelvis, a rearward-positioned scapula attached to the rib cage, and a shoulder joint facilitating extensive abduction (Crompton, 2008; Larson, 1998). In exploring trabecular response patterns in the clavicle, these trabecular parameters (which are indicative of locomotion unique to each genera) offer valuable insight into the role of evolutionary adaptations within the shoulder complex (Georgiou et al., 2019).

MATERIALS AND METHODS

Micro-CT scans of 31 adult, wild-origin hominoid clavicles (*Gorilla gorilla*, *Pan troglodytes*, *Homo sapiens*; **Table 1**) were obtained and analysed using the medtool 4.5 software (v. 4.5; www.dr-pahr.at/medtool). The specimens used for this study originate from the Cleveland Museum of Natural History (CMNH), Field Museum of Natural History (FMNH), and American Museum of Natural History. All non-human apes are of wild-origin, with their collection locality specified in museum records. Human clavicles were sampled from the Hamann-Todd Collection (HTH) at the Cleveland Museum of Natural History. This collection comprises over 3,000 individuals who died in Cleveland, Ohio between 1893 and 1938 and most of those in the collection come from Ohio's public institutions such as hospitals, poorhouses, and prisons (Williams & Ross, 2021). Despite these individuals having been legally accumulated at the time of the collection's conception, the legislation, at the time, was a part of a societal framework that restricted the consent of those involved. Trabecular thickness, trabecular spacing, and trabecular number (**Figure 2**) were measured across the entire clavicle, employing a multiple volume of interest approach.

Micro-CT scans were obtained at the University of Chicago utilising a Phoenix Nanotom (180–240 kV) and V|tome|x (350–400 kV) combination, a high-resolution CT scanner. Scans were conducted with a resolution ranging between 60.106 to 89.203 microns. CT scan data were manually segmented to delineate the medullary cavity space and the trabecular bone structure it encompasses (**Figure 2**). This segmentation process was carried out using Avizo Lite (v. 2020.2, Thermo Fisher), resulting in meticulously defined TIFF stacks. The segmented TIFF stacks served as the primary input for subsequent analysis using medtool 4.5. For quantitative comparison, the clavicles were divided into five regions of interest; acromioclavicular joint, acromial diaphysis, mid-diaphysis, sternal diaphysis, and sternoclavicular joint (**Figure 2**). A multiple volume of interest approach (described further in Tsegai et al.

Table 1

Taxon, sex, number, and locomotive regime by genus

Taxon	*N*; wild/captive	Locomotive regime	Sex
Gorilla gorilla	*N* = 10; all captive (FMNH)	Quadrupedal knuckle walking	5 M, 5 F
Pan troglodytes	*N* = 13; all captive (FMNH)	Bipedal and quadrupedal	8 M, 5 F
Homo sapiens (anatomically modern)	*N* = 8; all anatomically modern (CMNH HTH collection)	Bipedal	1 M, 7 F

2013) was then used to quantify trabecular thickness (Tb.Th), trabecular separation (Tb.Sp), and trabecular number (Tb.N)) within each of the defined regions (**Figure 2**).

RESULTS

Across these three hominoid taxa, the subarticular trabecular bone displayed higher trabecular number and lower trabecular separation (**Figure 3**). Additionally, the sternal end displayed an even higher trabecular number and lower trabecular separation than the acromial end. Consistent repetitive microfracturing from compressive force may be responsible for the higher trabecular number in joints (see **Discussion**).

Generally, regions of muscular and ligament attachments display visible differences in trabecular density (e.g. Ryan & Shaw, 2013; Tsegai et al. 2013; Skinner et al. 2015), and the work here showed that this is achieved through a combination of increased trabecular separation and trabecular thickness. This heightened thickness appears to be a response to the loading environment created by the tensile forces generated by attaching muscles and ligaments, effectively reinforcing the cortical structure during periods of increased muscular activity. Separation may represent a response to strut reorientation in an anisotropic (directional) reaction to tension. This aligns with Saers et al. (2022) in findings concerning trabecular growth patterns post-initial ossification: trabecular bone, which first forms orthogonal to the growth plate and ossifies into a dense, anisotropic structure, undergoes remodelling by removing elements that experience minimal loading. This captures the idea that increased separation is based on resorption of unneeded (unstressed) trabeculae, while trabeculae thicken in response to locomotive stress.

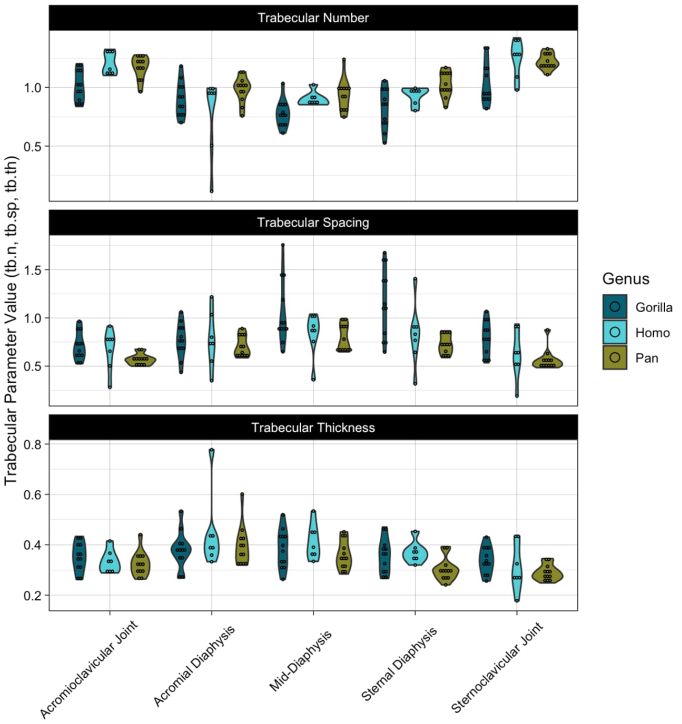
When looking at genus-based comparisons, the most intraspecific species differences across all three factors — trabecular thickness, trabecular separation, and trabecular number — were evident in *Gorilla*. This distinction was not solely attributed to inherent variability but was also further examined by sex (as depicted in **Figure 4**). Moreover, within the clavicle, gorillas exhibited notably higher values in trabecular thickness along the mid to sternal diaphysis in comparison to chimpanzees and humans. Gorillas displayed marginally greater trabecular separation in the acromial diaphysis region compared to chimpanzees and humans. Conversely, chimpanzees exhibited relatively higher trabecular number in the acromial diaphysis compared to both humans and gorillas.

DISCUSSION

The higher trabecular number and lower trabecular separation (**Figure 3**), coupled with decreased trabecular thickness, may be indicative of a reaction to compression in line with microfracturing for repair mechanisms in a partial volume effect (Hernandez et. al, 2005). Areas of higher separation and thickness may reflect reaction to tensile forces with thicker, more distanced and oriented struts (Best et. al, 2017). This combination strongly suggests that subarticular trabecular bone is exceptionally well-suited to withstand and absorb compressive forces frequently encountered at joint surfaces (Goulet et al., 1994). Additionally, the sternal end displayed an even higher trabecular number and lower trabecular separation than the acromial end. Consistent repetitive microfracturing from compressive forces may be responsible for the higher trabecular number in joints.

Figure 3

Findings across three hominoid taxa concerning subarticular trabecular bone



Note. Notably, the joint region exhibits a higher trabecular number and lower trabecular separation, indicating exceptional resilience to compressive force. Conversely, at entheses, sites where muscles and ligaments attach, decreased trabecular number and increased trabecular thickness oppose a higher Tb.Sp.

Based on the trabecular structure, the sternal end may be subjected to heightened compressive loading at the sternoclavicular joint, whereas the acromial end may undergo greater tensile loading, particularly during activities involving suspension and vertical climbing.

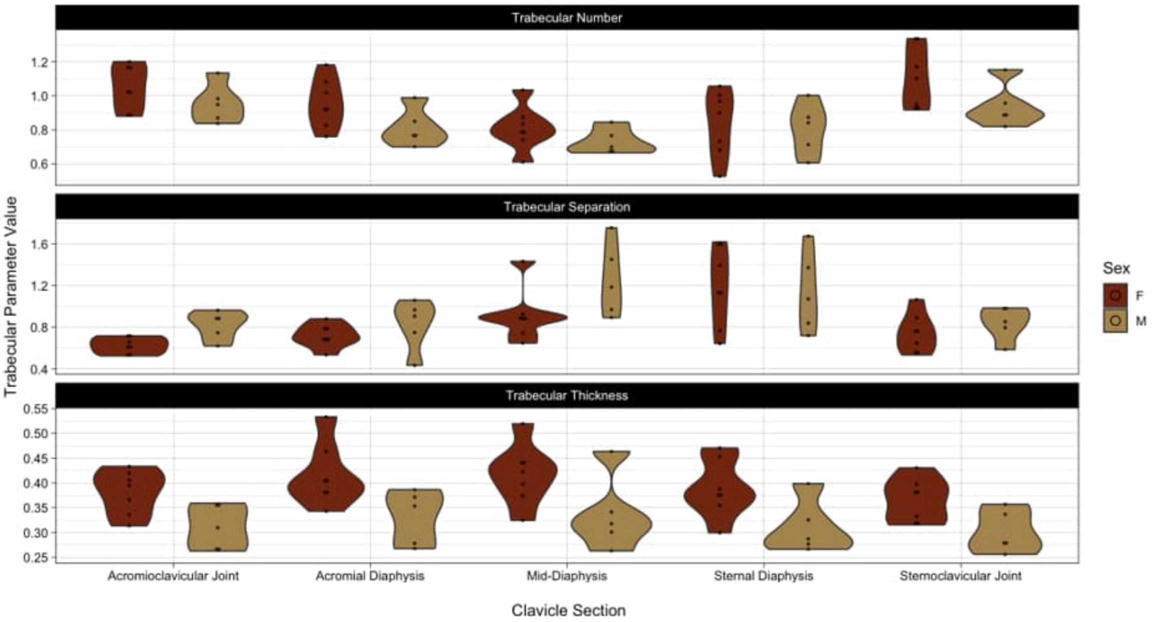
Of significance is the unique location of the pectoralis major (and deltoid) insertion on the clavicle found in humans (see **Appendix**) and chimpanzees, a feature which distinguishes these genera from *Gorilla* (Potau et al., 2018; Ashon & Oxnard, 1963). This distinct insertion pattern may influence arm flexion dynamics, as demonstrated in humans and gibbons (Gagey, 1985; Stern et al., 1980). The associated action of the pectoralis major, coupled with the internal curvature (ventrally/anteriorly projecting) of the clavicle acting as a "crank", facilitates the rotation of the glenoid cavity of the scapula. Variations in this curvature could potentially impact the efficiency of such muscular actions (Gagey, 1985; Stern et al., 1980).

For the variation in the acromial end, one could attribute the chimpanzee clavicular deviation to deltoid insertions — which set chimpanzees apart from gorillas and humans in their assistance with more arboreal behaviours such as brachiation (Voisin, 2006). The majority of the deltoid muscle attachment is located on the cranial surface of the acromial end in chimps while it is more on the ventral/anterior in *Homo* (see **Appendix**). While the muscular insertions on the clavicle may not explicitly indicate differences in locomotor behaviour, they likely reflect adaptations to similar forces (Stern et al., 1980). This notion aligns with observed differences between tree-dwelling and ground-dwelling primates. For instance, *Gorilla spp.* less frequently inhabit trees, which may result in less pronounced arm elevation, resulting in a clavicle with a diminished internal curvature (Voisin, 2006).

Voisin and Balzeau (2004) further highlighted disparities in the arrangement of bony structures within the clavicle among humans, chimpanzees, and gorillas, indicating heightened resistance in the chimpanzee clavicle compared to its human counterpart. This underscores the potential influence of clavicle morphology on force distribution and, consequently, locomotion within each primate species.

Figure 4

Variability within Gorilla *separated by sex*



Note. Due to the dramatic difference between *Gorilla* male and female specimens relative to chimpanzees and humans, a separate graph was made to illustrate the distinction. The factor observing most variation was thickness, finding males on average 0.1 units of thickness less than females.

The observed variations in trabecular bone microstructure may be associated with these diverse adaptations in muscle placements on the clavicle, contributing to the nuanced biomechanics and distinct locomotor behaviours evident across different primate species.

The differences in trabecular bone microstructure among gorillas, chimpanzees, and humans are intricately linked to unique muscular attachments on the clavicle, influencing arm flexion dynamics and scapular rotation (Gagey, 1985; Stern et al., 1980). These adaptations, coupled with variations in clavicular morphology and bony structures, underscore the potential influence of muscle placements on the clavicle, shaping nuanced biomechanics and diverse locomotor behaviours among primate species (Voisin & Balzeau, 2004; Voisin, 2006).

In further investigations, a valuable path for research may include study of the microarchitecture involved in these responses, such as the specific forces and directions implicated in catastrophic bone failure (Crane et al., 2019). While this study primarily delved into understanding medial-to-lateral variations in bone modelling, remodelling, and overall organisation, acknowledging the complex nature of observed fracture patterns is crucial. Factors such as bone mineral density stand among numerous elements that could substantially contribute to these patterns (Andermahr et al., 2007).

CONCLUSION

Ultimately, the findings underscore the importance of employing internal morphological assessments to decipher the intricate relationship between clavicle morphology, internal microarchitectural response, and locomotor behaviours. Developing a more robust understanding of the mechanisms underlying subarticular response will not only improve the theoretical framework behind study of Hominoidea (and therefore the broader evolution of locomotive behaviour and anatomy), it can contribute to the wider context of bone mechanics. The intricate relationship between bone microstructure and mechanical loading holds crucial implications for the prevention and treatment of skeletal disorders, including osteoporosis. The complexities of bone response and elasticity are studied as distinct combinations of trabecular parameters, which underscore the nuanced nature of bone modelling in response to different mechanical loading environments. To better develop strategies for medical treatment, methodologies for understanding osteological response to muscular loading, and for the broader study of palaeoanthropology, it is imperative to understand the intricacies of interaction between these parameters. Trabecular number, separation, and thickness hold great significance in the wider discussion of trabecular bone morphology and how it contributes to understanding locomotive behaviour. Additionally, the potential utilisation of trabecular assessments in scrutinising fossil primate and hominoid clavicles offers invaluable insights into the evolutionary changes within the shoulder complex, opening promising avenues for further comprehending the adaptations and biomechanical dynamics of the clavicle across evolutionary timescales.

NOTES

1. “Enthesis” refers to any insertion of connective tissue to a bone, including tendons, ligaments, fascia, and joints.
2. “Brachiation” refers to the action of swinging using only one’s arms.

SUPPLEMENTARY MATERIALS

Appendix

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