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Diplomová práce

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Prohlašuji, že jsem práci zpracoval(a) samostatně a použil(a) jen uvedených pramenů a literatury.

Plzeň, květen 2020 ………………………

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1 INTRODUCTION

Extant primates are identified by a wide range of locomotor and postural behaviors (Almécija et al., 2007). The morphology of hands of some of our ancestors has been traditionally described as mosaic (e.g., Begun, 1992; Demes et al., 1994; Susman, 1998). The primitive characteristics referred to the use of hands during locomotion, whereas the derived features were associated with manipulative behavior (Susman, 1998; Tocheri et al. 2007; Green and Gordon, 2008 Skinner et al., 2015). Thus, it can be assumed that such mosaic pattern was likely an intermediate morphology that gradually disappeared over evolutionary time (Marzke, 1997; Susman, 1998; Schmitt, 2003; Richmond et al., 2001; Begun, 2007; Daver et al., 2012; Skinner et al., 2015).

However, studies describing the mosaic morphology were often based on external bone morphology (Bloch and Boyer, 2002; Ward, 2002; Kirk et al., 2003; Deane and Begun, 2008; Alba et al., 2010). Because of that, the long-held discussion about locomotor and manipulative activities of our ancestors remains unresolved. Investigation of internal bone structure, such as trabecular bone, in connection with the locomotor behavior of extant primates, can offer a unique insight into the behavior of our ancestors.

Trabecular bone tissue responds to local stress and adapts to its mechanical environment (Ruff et al., 2006). In places where stress is lower, there is a gradual decline in the amount of trabecular tissue, resulting in a weaker structure. Conversely, in places where stress is higher, there is a gradual increase in trabecular tissue (Pontzer et al., 2006; Barak, 2011; Sinclair et al., 2013). Therefore, we assume, that the analysis of internal structure may reflect the actual biomechanics of an individual during its lifetime as opposed to what the individual would be morphologically capable of, as is the case with the analysis of external bone morphology (Schilling et al., 2014). Although the structure of trabecular bone is partially genetically determined (Currey, 2002), remodelling is at peak during growth and development and gradually declines into the adulthood (Martin et al., 1998).

The primate hand has a high informative value because it is directly involved during both arboreal and terrestrial locomotion (except for bipeds like humans). Following the assumption of local stress determination, the trabecular tissue parameters should be different depending on how the hand is employed and loaded during locomotion. Specifically, the trabecular structure likely reflects differences in load (i.e., differences in load direction, magnitude, and frequency) and differences associated with different hand positions during the locomotion. The parameters should differ depending on the type of action performed by the hand and its associated load. Further factors that likely influence or contribute to the variability of trabecular traits are the body size, age, sex, genetic makeup, and fitness of the individual, among other factors.

Studies mapping the internal trabecular patterns of primate bones focus almost exclusively on metacarpals or phalanges (e.g., Marchi, 2005; Lazenby et al., 2011; Tsegai et al., 2013). However, almost no such studies have been performed on primate wrist bones (except, for example, Schilling et al., 2014; Williams-Hatala et al., 2018; Stephens et al., 2018), even though it is the wrist that must endure the highest stress during terrestrial and arboreal locomotion (Schilling et al., 2014).

In this study, the trabecular bone tissue of the scaphoid, lunate, and capitate bones of *Ateles*, *Gorilla*, *Hylobates*, *Pan*, *Papio*, *Pongo,* and *Homo* will be investigated. The reason why these genera have been chosen is because of their different body sizes and types of locomotion. The three bones have been selected because of their role in transferring the weight between forearm and metacarpals during the locomotion, where the radiocarpal and mediocarpal joints are involved. The radiocarpal joint is responsible for more than a half of the range of wrist movements (Crisco et al., 2005) and the mediocarpal joint is a functional unit that allows for wrist movements in all directional planes (Tortora and Derrickson, 2011). Motion and loading during locomotion directly affect the internal morphology of the wrist, and it can be assumed that the selected bones are likely to preserve this functional signal (Schilling, 2014).

Questions about limb bone loading during locomotion have been addressed in paleoanthropology for more than a century (Huxley, 1863; Keith 1902). Attention has particularly been brought to this topic because of an effort to map the evolutionary trajectory of bipedalism (Strait et al., 1997; Corruccini, 1975; Richmond and Strait, 2000; Corruccini and McHenry, 2001).

The capitate is loaded in tension during arboreal locomotion. It is probably loaded less than during terrestrial locomotion because the weight is distributed more evenly between all carpal bones, especially between scaphoid and lunate. On the other hand, the capitate is loaded in compression during terrestrial locomotion, as the forelimb must carry much more weight of the upper half of the body (Schilling, 2014). This means that the morphology of the midcarpal joint surface in terrestrial taxa has evolved to withstand high compressive loads. The articular surfaces between the capitate, scaphoid, and lunate are relatively broad and allow these bones to act as one functional unit (Tortora and Derrickson, 2011). That makes them highly resistant to mechanical loads. In contrast, these bones are rather small and more 'spherical' in shape in arboreal taxa, because they are not under such high compression during locomotion (Sarmiento, 1988; Richmond and Begun, 2001). Accordingly, these differences in loading should be reflected in the distribution of the trabecular tissue between the groups based on the locomotor patterns.

Therefore, wrist loading regimes should differ between species that use their hands mostly for suspensory locomotion and terrestrial quadrupedal locomotion (Carlson and Patel, 2006). Thus, we predict that suspensory taxa will have a lower bone volume fraction (bone volume/tissue volume) than quadrupedal taxa. The carpal bones of *Homo sapiens* serve as a control in our comparison of primate species because humans rarely use their hands for locomotion. That is the reason why we assume that *H. sapiens* will have a lower bone volume fraction than all other taxa. We also assume that the differences in body mass and body size between species may reflect some differences between trabecular bone parameters.

The first aim of this thesis is to test the assumption that variability in carpal bone trabecular structure correlates with locomotor type, regardless of the evolutionary trajectory of selected species. The second aim of the thesis is to explore how the internal structure of the wrist bones differs among the selected taxa, especially with regards to differences in wrist size. The prediction is that the internal structure will vary according to bone size in a similar manner as the trabecular structure of long bones in mammals (Ryan and Shaw, 2013).

2 ANATOMY OF THE WRIST

2.1 Fetal Growth of the Wrist Bones

O´Rahilly and Müller (1987) defined 23 developmental stages reflecting the morphological changes of the hand during prenatal development. The origin of morphological development begins at the 26th to 27th day of pregnancy (Malas et al., 2006). The wrist‘s growth is classified as beginning from stage 17, approximately at day 41 of pregnancy and ending at stage 23 during the 8th week of pregnancy when the embryonic period is completed and the fetal period begins (O'Rahilly a Müller, 2010). At stage 17, mesenchymal condensation of future metacarpals begins and later proceeds during stage 18 to gradual carpal chondrogenic differentiation. The structure of the capitate begins to appear at stage 20, and at stage 21 the structures of scaphoid, lunate, hamate, and triquetral are also evident (Caba et al., 2012).

In phase 21 (approximately 52 days into the embryonic development), the bases for radial and ulnar collateral ligaments are formed, which are clearly visible in the fetal period. Stage 22 is characterized by laying the foundations of the *retinaculum flexorum* (*ligamentum carpi*), under which the carpal tunnel begins to form (at 9 weeks). At stage 23 radiocarpal and ulnocarpal ligaments are formed on the palmar side of the wrist and at week 10 on the dorsal side of the wrist. At the beginning of the fetal period (week 9), the joints between the scaphoid and lunate and between the trapezoid and capitate are formed. Around 11 weeks, the connections between lunate and triquetral and between capitate and hamate are shaped (Caba et al., 2012).

The cartilaginous form of the future articular disc is visible at stage 21 and the disc is morphologically complete at week 14. Pre-muscle blastems are evident in phase 20. *Musculus flexor digitorum superficialis*, *m. flexor digitorum profundus*, *mm. lumbricales,* and *m. extensor* *digitorum* are developted during stage 22, and *m. adductor pollicis* and *m. flexor carpi radialis* are developed during stage 23. This completes the classic circular pattern of the hand muscles. During the 10th week, the organization of the fibrous joints of the wrist begins, and *m. extensor carpi ulnaris* appears as well. The development of the hand muscles is complete by week 12, and at week 14, blood vessels begin to appear in the lunate; thus, the osteogenic process starts and is later completed after birth (Caba et al., 2012).

2.2 Postnatal Development of the Wrist Bones

Although the functional anatomy of the hand has been discussed and studied quite thoroughly and carefully (e.g. Marzke, 1997; Almécija et al., 2015; Williams-Hatala et al., 2016; Karakostis et al., 2018), only a few such studies have been focused on the carpal bones (with exceptions, such as Napier and Davis [1959] and Schwartz et al. [1998]). This may be due to taphonomic reasons, such as the low number of fossil specimens, as well as to the difficulty of studying these small bones. However, the interest in this topic is gradually rising, especially around questions concerning the evolutionary pathways of wrist bones in hominoids or functional adaptations (e.g. Channon et al., 2009; Michilsens et al., 2009; Myat et al., 2012; Daver et al., 2012; Kivell et al., 2013).

Primates exhibit high degree of anatomical variation, which also pertains to the variability of hand proportions, including the wrist. The anatomical differences reflect the evolutionary trajectory related to motion capabilities of the hand and wrist. Some of this anatomical variation likely allows the hand to withstand excessive stress during locomotion. The anatomy of the wrist may also be adapted to the locomotor habits of particular species (Selby at al., 2016).

Although the eight or nine carpal bones that constitute the primate wrist have been described in conjunction with the forearm bones as functioning as an anatomical module, the results of recent studies demonstrate that the morphology of individual wrist bones follows different evolutionary pathways (Kivell et al., 2013). These results support the opinion that the wrist acts as an integrated complex system of joints, in which the individual bones have some degree of functional and evolutionary independence (Daver et al., 2012). Some morphological changes indicate the type of locomotor behavior, and we can see the pattern of these changes across different taxa. However, other morphological changes indicate taxon-specific or clade-specific synapomorphic patterns (Kivell et al., 2013). For instance, the morphology of the lunate separates the great apes from the other primates and the different evolutionary pathway of the hamate separates *Hylobates* from other genera. It seems that these examples reflect autapomorphic morphological trait changes and not the evolutionary changes caused by the different types of locomotion within primates (Drapeau et al., 2007; Kivell et al., 2013).

New World and Old World monkeys retain the primitive form of the wrist. The distal end of the ulna is a part of the wrist joint that abuts the triquetral and pisiform. Also, the synovial radioulnar joint is not fully developed in these groups of primates. In contrast, in anthropoid monkeys, an intraarticular disc is present between the ulna and carpal bones. The intraarticular disc is completely separated from the pisiform and partially from the triquetral. The disc articulates with the lunate, but it is completely separated from the radioulnar joint (Fig. 1).

Radioulnar joint is fully ossified in gibbons, but it occurs as a single unit (lunula) or becomes a part of the concave proximal articular surface in chimpanzees (Fig. 1). This phenomenon can be observed also in gorillas. However, the joint is still surrounded by the articular cartilage and lies in the proximal synovial space. It is also in contact (at least partially) with the wrist joint (Lewis and Hamshere, 1970; Schwartz et al., 1998).

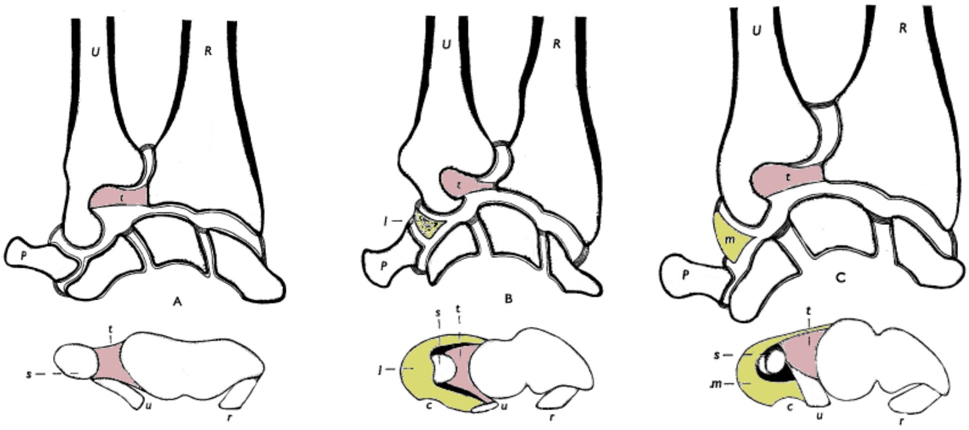


Fig. 1: The radiocarpal joint of the right upper limb; (A) Old World monkeys (*Cercopithecus nictitans*), (B) gibbons (*Hylobates lar*), and (C) chimpanzees (*Pan troglodytes*). (R) radius; (U) ulna; (P) pisiform; (t) triangular disc; (m) intraarticular disc; (l) lunula; (r) palmar radiocarpal ligament; (u) palmar ulnocarpal ligament; (s) styloid process of ulna; (c) spot where the pisotriquetral and radiocarpal joints are connected. The figure was taken from Hamshere and Bucknill (1970) and modified.

In most primates, there is *os centrale*, an accessory ossicle of the wrist typically positioned between the bodies of scaphoid, trapezoid, trapezium, and the head of capitate, which is fully ossified to the scaphoid body in the human wrist. As we can see in Fig. 2, in the Old World monkeys, the body of centrale articulates (at least partially) with the head of the capitate. Sometimes the triquetral may also contact the head of the capitate, however this is unusual. The scaphoid is proximal to centrale and may slightly overlap it dorsally. The capitate is longer than hamate. The lunate articulates primarily with the head of the capitate, though sometimes it may be in contact with the hamate. The centrale is long and expands ventrally under the trapezoid, as well as beyond the dorsal surface of the head of the capitate and the distal end of the lunate. The mesiodistal corner of the centrale encroaches between the trapezoid and the capitate (Orr, 2018).

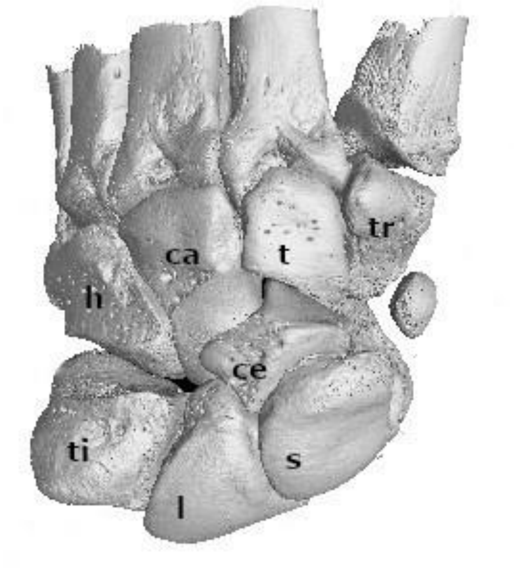


Fig. 2: The dorsal view of the left wrist of Old World monkeys (*Papio hamadryas*). (h) hamate; (ca) capitate; (t) trapezoid; (tr) trapezium; (ce) centrale; (ti) triquetral; (l) lunate; (s) scaphoid.

In gibbons, the centrale may fuse with scaphoid in very young as well as older individuals (Schwartz et al., 1998). Also, *Hylobates* have a proximo-distally shorter and medio-laterally narrower lunate with a proximo-distally and medio-laterally smaller radial facet and proximo-distally and dorso-palmarly larger scaphoid facet. They share this pattern with all Miocene apes (Kivell et al., 2013).

In chimpanzees and orangutans, the scaphoid surrounds the centrale rather dorsally. The centrale is very narrow and surrounds the head of the capitate. In its shape and articulations, the centrale closely resembles the centrale of the Old World monkeys. Also, as in Old World monkeys, the lunate of chimpanzees and orangutans articulates primarily with the head of the capitate. In contrast, the centrale is usually fused to the scaphoid (Schwartz et al, 1998). Gorillas generally exhibit the ancestral hominid condition. On the other hand, chimpanzees and orangutans have evolved in parallel a slightly dorso-palmarly taller and medio-laterally wider lunate with a proximo-distally and medio-laterally larger radial facet and a proximo-distally and dorso-palmarly smaller scaphoid facet (Kivell et al., 2013).

Triquetral and capitate morphology indicates several occurrences of parallel evolution within hominoids. In the triquetrum, *Pongo* and *Hylobates* have a short proximo-distal length of the lunate facet, which indicates greater mobility and greater tensile loading during suspensory locomotion. In the capitate, *H. sapiens* and fossil hominis and *Gorilla* have the body of capitate proximo-distally shorter and medio-laterally broader, which indicates greater stability and compressive loading during quadrupedal locomotion. Similar morphology of the wrist bones indicates behavior (e.g. locomotor behavior) shared between clades. Within the wrist bones, these indications can be observed in particular on scaphoid, triquetral, and capitate. Compared to that, morphology of lunate and hamate is most likely synapomorphic for the clade. Overall, there is an increased variability of morphological carpal traits in hominoids across carpal bones, compared with other primates, and some traits indicates parallel evolution, especially between orangutans and gibbons, and among extant African apes, recent and fossil humans (Orr et al., 2010; Kivell et al., 2013). *Pan* retains the ancestral hominoid pattern of the capitate, while *Gorilla* has evolved in parallel with *H. sapiens* and fossil hominins and shares some morphology with hominins. For example, the body of the capitate in *Gorilla* is proximo-distally shorter with a medio-laterally wider proximal facet (Kivell et al., 2013). In contrast, *Pongo* and particularly *Hylobates* have a proximo-distally longer but dorso-palmarly shorter capitate body and medio-laterally and dorso-palmarly smaller proximal facet (Kivell and Begun, 2009).

The evolution of the scaphoid morphology is described as more complex compared with the other wrist bones, with this complexity being ascribed to the variation in locomotor behaviors or to the fusion of the centrale to the scaphoid in hominins (Richmond et al., 2001). *Gorilla*, *Pan,* and *H. sapiens* share a smaller lunate articulation and a larger scaphoid body, which reflects fusion of the centrale to the scaphoid body (Kivell et. al., 2013).

In general, the proximal edge of the wrist bones creates the radiocarpal joint and the distal edge creates the midcarpal and carpometacarpal joints (Reddy & Compson, 2005). Both proximal and distal edges together create a functional unit, which allows for movements in all planes and directions (Ombregt, 2013). The arrangement of the wrist bones creates the carpal tunnel where flexor tendons (*m. flexor digitorum superficialis et profundus*) and *n. medianus* run (Reddy and Compson, 2005).

There are six osteofibrous channels on the dorsal side of the wrist that hold tendons of wrist and finger extensors and thumb abductors. The first channel contains tendons of *m. abductor pollicis longus* and *m. extensor pollicis brevis*, which allow for radial and palmar flexion of the wrist. The second channel contains tendons of *m. extensor carpi radialis longus* that gets involved while extensing the wrist, and *m. extensor carpi radialis brevis* that also extends the wrist and brings it back to the neutral position. The tendons of *m. extensor pollicis longus* go through the third channel and allow for thumb movements. In the fourth channel, there are tendons of *m. extensor indicis proprius* (extension of the second digit) and tendons of *m. extensor digitorum*, which allow for the movement of the second to fifth digit, especially their proximal phalanges. Their secondary function is to adduct the wrist medially towards the ulna. The tendon of *m. extensor digiti minimi* goes through the fifth channel and serves the same function as the tendon of *m. extensor digitorum*. *M. extensor carpi ulnaris* passes through the sixth channel and acts as a strong deviator of the ulnar side of the wrist and also serves as an opponent to *m. abductor pollicis longus*. However, *m. extensor carpi ulnaris also allows for* many secondary wrist functions (Ombregt, 2013).

Crisco et al. (2005) defined the radiocarpal joint as a functional unit that allows for more than half of the wrist's range of motion. This joint is based on multiple articulations of scaphoid, lunate, triquetral, and of the distal end of the radius. These bones create the joint's characteristic elliptical shape where the concave part is formed as carpal articular surface at the distal part of the radius. Radius has two facets for scaphoid and lunate and it continues as an articular disc on the ulnar side (Fig. 3).

Crisco et al. (2005) suggest that despite the complex movements of the wrist, the scaphoid and lunate function mostly in flexion or extension, an idea shared with some of the other studies (Ruby et al., 1988; Short et al., 1997; Werner et al., 2004). Crisco et al. (2005) also found that rotation of scaphoid and lunate increases linearly with the degree of wrist motion regardless of its directionality, which is also supported by previous studies (Patterson et al., 1998; Wolfe et al., 2000). Finally, as fusion of scaphoid and centrale significantly reduces flexion, extension, and both abduction and adduction, the results of previous studies demonstrate the importance of individual bones of the radiocarpal joint to wrist motion (Sturzenegger et al., 1991; Beyermann et al., 2000).

The radiocarpal joint cooperates with the midcarpal joint that is traditionally defined as a functional unit and not as a single anatomical joint. The articulation is between the proximal and distal rows of carpal bones. The proximal row is ulnarly concave for hamate and capitate and radially convex for trapezium and trapezoid (Fig. 3). The site of articulation is the distal part of radius and the scaphoid, lunate and triquetral (Tortora and Derrickson, 2011).

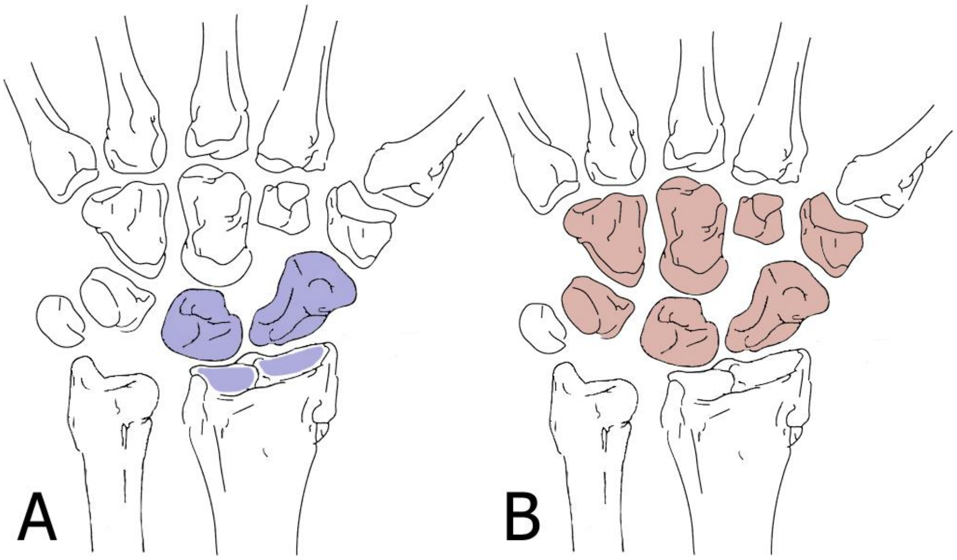


Fig. 3: The radiocarpal (A) and midcarpal (B) joint of human wrist.

Moritomo et al. (2006) found that the direction of movement of the capitate towards the scaphoid is always oblique and it extends from radio-dorsal to ulno-palmar in radioulnar deviation. It holds for the direction of movement of the capitate relative to the lunate and triquetrum as well. The range of movements remains almost without changes in both cases though. When coming from flexion to extension, the extent of rotation of the capitate decreases with respect to the scaphoid and increases with respect to the lunate. This ultimately means that the midcarpal joint basically includes three types of joint systems – the uniaxial joint between scaphoid and distal row of the carpal bones, the biaxial joint between lunate, triquetral, and distal row of carpal bones and finally the multiaxial intercarpal joints of the proximal row of the carpal bones (Moritomo et al., 2006).

The arrangement of muscles, tendons, and bones allows for a fully functional hand as a unit and reflects the specific requirements of a species during locomotion, and postural and manipulative behaviors (Sarmiento et al., 1988).

2.3 Remodelling of the Trabecular Tissue

Some experimental studies have shown the ability of bones to adapt to extreme conditions, particularly to the point, in which loads are applied to the bone without breaking or irreversibly damaging it (e.g. Ehrlich and Lanyon, 2002; Barak et al., 2011; Wallace et al., 2013; Tsegai et al., 2018). This process is most commonly described as bone functional adaptation (Ruff et al., 2006). The study of bone internal structure is used for medical and orthopedic purposes (e.g. Klawitter and Hulbert, 1971; Hart et al., 1988; Hniskes and Hollister, 1993; Pettermann et al., 1997; Uhthoff et al., 2006; Chen et al., 2007), to understand the biomechanical adaptation of modern human population (e.g. Sievänen et al., 2007), to understand the remodelling and biology of the bones (e.g. Cowin, 1984; Bagge, 2000; Jacobs, 2000; Miller et al., 2002; Coelho et al., 2009) etc. In addition, it is also used to understand the lifestyle of human ancestors. The differences in trabecular bone in extant species are identified with an attempt to associate them with different behaviors. Once the relationship between structure and behavior is established, such knowledge can be applied to the study of different lifestyles of human ancestors (e.g. Ryan and Ketcham, 2002b; Griffin et al., 2010; Ryan et al., 2012; Tsegai et al., 2013; Skinner et al., 2015; Stephens et al., 2016; Tsegai et al., 2018).

However, the relationship between bone internal structure and behavior is oftentimes rather unclear. This may be a result of studies that have traditionally focused mainly on the proximal femur (e.g., Ryan and Ketcham, 2002a, 2002b; Ryan and Walker, 2010) and/or on the proximal humerus (e.g., Ryan and Walker, 2010; Scherf et al., 2013, 2015), with conflicting conclusions being reached. The results can be misleading precisely because neither bone is directly associated with the highest loads during manipulative tasks or locomotion. Therefore, we suggest, in line with some recent studies (e. g. Schilling et al. 2014; Stephens et al., 2018; Williams-Hatala et al., 2018) to focus the attention on the bones of the wrist.

There are some known interspecific patterns in the variation of trabecular structure, such that a species can exhibit a similar trabecular structure across several elements of their skeleton. For example, recent humans may be described as having a low volume of trabecular bone across the postcranial skeleton, including a heavily loaded lower limb bones, such as the femur. In contrast, chimpanzees tend to have a high volume of trabecular bone across different skeletal elements as compared to other hominoids (e. g. Griffin et al., 2010; Tsegai et al., 2013).

Trabecular and cortical bone remodelling, known as targeted remodelling, is strictly regulated and ensures the repair of microdamage. It is a replacement of older bone tissue with newer one through sequential osteoclastic resorption and osteoblastic bone formation. Though the rate of remodelling is regulated by a wide variety of calciotropic hormones, such as parathyroid hormone (PTH), thyroid hormones, sex steroids etc., bone remodelling is based on the action of resorptive and formative cell populations (Eriksen, 2010). The cells responding to mechanisms of loading are osteocytes and osteoblasts. Not all bone cell reactions are part of the remodelling process. The specific mechanical stimuli to which osteocytes and osteoblasts respond are probably changes in strain itself and strain-generated changes in their fluid environment (Ehrlich and Lanyon, 2002). It is necessary that older bone is replaced by newer bone to ensure the integrity of the skeleton. This process must be strictly regulated, as deviations from the neutral balance between resorption and formation could entail disproportionate bone loss or incremental bone mass, thus increasing the risk of fractures or compression syndromes (Eriksen, 2010).

The remodelling of trabecular bone occurs on the surface of the trabeculae and lasts approximately 200 days (Eriksen, 2010). Remodelling is initiated by osteoclastic resorption that erodes the resorption gap and lasts approximately 30-40 days, followed by bone formation itself (Eriksen et al., 1984). We can see a complete renewal of the resorption gap with the new bone at the end of the whole process (Eriksen et al., 1990).

Unlike trabecular bone remodelling sites that are close to red bone marrow, the cortical bone remodelling sites are distant from the red bone marrow (Partiff, 2000). Therefore, it has been assumed that the mechanisms of bone remodelling are different in trabecular versus cortical bone, (i.e., cells responsible for trabecular bone remodelling go directly from red bone marrow to the bone surface, whereas the cells responsible for cortical bone remodelling reach the cortical bone through the vasculature [Eriksen, 2010]).

In general, spongy bone reacts to stress with relatively rapid remodelling, approximately 120 days (Ehrlich and Lanyon, 2002), in contrast to compact bone (Eriksen, 2010). Compact bone adapts to external conditions especially in its thickness, thereby improving the resistance to bending forces, whereas trabecular bone maintains thickness so that the kinetic energy transfer is most efficient (Keaveny et al., 2001; Sugiyama et al., 2010; Reznikov et al., 2015).

Several genetic and environmental factors, apart from specific locomotor behaviors that could affect remodelling of the internal structure of bones have been identified (Ruff et al., 2006). These aspects include loading magnitude due to body mass (Ryan et al., 2013), differences in load frequency in conjunction with overall activity levels (Liberman, 1996), and other factors that may affect the frequency or orientation of load (Wallace et al., 2013).

In addition, genetic factors, such as hormonal differences or differences in bone regulation, even among closely related species, may influence the remodelling of trabecular bone (Lovejoy et al., 2003). Equally, there may be differences between females and males or across the life stages of an individual (Reginster and Burlet, 2006). These genetic differences may manifest as phylogenetic differences in internal structure (Ryan and Shaw, 2013). Other aspects affecting remodelling of the structure may be diet and the intestinal microbiome (McCabe et al., 2015). At the same time, it is important to mention that remodelling is more effective during an individual's ontogenetic growth than during adulthood (Sarringhaus et al., 2014). It is particularly important for African apes, in which the structure is remodelled primarily during development and is significantly lower (but still evident) in adulthood (Ruff et al., 2013). There are many known factors affecting the remodelling of the internal structure and therefore, it is not always possible to accurately determine the relationship between structure and behavior of an individual, which may distort the final interpretation of results. It is especially difficult to determine what kind of behavior or combination of behaviors is reflected in trabecular bone structure.

3 LOCOMOTOR AND POSTURAL BEHAVIOR

The wrist is a morphological complex involving many bones, muscles, and ligaments (Sarmiento, 1988). Therefore, any functional interpretation of morphological variation must be supported by accurate description of the carpal bones and their mobility (carpal kinematics) within their anatomical complex. Previous studies of primates have focused primarily on great apes, mainly because of their close relationship with humans (e.g. Jenkins and Fleagle, 1975; O´Connor and Rarey, 1979; Orr et al., 2010), while neglecting other primates. Functional anatomy of the anterior/upper limb plays a decisive role in the reconstruction of locomotor and postural behavior and adaptations of human ancestors, which can be studied by understanding the functional anatomy of extant primates.

The genera selected for comparison were divided into broader locomotor groups and this allows for categorizing the involvement of the hand during locomotion and loading regimes acting on the selected bones.

1) Suspensory behavior, including the semi-brachiating *Ateles sp*., brachiating *Hylobates agilis*, *H. muelleri, H. lar,* and ratcheting *Pongo pygmaeus*;

2) Quadrupedal behavior, including the knuckle-walking *Gorilla beringei*, *G. gorilla*, *Pan troglodytes,* and digitigrade *Papio ursinus, P. anubis,* and *P. hamadryas*;

3) Bipedal behavior, comprised solely of *H. sapiens*, which serves as a null model for comparison.

It is also important to note that although these broad locomotor groups reflect basic differences in locomotion, postural behavior, and wrist load, each category may also reflect differences in the external morphology of the wrist bones. As such, it is possible that this variation in external morphology may affect the inner structure of carpal bones. For example, the „suspensory“ category in fact involves three types of locomotor behavior (semi-brachiation, brachiation, and ratcheting), and differences are present among these three types, such as the amount of time spent in locomotion in the trees versus on the ground or the use of tail during locomotion etc. (see below). Similarly, we can observe the differences between knuckle-walking and digitigrade foot postures in the „quadrupedal“ category (see below).

3.1 Suspensory Behavior

Suspensory locomotion is a form of arboreal locomotion during which the primate’s body is suspended below or among tree branches (Michilsens et al., 2009). There are in fact three subcategories in this category: brachiation, semi-brachiation, and ratcheting behavior.

Hollihn (1984) defined brachiating behavior as „bimanual progression along or between overhead structures for a distance of several meters without the intermittent use of other types of positional behavior and without support by the hind limbs or tail.” This definition is widely accepted. It is well known that brachiation is mainly used by gibbons (family *Hylobatidae*) (up to 80% of their traveling time) (Hollihn, 1984). If we apply Hollihn's definition of brachiation to all extant primates, the gibbons are the only group of true brachiators (Michilsens et al., 2009).

Brachiation is relatively widely studied with a special focus on the shoulder girdle and consequently on the muscles of the upper limb and the limb’s biomechanical mobility (e.g., Chang et al., 1997; Chang and Bertram, 2000; Gomes and Ruina, 2005) and on the anatomical characteristics of extant primates (e.g., Tuttle, 1972; Fleagle, 1979;

Hollihn, 1984). However, almost no studies have focused on the loading of wrist bones during brachiation (except Schilling, 2014).

Previous studies have highlighted, in particular, some myological characteristics of brachiators, such as large *m. flexor digitorum profundus, m. flexor digitorum superficialis* and *m. flexor digitorum longus*, large *m. biceps brachii* (Tuttle, 1972), and large *m. lattissimus dorsi* and *m. teres major* (Fleagle, 1979). Generally, it is also assumed that the gibbon forelimb is characterized by elbow and wrist flexors with a high power generating capacity and that the wrist flexors are connected to long tendons to maximize the energy storage and recovery during the locomotion (Michilsens et al., 2009).

When hylobatids use the hand during terrestrial locomotion, the wrist is in a similar position to palmigrade species (see below). It is significantly dorsiflexed and the palm touches the substrate. The hand is characteristically used as a hook during arboreal locomotion, in which the middle phalanges are on top of the support and the distal phalanges touch the side of the support opposite to the proximal phalanges and the metacarpophalangeal joint is in slight flexion (Sarmiento, 1988).

Jenkins (1981) reported that the distal row of wrist bones remains stable and the proximal row rotates around it during brachiation. Also, considerable ulnar and radial deviations of the radiocarpal and the midcarpal joints are evident and increased wrist flexion, mostly at the end of the support phase and especially on larger diameter supports. This is due to the area where the palm touches the support moving distally with increasing support diameter (Sarmiento, 1988).

Some studies also show that all extant hominoids have a unique wrist structure because the lineage evolved an intraarticular meniscus, which prevents direct articulation of the ulna with the wrist. This meniscus prevents articulation to different degrees among hominoid species, depending on the type of locomotion (e.g. Lewis, 1969; 1970). Yet some studies assume that this evolutionary modification correlates functionally with brachiation in which the body of the primate is suspended from one of the upper limbs and the wrist structure must allow for an increase range of supination (e.g. Lewis, 1971).

The New World monkeys exhibit anatomical features of suspensory behavior, which are not evident in gibbons or orangutans (Rosenberg and Strier, 1989; Larson, 1998). This can be referred to as the semi-brachiating motion, which is characteristic for extant primates that involve the tail and lower limbs during the locomotion (Cant et al., 2001). The greatest biomechanical difference distinguishing their movements is the distinct involvement of the tail and forelimbs during both, terrestrial and arboreal locomotion (Cant, 1986).

Also, New World primates, including the semi-brachiating ones, retain a primitive type of wrist in which the styloid process of the ulna articulates directly with the pisiform and triquetral, and the articular surface of the styloid process of ulna faces inward. The triquetral is subject to a relatively high load and the hamate lies rather obliquely from the triquetral in such a way that it often disrupts the articulation of the capitate with the lunate (Lewis, 1971).

According to Cant et al. (2001), *Ateles* (the spider monkeys) combine three types of locomotor habits: quadrupedal/terrestrial (21 %), suspensory (23 %), and clambering (28 %). This variety of locomotor behaviors may cause the absence of some anatomical features that can be seen in other suspensory primates. For example, the hamate is not prolonged or distally expanded as is typical for hylobatids (Corruccini et al., 1975). However, previous studies show that most anatomical differences between these two groups are mainly in the shoulder and elbow joints (Larson, 1998; Young, 2003), with hylobatids having more pronounced traits than *Ateles* (Youlatos, 1996).

Ratcheting behavior is a type of behavior that is typical mostly for orangutans when using slow (cautious) brachiation to move. Movement is characterized by swinging and catching under the branch with the help of upper limbs but it is significantly slower than the true brachiation displayed by for instance gibbons (Sarmiento, 1988).

Orangutans spend only about 11 % of their time using terrestrial locomotion, the rest being arboreal locomotion (Rodman, 1973). The hand is not necessarily used for ground locomotion, but if it is, the wrist is in pronounced dorsiflexed position (Sarmiento, 1988). Orangutans prefer to use branches of narrower diameter during arboreal locomotion (Rodman, 1973; Mackinnon, 1974), and therefore there is not such pronounced ulnar and radial deviation as in, for example, hylobatids (Sarmiento, 1988).

Generally, at the beginning of the support phase, the wrist reaches the most prominent ulnar deviation and is markedly dorsiflexed at the end of the support phase. During the swing, the hand is typically used as a hook and the wrist is rather in a neutral position. The hand is almost always parallel to the support and strongly adducted during the ascent upward. It is only at this point that the wrist can wrap around the entire diameter of the support by being markedly flexed (Sarmiento, 1988).

In both, gibbons and orangutans, the degree of wrist pronation or supination is influenced by the diameter of the support, in such a way that with a larger support diameter we can observe a higher degree of wrist supination (Wallace 1980; Sasrmiento 1988). In primates that have a free centrale (including *Ateles*, *Pongo* and Hylobatidae), it is apparent that soft tissues around the centrale are arranged for stabilization of the centrale and scaphoid with ligaments (Orr, 2018).

3.2 Quadrupedal Behavior

Quadrupedal locomotion or posture is a form of terrestrial locomotion in primates using four limbs. Terrestriality evolved independently and repeatedly in various primate taxa (Fleagle, 1979). Generally, the most unusual forms of terrestriality in primates are knucle-walking (typical of *Gorilla* and *Pan*) and bipedalism (typical of *Homo*). Though the large non-human primates move on the ground, they also spend a considerable amount of time moving through trees, and notably they retain a specific wrist bone morphology that allows them to be effective during both arboreal and terrestrial locomotion (Richmond, 2006).

Knuckle-walking is a form of terrestrial locomotion and body posture that is exceptionally rare among mammals. During knuckle-walking, gorillas and chimpanzees curl the fingers towards their palms and carry their weight on the dorsal surface of the middle phalanges. The metacarpophalangeal joints hold the hand in the extended position and the wrist helps to maintain a slightly upright body posture (Tuttle, 1967). Some experimental studies show that some morphological structures, especially the fusion of scaphoid and capitate, may limit radiocarpal and midcarpal joint extension (Tuttle 1967, 1969; Lewis, 1972). It is generally believed that during higher speeds, the strong muscles of the forearm primarily maintain wrist's stability and that the joint surfaces and ligaments are adapted for limited extension, being largely capable of doing so without muscle tension (Susman and Stern, 1979).

It is widely believed that knuckle-walking is an autapomorphy of gorillas and chimpanzees, an adaptation that occurred independently in chimpanzees and gorillas (Kivell and Schmitt, 2009). The African apes are a group of closely related genera, which differ mainly in body size and in some characteristics of behavior, especially social behavior. However, their morphological features are very similar, and some morphological differences are ascribed to body size differences (Doran, 1996).

In apes that use knuckle-walking, both adult and juvenile individuals use this locomotor mode. However, morphological changes of the wrist are evident only in adult individuals. For example, the scaphoid is concave in the vast majority of chimpanzees on the dorsal side and has a prominent process. In gorillas, these traits occur only in about 6 % of individuals, regardless of sex or body size. If this trait occurs in gorillas, it appears relatively late in the development and is not as prominent as in chimpanzees (Kivell and Schmitt, 2009). Compared to other primates, capitate is more elongated in both chimpanzees and gorillas. This feature has been interpreted as an adaptation to increased stability of the wrist when loaded in knuckle-walking (Schmitt, 2003). However, this statement is very problematic because some monkeys that do not use knuckle-walking exhibit a prolonged capitate as well (Kivell and Schmitt, 2009).

Another feature not entirely understood is the fusion of centrale and scaphoid, which makes the wrist (especially its radial side) stronger and more resistant (Orr, 2018). The centrale is located between the scaphoid and the capitate in most primates. Only great apes, including humans, show almost ubiquitous fusion of centrale to scaphoideum (rare and isolated exceptions exist for various taxa) (Kivell and Begun, 2007). Schultz (1936) determined that fusion occurs in great apes between the end of the fetal stage and the first postnatal three years.

The functional meaning is unclear. Some (e.g. Jouffroy and Lessertisseur, 1960; Yalden, 1972; Lewis, 1989) argue that fusion restricts wrist movement, whereas others (e.g. Marzke, 1971; Richmond et al., 2001; Begun, 2004; Orr, 2018) argue that it makes the wrist more load-resistant. Thus, during knuckle-walking, wrist mobility is limited in extension and at the same time the wrist is more resistant to the strong pressure exerted upon it (Orr, 2005; 2017). Lewis (1989) argues that the carpal bones are strongly connected by ligaments, thereby preventing movements between the centrale and the scaphoid. In his opinion, it is likely that the non-fused centrale facilitates movements between the scaphoid and the capitate at their articulation. Conversely, fusion reduces the number of joints, giving the wrist greater stiffness and resistance to stress.

Digitigrade hand/foot posture is usually associated with quadrupedal terrestrial species that are morphologically adapted to move at relatively high speeds. Such adaptation is often described as being biomechanically advantageous (Brown and Yalden, 1973) because shorter hand or foot can minimize locomotor costs at higher speeds. Equally, effective limb lengths can alleviate the external load on the wrist at high speed (Brown and Yalden, 1973). However, other studies have shown that forelimb digitigrady is not necessarily an adaptation for high-speed mobility (Patel and Wunderlich 2010), leaving this topic to warrant further study.

Digitigrade taxa include all primates standing or walking on their digits or toes. These are only large bodied cercopithecines such as *Papio*, *Theropithecus*, *Mandrillus*, *Erythrocebus,* and some *Macaca* and *Cercocebus* species (Patel and Polk, 2010). Short fingers minimize potentially harmful bending moments at the fingers and help to reduce limb length, particularly at its distal extremity (Nieschalk and Demes, 1993).

During terrestrial locomotion, *Papio* (baboons) alternates between digitigrade and palmigrade hand postures. A relationship exists between speed and hand posture (Patel and Wunderlich, 2010), with a digitigrade hand posture occurring during relatively slow speeds with a flexed wrist joint and dorsiflexed metacarpophalangeal joints. With higher speeds, there is a change towards a palmigrade hand posture and the angle between the metacarpal segments and the ground decreases and the wrist gradually approaches maximum dorsiflexion (Patel and Polk, 2010).

Hand posture can be associated with the absolute magnitude of the ground reaction force during locomotion, as high-speed locomotion is usually associated with higher ground reaction forces (Hanna et al., 2006). In contrast, semiterrestrial primates may not be able to respond to such a change in velocity during locomotion as efficiently as terrestrial primates, because their wrist has evolved to prioritize mobility over stability (Yalden, 1972).

Baboons tend to hold the so-called anatomically neutral wrist positions, with extended postures occurring during terrestrial locomotion and flexed wrist positions occurring during arboreal locomotion (Schmitt, 1994). The wrist’s range of motion stems from the radiocarpal, transversointercarpal, and carpometacarpal joints. The dorso-lateral part of the radiocarpal joint is a large semilunar intraarticular meniscus allowing flexion (80°), extension (10°), and radial and ulnar deviations (about 30°). The proximal joint surface of the transversointercarpal joint consists of the scaphoid, centrale, lunate, and triquetral, and the distal joint surface consists of the trapezium, trapezoideum, capitate, and hamate. This joint allows for flexion (30°), extension (30°) and radial and ulnar deviations (about 20°). Finally, the carpometacarpal joint allows for several degrees of flexion, extension, as well as radial and ulnar deviations (Jones, 1967).

However, it is important to note that digitigrade postures differ slightly from other quadrupedal postures because the palm does not contact the support during the pose phase (Patel and Polk, 2010). This type of hand posture is sometimes associated with a restriction of wrist mobility in extension and ulnar deviation (Lemelin and Schmitt, 1998;

Richmond, 2006). The limitations have a morphological basis in that, unlike knuckle-walkers, the digitigrade monkeys share a radial dorsal process, as well as a meniscus interposed between the dorsal parts of the radius and the scaphoid (Jones, 1967; Yalden, 1972). However, we do not assume that these differences have a great influence on the orientation of the load acting upon selected carpal bones and consequently on the bones’ internal structure. Therefore, we classify this type of locomotion into a common locomotor group with the knuckle-walking taxa (same as in Schilling, 2014).

3.3 Bipedal Behavior

Homo sapiens is an obligate biped with upright body posture and hands freed from locomotion. Humans are almost exclusively terrestrial. This unique behavior is associated with a number of very specific anatomical features, especially with changes to the orientation of the foramen magnum, the curvature of the spine (S-shaped), shape of the pelvis, interlimb proportions, possession of the pedal arch and specific muscle arrangement (Harcourt and Smith, 2010). However, a wide range of behaviors characterizes humans. Therefore, even in humans we can observe ways in which the hand is involved in locomotion. They are relatively scarce though.

One of these behaviors is the digitigrade posture practiced during sport activities where four fingers are deviated laterally with the digital pads of their distal phalanges touching the ground, the thumb is oriented with its distal phalanx directed postero-radially and also contacts the ground only through the digital pad of distal phalanx (Sarmiento, 1988). The radiocarpal joint is in an almost neutral position, keeping the wrist in a stretch. The wrist is more in radial deviation than ulnar deviation. This hand holding usually does not accompany any movements but is mainly used in static postures (such as athletes) (Muybridge, 2012). As with

Gorillas, the front half of the body is evenly loaded without ulnar or radial preference (Sarmiento, 1988).

Humans can also move on the ground with the involvement of their upper limbs and hands clenched into a fist. This movement may resemble knuckle-walking in gorillas or chimpanzees but most closely resembles terrestrially locomoting orangutans (see above), except that people usually involve the thumb to stabilize the body (Sarmiento, 1988).

Finally, we can also describe arboreal behavior in humans, albeit not at high frequencies. Generally, when the upper limbs are in suspension, the hand is loaded in a similar manner to other primates (see above). The difference is again the involvement of the thumb, which is widely used in humans (Sarmiento, 1988).

3.4 Mechanical Predictions

It is apparent that the suspensory taxa (*Hylobatidae*, *Ateles* and *Pongo*) use arboreal locomotion rather than terrestrial. On this basis, it can be expected that the wrist is subjected to the overwhelming majority of tensile forces and must therefore be very tensile resistant. On the other hand, the quadrupedal taxa (*Gorilla*, *Pan* and *Pongo*) use terrestrial locomotion rather than arboreal. Therefore, it can be expected that the wrist is subjected in particular to compressive forces and must be resistant to compression.

However, it is important to note that there is substantial variation within each category in frequency of terrestrial versus arboreal locomotion. Those differences are likely reflected in the external morphology and probably also in the trabecular structure of the wrist bones. For example, among the suspensory taxa, *Ateles* use prehensile tail during suspensory locomotion but other suspensory taxa (i.e. *Hylobates* or *Pongo*) do not have a tail. Also, *Ateles* engage in a substantial amount of quadrupedal and tripedal walking (21% of locomotor time), in vertical climb and descent (13%), in orthograde clamber and transfer (28%), and in brachiation and forelimb swing (22%) (Fleagle, 1979; Cant et al., 2001). *Pongo* engages in quadrupedal walking (18% of locomotor time), vertical climbing (16%), and vertical descent (9%). Hylobates engage in vertical climb and descent (36%), in bipedal walk (8%), in brachiation and forelimb swing (59% of locomotor time), and in dropping and leaping (2% of locomotor time).

Among the quadrupedal taxa, *Gorillas* engage in quadrupedal and tripedal walk (53% of locomotor time), in vertical climb and descent (40%), in bipedal walk (2%), and in brachiation and forelimb swing (5%). *Pan* engages in quadrupedal and tripedal walk (22% of locomotor time), in vertical climb and descent (68%), in bipedal walk (3%), in brachiation and forelimb swing (7%), and in dropping and leaping (1%). Finally, *Papio* engages in quadrupedal and tripedal walk (68% of locomotor time), in vertical climb and descent (21%), and in dropping and leaping (10%) (Thorpe and Crompton, 2006).

It can be assumed that precisely these differences in tension and compression appear in the representation and distribution of the trabecular structure. Bone generally is stronger in compression than tension. So, if one bone is primarily loaded in tension and another is loaded primarily in compression, we might expect that the trabecular bone will be stronger and thicker in bones loaded under the compression rather than under tension (Schilling, 2014). Therefore, we assume that knuckle-walkers will show thicker trabecular bone structure than other groups.

However, in some studies (Currey, 1968; Tattersall, 1974; Cartmill and Milton, 1977), it has been argued that during suspensory locomotion, compressive forces apply to the bones and joints at some stages as well. Thus, at times, the wrist bones may actually be compressed. This comes downs to the distribution of forces in bending, in which both compression and tension occur, although at different sites along the bone. Compressive forces occur mainly when the wrist "exhausts" the possible range of motion or when the primate pulls up during suspensory movements (Sarmiento, 1985). Likewise, some studies show that tensile forces can occur and are likely at work during terrestrial locomotion. Thus, during specific stages of terrestrial locomotion, the wrist bones may face more tensile forces but overall, the compressive forces significantly prevail (Sarmiento, 1986).

4 MATERIALS AND METHODS

4.1 Sample

The sample analysed in this study includes 56 adult individuals (both female and male, Tab. 1). The sample of suspensory and quadrupedal species comes from the Museum für Naturkunde, Berlin, Germany. All bones come from free-ranging primates from localities in Africa (*Gorilla*, *Pan*, *Papio*), in Asia (*Pongo*, *Hylobates*), and in America (*Ateles*). The sample of human bones is housed at the Department of Anthropology, University of West Bohemia, Pilsen, Czech Republic. The sample comes from the archaeological rescue excavation in Litomyšl (five individuals) and Teplá (six individuals). Both archaeological sites were dated to the 12th to 15th centuries (Kuchařík et al., 2012; Nováček et al., 2015).

We selected only individuals without any obvious pathology and with long bones fully ossified. We preferentially selected disarticulated bones, because it is faster and cheaper to scan them. However sometimes, especially in *Ateles* and *Hylobates*, we had to scan articulated wrists. We analysed the scaphoid, lunate, and capitate because of their role in transferring the weight between metacarpals and wrist and because of the load distribution between the proximal and distal portion of an extremity during locomotion. Motion and loading during locomotion directly affect internal morphology of the selected bones. Thus, it can be assumed that these bones are likely to preserve the functional signal. Therefore, we have chosen bones for analysis based on their functional involvement during locomotion. We preferred to scan individuals, in which all three bones were present, which unfortunately was not the case for all individuals (Tab. 1). Furthermore, if both hands were present, we preferred to select the better preserved one, and if both hands were well preserved, we preferred to select the left hand since it comes from a non-dominant limb (at least in most humans) and represents a baseline for mechanical demands put on hands.

The selected taxa were divided into broader locomotor groups according to the type of locomotion and involvement of the hand during locomotion (Tab. 1). We assume that different types of locomotion manifest differently on the trabecular anatomy of the selected carpal bones.

1) Suspensory behavior (20 individuals), including the semi-brachiating *Ateles sp*., brachiating *Hylobates agilis*, *H. muelleri,* and *H. lar,* and ratcheting *Pongo pygmaeus*;

2) Quadrupedal behavior (25 individuals), including the knuckle-walking *Gorilla beringei, G. gorilla, Pan troglodytes,* and digitigrade *Papio ursinus, P. anubis,* and *P. hamadryas*;

3) Bipedal behavior (11 individuals), comprised solely of *H. sapiens*, which serves as a null model for comparison.

Tab. 1: Sample composition.

Taxon	Body mass [Combined (kg)]*	Locomotor behavior	Locomotor group	Capitate	Lunate	Scaphoid
Ateles sp.	5.0-9.1	Semibrachiator	Suspensory	4	6	5
Hylobates agilis	5.7	Brachiator	Suspensory	4	3	3
Hylobates lar	5.6	Brachiator	Suspensory	1	1	1
Hylobates muelleri	6.0	Brachiator	Suspensory	2	2	1
Pongo pygmaeus	56.8	Ratcheting	Suspensory	8	7	8
Gorilla beringei	130.0	Knuckle walker	Quadrupedal	1	1	1
Gorilla gorilla	131.6	Knuckle walker	Quadrupedal	7	7	7
Pan troglodytes	42.5	Knuckle walker	Quadrupedal	8	9	8
Papio Anubis	19.2	Digitigrade	Quadrupedal	2	3	2
Papio hamadryas	21.3	Digitigrade	Quadrupedal	4	4	4
Papio ursinus	22.3	Digitigrade	Quadrupedal	1	1	1
Homo sapiens	60.0	Biped	Bipedal	11	11	11
Total				53	55	52

*Body mass estimation from (Smith and Jungers, 1997; Smith et al., 2003). Combined refers to female and male individuals.

4.2 CT-Scanning and processing

Selected wrist bones were scanned using the YXLON FF35 CT (microCT) scanner housed in the Micro-CT Laboratory, Museum für Naturkunde, Berlin, Germany. The scans were obtained with the resolution of 144 pixels per inch with slice thickness ranging between 0.007 and 0.014 inch; voxel width between 0.007 and 0.016 inch; voxel height ranging from 0.006 to 0.009 inch with final voxel size of 0.0069^3 inch. Each scan was processed in Volume Graphic Studio Max software and all slices were then reconstructed as 8-bit Tagged Image File Format (TIFF) image stack for opening in ImageJ software.

A cubic volume of interest (VOI) was quantified in a specific anatomical region for each carpal bone. The size of the VOI has been set at 5 mm^3 for every species regardless of their respective body masses. The placement of VOI was critical because of small size and irregular shape of selected bones and therefore, we placed the VOIs, based on the same mechanical and anatomical reasons as Schilling at al. (2014), in the centre of the body of lunate, between the radial and capitate/centrale articular surface of scaphoid, and centrally under the proximal articular surface of capitate (Fig. 4).

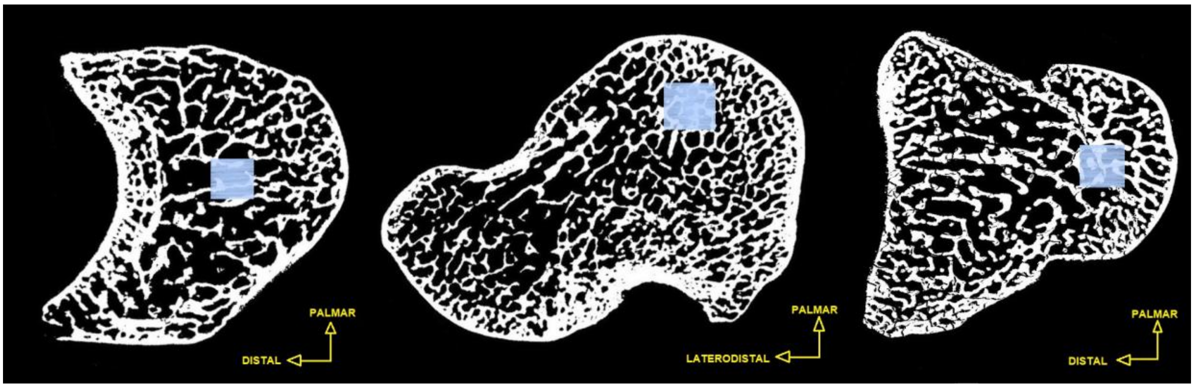


Fig. 4: Volume of interest position in lunate, scaphoid, and capitate of *Homo sapiens*.

Based on Kivell et al. (2011), we measured bone volume fraction (BV/TV), trabecular thickness (Tb.Th), trabecular spacing (Tb.Sp), degree of anisotropy (DA), and connectivity (Conn.D) within the selected VOI for each carpal bone with BoneJ2 in ImageJ software (see the results section, Tab. 2).

BV/TV is the volume of mineralized bone per unit volume of the sample, which is measured by dividing bone volume with total volume of the VOI. Therefore, this parameter can be used to evaluate relative changes in bone volume density within the selected VOI (e.g. Kivell et al, 2011; Kivell et al., 2013). Tb.Th indicates trabecular thickness and Tb.Sp trabecular spacing. With those parameters we can compare the thickness of trabecular structure but also the separation of the struts (e.g. Hildebrand and Rüegsegger, 1997; Dougherty and Kunzelmann, 2007). DA is a measure of how highly oriented the struts are within VOI. This parameter is influenced by mechanical loading and by its direction. Bone that is loaded can become anisotropic (i.e. unequally strong in all directions) and the direction of the struts indicates the direction of the loading (e.g. Harrigan and Mann; Odgaard, 1997). Conn.D indicates the number of connected structures within the VOI but it is not simply related to volume fraction (e.g. Odgaard and Gundersen, 1993). The index of connectivity allows for characterizing the redundancy of the trabecular connections but since the connectivity depends on structure size, it is more accurate to present it as a density (e.g. Bouxsein et al., 2010).

4.3 Allometric scaling

The mechanical properties of mammal bones vary within and among species (Currey, 2003). While intraspecific diversity is mainly due to heterogeneity of hydroxyapatite volume (Weiner and Wagner, 1998; Currey, 2003; Ruffoni et al., 2007), differences between species are strongly influenced by body mass. Mechanical forces act on bones of small animals differently than on bones of large animals because bone strength scales to the power of two and mechanical loading scales to the power of three. Hence, whole bones scale their length and diameter relative to body mass with close to isometry ($\propto BM^{0.33}$; i.e. the slope of the regression between the log of bone length or diameter and the log of body mass is close to 0.33) (Alexander et al., 1979; Biewener, 1983; Steudel and Beattie, 1993). It can be assumed that trabecular parameters will change with body mass because trabecular structure contributes to the mechanical properties of whole bones (Werner et al., 1988; Rogers and LaBarbera, 1993; Sharir et al., 2008*;* Barak et al., 2010).

Doube et al. (2011) found that BV/TV and DA do not scale with body mass, while Tb.Th, Tb.Sp, and Conn.D decrease with body mass among mammals. Ryan and Shaw (2013) concluded that BV/TV, Tb.Th, and Tb.Sp increase with body mass, while Tb.N (trabecular number, a parameter not used in this study, is the number of traversals made per unit length by a random linear path across the trabecular structure), Conn.D, and DA scale inversely with body mass. In summary, some studies show that small animals have thicker trabecular structure relative to body mass than large animal, which have thinner and more tightly packed trabecular structure while others show the opposite. Also, some studies (e.g. Mullender et al., 1996; Swartz et al., 1998) show none or weak relationship between trabecular parameters and body mass.

Given the various unsolved questions regarding how trabecular structure scales with body mass, we decided to look at issues of scaling and test the relationship between trabecular parameters and body mass to see how trabecular parameters correlate with it, because if Tb.Th, Tb.Sp, and Conn.D decreased or increased with body mass, the standardization of those parameters would be necessary. We calculated bone volume of each bone as a proxy for body mass (since we did not have direct or indirect data to derive body masses) for every individual in

ImageJ and then, we calculated Pearson´s correlation coefficient to see how the trabecular parameters correlate with it. We tested the correlation only in Tb.Th, Tb.Sp, and ConnD. parameters because the BV/TV and DA parameters are not affected by body size (Doube et al., 2011; Schilling et al., 2014). Based on Ryan and Shaw (2013), the regression slopes for thickness linear variables should be equal to 1 (isometric scalling). Therefore, values greater than 1 indicate positive allometry and values smaller than 1 indicate negative allometry.

As we expected, all trabecular parameters that we tested are significantly correlated with bone volume (Tab. 2). Trabecular thickness (Tb.Th) and trabecular spacing (Tb.Sp) are significantly negatively correlated (negative allometry) in all carpal bones, and the trabecular connectivity (Conn.D) is significantly positively correlated (positive allometry) in all carpal bones (Tab. 3). Since there is a significant correlation between bone volume and connectivity and thickness parameters, we standardized them by dividing the value for each parameter by bone volume for each bone. Figure 5 shows the dispersion of the groups and their respective regression lines to demonstrate the scaling of each of the trabecular parameters (Conn.D, Th.Tb, and Tb.Sp).

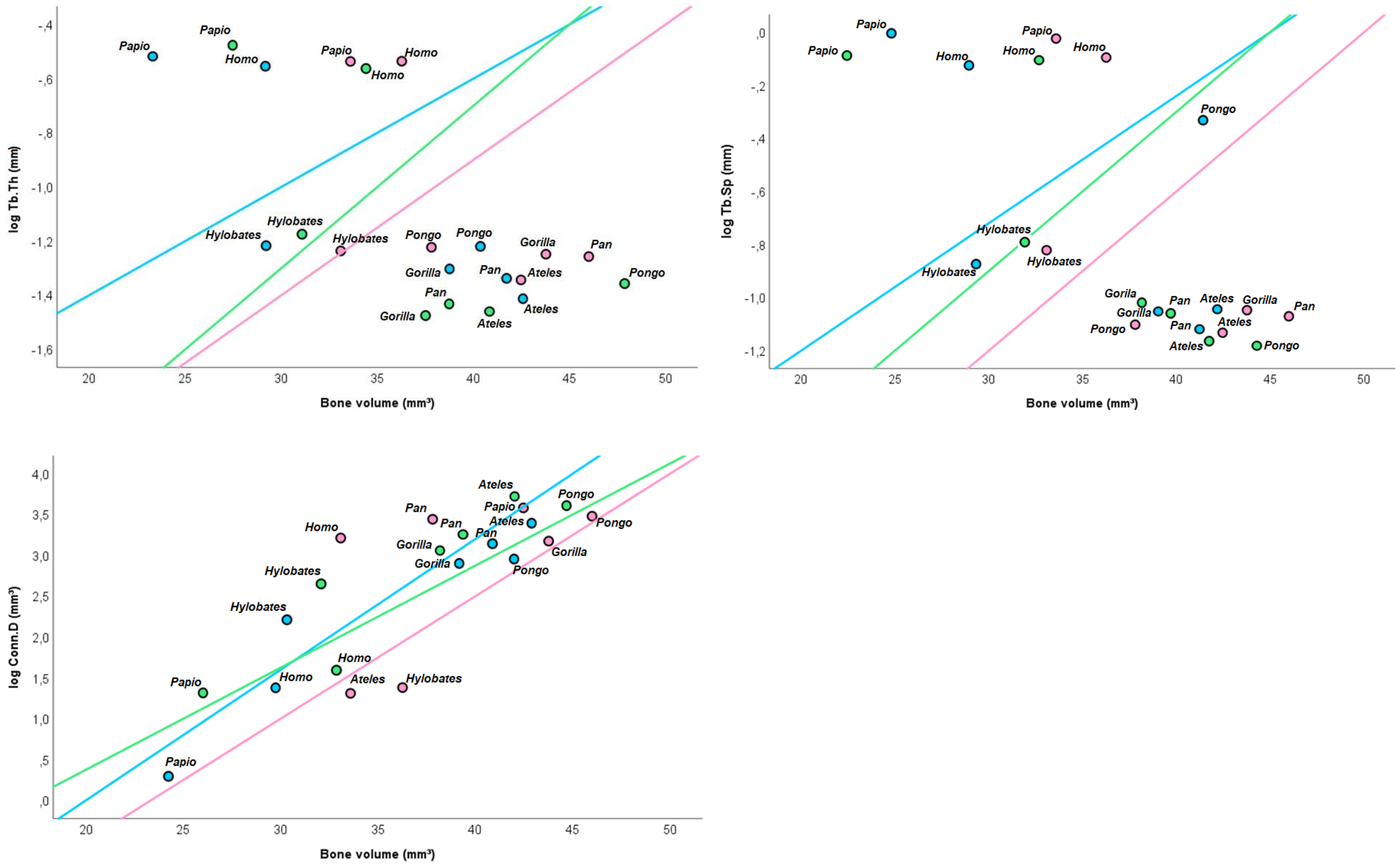


Fig. 5: Scaling of trabecular parameters (Conn.D, Tb.Th., and Tb.Sp) with bone volume based on median for capitate (pink), lunate (blue), and scaphoid (green).

4.4 Hypotheses

We have tested five trabecular parameters to achieve two main aims of this study. Firstly, we tested the assumption that variability of trabecular parameters correlates with the type of locomotion. We expect that there would be a noticeable difference in trabecular parameters between groups caused by different involvement of the hand during locomotion. Specifically, we expect that BV/TV and Tb.Th would be lower in suspensory taxa (carpal bones loaded primarily in tension) than in quadrupedal taxa (carpal bones loaded primarily in compression) and the lowest in *Homo* (no loading during locomotion). In contrast, we expect that Tb.Sp would be highest in *Homo* and lowest in quadrupedal taxa. We do not predict distribution of other parameters, because they are not directly reflecting the mechanical loading but we expect significant differences.

Secondly, we tested how the internal structure differs among selected species within each locomotor category. We expect that there would not be any difference among suspensory as well as among quadrupedal taxa. Respectively, we expect that there would be no significant difference in all trabecular parameters among suspensory taxa and among quadrupedal taxa. However, we expect a certain degree of overlap because selected species use several types of locomotion (see above).

4.5 Statistical procedures

The expectations have been tested using Kruskal-Wallis test for each trabecular parameter and each selected bone. The non-parametric Kruskal-Wallis test was used because of the small sample sizes. Trabecular parameters were log transformed (log10) to bring the vastly different values for some parameters to similar scales. Also the Tb.Th., Tb.Sp, and Conn.D were scaled with bone volume. We used the log-transformed data as input data for Kruskal-Wallis test and boxplots. We then used pairwise comparisons (*post-hoc* Mann-Whitney U tests) to explore differences between individual groups. All statistical procedures have been performed in IBM SPSS Statistics 26, and all figures have been modified in GIMP 2.10.14.

Tab. 2: Scaling of trabecular parameters in capitate, lunate, and scaphoid with bone volume (Pearson´s correlation).

					95 % CI for slope			
Bone	Trabecular parameter	N	*r*	Slope	Lower	Upper	*p*	Allometry
Capitate	Conn.D (mm³)		0.42	1.52	1.00	2.54	**0.00**	+
	Tb.Th (mm)	53	-0.41	-0.53	-0.55	-0.51	**0.00**	-
	Tb.Sp (mm)		-0.37	-1.47	-1.53	-1.41	**0.01**	-
Lunate	Conn.D (mm³)		0.65	1.93	1.21	2.65	**0.00**	+
	Tb.Th (mm)	55	-0.33	-0.30	-0.32	-0.28	**0.01**	-
	Tb.Sp (mm)		-0.50	-1.69	-1.75	-1.63	**0.00**	-
Scaphoid	Conn.D (mm³)		0.47	1.31	0.17	2.45	**0.00**	+
	Tb.Th (mm)	41	-0.51	-0.64	-0.66	-0.62	**0.00**	-
	Tb.Sp (mm)		-0.69	-2.80	-2.85	-2.75	**0.00**	-

Allometry: + positive, - negative.

5 RESULTS

Table 3 presents descriptive statistics for each trabecular parameter across different genera and locomotor groups. Overall, there is a substantial amount of overlap across taxa and locomotor groups in each trabecular parameter in all selected carpal bones. Several taxa show a large degree of intrageneric variation in certain trabecular parameters (see the standard deviation values). Figure 6 shows the distribution of trabecular parameters across locomotor groups. Figure 7 shows the distribution among suspensory and quadrupedal taxa. Again, we can see a substantial amount of overlap, except for trabecular thickness and spacing, in which *Ateles* and *Hylobates* are not overlapping with the other taxa.

Tab. 3: Descriptive statistics (mean and standard deviation) for the distribution of trabecular parameters in capitate, lunate, and scaphoid.

Species	Bone	BV/TV (%)	Tb.Th (mm)	Tb.Th (mm/mm³)*	Tb.Sp (mm)	Tb.Sp (mm/mm³)*	DA	Conn.D (mm³)	Conn.D (mm³)*
SUSPENSORY									
Ateles	capitate	0.34 (0.04)	0.29 (0.06)	0.83 (0.01)	0.95 (0.40)	0.91 (0.06)	0.39 (0.19)	21 (3)	3.13 (0.43)
	lunate	0.26 (0.07)	0.29 (0.04)	0.88 (0.02)	1.02 (0.21)	0.92 (0.06)	0.21 (0.07)	3 (2)	8.89 (13.58)
	scaphoid	0.28 (0.08)	0.30 (0.04)	0.89 (0.00)	0.81 (0.16)	0.98 (0.03)	0.32 (0.10)	18 (15)	1.21 (0.33)
Hylobates	capitate	0.36 (0.08)	0.29 (0.52)	0.92 (0.01)	0.80 (0.34)	1.00 (0.06	0.42 (0.14)	24 (31)	4.52 (5.32)
	lunate	0.30 (0.06)	0.25 (0.04)	0.89 (0.00)	0.85 (0.36)	0.97 (0.05)	0.49 (0.15)	19 (14)	3.83 (1.88)
	scaphoid	0.32 (0.09)	0.26 (0.03)	0.89 (0.01)	0.78 (0.32)	0.98 (0.05)	0.25 (0.12)	18 (10)	3.68 (2.33)
Pongo	capitate	0.39 (0.15)	0.06 (0.01)	0.89 (0.00)	0.08 (0.03)	0.89 (0.00)	0.32 (0.13)	2775 (2952)	44.31 (51.97)
	lunate	0.45 (0.19)	0.06 (0.02)	0.88 (0.00)	0.10 (0.04)	0.88 (0.00)	0.22 (0.10)	4294 (7712)	35.29 (36.05)
	scaphoid	0.45 (0.08)	0.05 (0.01)	0.88 (0.00)	0.07 (0.03)	0.88 (0.00)	0.20 (0.12)	2279 (1817)	67.02 (135.77)
QUADRUPEDAL									
Gorilla	capitate	0.46 (0.04)	0.06 (0.01)	0.89 (0.00)	0.09 (0.04)	0.89 (0.00)	0.40 (0.16)	3021 (2025)	21.42 (15.48)
	lunate	0.41 (0.06)	0.05 (0.01)	0.89 (0.00)	0.10 (0.03)	0.89 (0.00)	0.26 (0.11)	2585 (3367)	8.39 (6.51)
	scaphoid	0.04 (0.06)	0.05 (0.01)	0.88 (0.00)	0.10 (0.02)	0.89 (0.00)	0.20 (0.03)	1093 (860)	18.46 (25.74)
Pan	capitate	0.44 (0.04)	0.02 (0.056)	0.89 (0.00)	0.03 (0.09)	0.89 (0.00)	0.30 (0.14)	1496 (1384)	64.52 (66.24)
	lunate	0.39 (0.06)	0.05 (0.01)	0.90 (0.00)	0.10 (0.03)	0.90 (0.00)	0.27 (0.09)	11776 (2003)	128.78 (255.57)
	scaphoid	0.39 (0.06)	0.05 (0.01)	0.89 (0.00)	0.10 (0.02)	0.90 (0.00)	0.17 (0.06)	3058 (5732)	79.68 (94.22)
Papio	capitate	0.43 (0.03)	0.05 (0.01)	0.88 (0.00)	0.07 (0.04)	0.88 (0.00)	0.30 (0.12)	3818 (2407)	79.47 (56.64)
	lunate	0.41 (0.05)	0.04 (0.01)	0.89 (0.00)	0.09 (0.01)	0.89 (0.00)	0.24 (0.05)	2030 (870)	44.00 (43.11)
	scaphoid	0.39 (0.04)	0.04 (0.01)	0.89 (0.00)	0.09 (0.03)	0.89 (0.00)	0.28 (0.04)	2839 (1416)	43.35 (20.47)
BIPEDAL									
Homo	capitate	0.33 (0.08)	0.06 (0.01)	0.92 (0.00)	0.15 (0.03)	0.92 (0.00)	0.19 (0.05)	1634 (2924)	25.88 (48.73)
	lunate	0.29 (0.08)	0.05 (0.01)	1.22 (0.00)	0.15 (0.04)	1.22 (0.00)	0.21 (0.08)	2424 (3719)	15.97 (23.45)
	scaphoid	0.27 (0.09)	0.05 (0.01)	0.92 (0.00)	0.15 (0.03)	0.92 (0.00)	0.16 (0.05)	902 (1202)	37.95 (61.99)

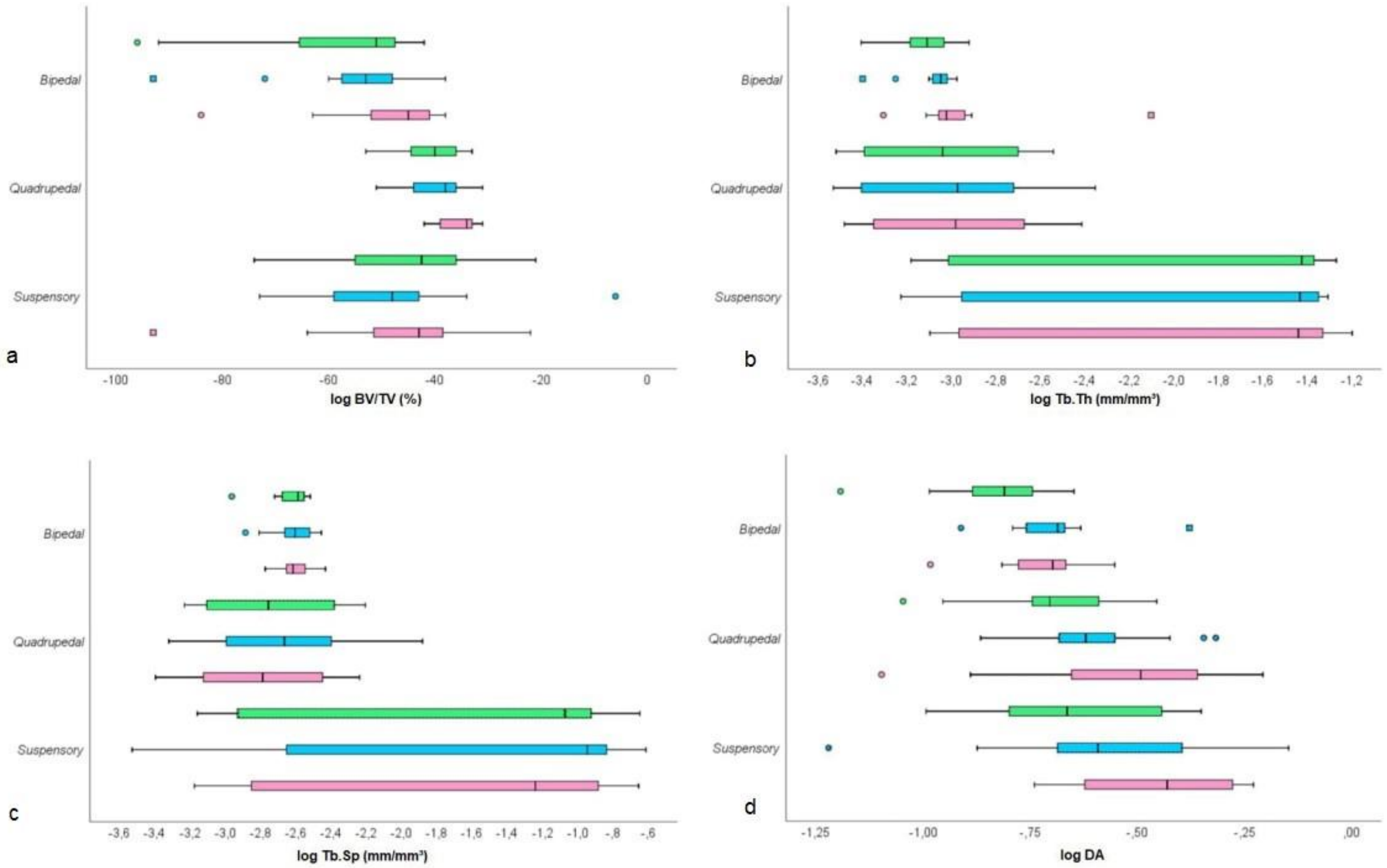
*Trabecular parameters standardized with bone volume by dividing the value of a parameter by bone volume.

5.1.1 Differences in trabecular parameters between locomotor groups

Table 4 shows results of differences between locomotor groups in all the trabecular parameters in all three carpal bones. All the parameters in all the bones are significantly different across locomotor groups, except anisotropy of lunate and trabecular spacing of scaphoid.

Specifically, Tab. 5 shows that the higher volume ratio, connectivity, and degree of anisotropy are associated with quadrupedal taxa compared to non-quadrupedal taxa, while higher trabecular thickness and spacing are associated with suspensory taxa rather than with non-suspensory taxa in capitate, lunate and scaphoid. However, trabecular structure in carpal bones seems rather variable between locomotor groups (Tab. 3).

Since there is clear pattern of variation in trabecular structure that distinguish locomotor groups from each other, we do find support for the first hypothesis that assumed systemic differences in trabecular structure that reflect locomotor behavior. Also, we do find the support for our expectation that bipedal *Homo* demonstrates the lowest mean values in all carpal bones for each parameter. However, there are notable exceptions. For example, trabecular parameters of *Pongo* are distinct from other suspensory genera in all three carpal bones. Moreover, the connectivity is highly variable across all genera and locomotor groups (Fig. 6 and 7). Figure 6 shows boxplots for the distribution of trabecular parameters across locomotor groups.


Bipedal
Quadrupedal
Suspensory
a
-100
-80
-60
-40
-20
0
log BV/TV (%)
b
-3,6
-3,4
-3,2
-3,0
-2,8
-2,6
-2,4
-2,2
-2,0
-1,8
-1,6
-1,4
-1,2
log Tb.Th (mm/mm³)
c
-3,6
-3,4
-3,2
-3,0
-2,8
-2,6
-2,4
-2,2
-2,0
-1,8
-1,6
-1,4
-1,2
-1,0
-,8
-,6
log Tb.Sp (mm/mm³)
d
-1,25
-1,00
-,75
-,50
-,25
,00
log DA

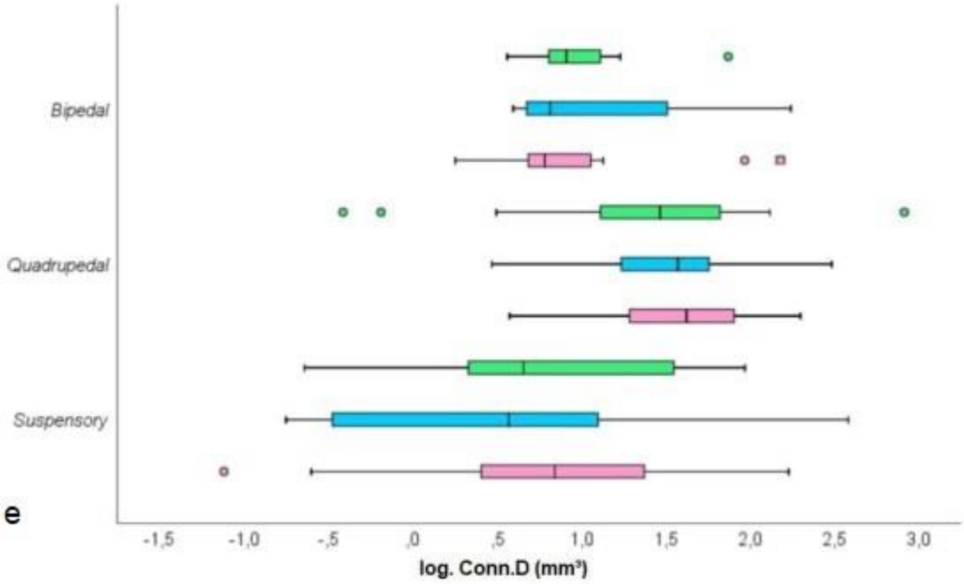


Fig. 6: Trabecular parameters for locomotor groups. Measured parameters are: a) trabecular spacing (Tb.Sp), b) anisotropy (DA fraction), c) trabecular thickness (Tb.Th.), d) volume ratio (BV/TV), and e) connectivity (Conn.D). The Tb.Th, Tb.Sp, and Conn.D were scaled with body mass and log transformed (log10), to bring the values to similar scale. The box represents the 25th and 75th percentiles, centre line is the median, points represent outliers and squares are the extreme outliers. Blue colour represents lunate, pink capitate, and green scaphoid.

Tab. 4: Differences of trabecular parameters between locomotor groups.

Bone	Trabecular parameter	N	Mean rank	Kruskal-Wallis H	*p*
Capitate	BV/TV (%)	53	24.69	18.34	**0.00**
	Tb.Th (mm/mm³)		26.51	12.57	**0.00**
	Tb.Sp (mm/mm³)		21.40	7.94	**0.02**
	DA		24.76	13.37	**0.00**
	Conn.D (mm³)		19.90	13.72	**0.00**
Lunate	BV/TV (%)	55	19.75	17.56	**0.00**
	Tb.Th (mm/mm³)		21.31	16.33	**0.00**
	Tb.Sp (mm/mm³)		22.19	10.24	**0.01**
	DA		20.66	5.07	0.08
	Conn.D (mm³)		21.09	13.98	**0.00**
Scaphoid	BV/TV (%)	52	24.19	12.37	**0.00**
	Tb.Th (mm/mm³)		25.78	13.29	**0.00**
	Tb.Sp (mm/mm³)		26.99	4.57	0.10
	DA		24.94	6.65	**0.04**
	Conn.D (mm³)		19.95	7 56	**0.01**

Values of Tb.Th, Tb.Sp and Conn.D were standardized with bone volume by dividing the value of a parameter by bone volume. $\alpha=0.05$

Tab. 5: Pairwise differences in trabecular parameters between locomotor groups.

Bone	Trabecular parameter	Locomotor groups*	Mann-Whitney U	SD	*p*	Bonferroni correction
Capitate	BV/TV (%)	1-2	-15.67	4.79	**0.00**	0.00
		2-3	21.54	5.66	**0.00**	0.00
		1-3	5.88	5.85	0.32	0.95
	Tb.Th (mm/mm^3)	1-2	15.40	4.79	**0.00**	0.00
		2-3	16.23	5.85	**0.01**	0.02
		1-3	0.83	5.66	0.88	1.00
	Tb.Sp (mm/mm^3)	1-2	13.47	4.79	**0.00**	0.01
		2-3	-6.90	5.66	0.22	0.67
		1-3	6.57	5.85	0.26	0.78
	DA fraction	1-2	3.68	4.79	0.44	1.00
		2-3	17.04	5.66	**0.00**	0.01
		1-3	20.71	5.85	**0.00**	0.00
	Conn.D (mm^3)	1-2	-16.32	4.79	**0.00**	0.00
		2-3	14.96	5.66	**0.01**	0.02
		1-3	-1.37	5.85	0.82	1.00
Lunate	BV/TV (%)	1-2	-15.48	4.88	**0.00**	0.00
		2-3	21.46	5.80	**0.00**	0.00
		1-3	5.98	6.07	0.32	0.97
	Tb.Th (mm/mm^3)	1-2	16.63	4.88	**0.00**	0.00
		2-3	4.52	5.80	0.44	1.00
		1-3	21.15	6.07	**0.00**	0.00
	Tb.Sp (mm/mm^3)	1-2	15.49	4.88	**0.00**	0.00
		2-3	-4.64	5.80	0.42	1.00
		1-3	10.85	6.07	0.07	0.22
	DA fraction	1-2	2.26	3.77	0.79	1.00
		2-3	16.65	4.56	**0.02**	0.07
		1-3	18.90	4.80	**0.02**	0.05
	Conn.D (mm^3)	1-2	-18.22	4.88	**0.00**	0.00
		2-3	8.32	5.80	0.15	0.45
		1-3	-9.90	6.07	0.10	0.31
Scaphoid	BV/TV (%)	1-2	-4.76	4.77	0.32	0.95
		2-3	19.44	5.56	**0.00**	0.00
		1-3	14.68	5.80	**0.01**	0.03
	Tb.Th (mm/mm^3)	1-2	14.30	4.77	**0.00**	0.01
		2-3	18.69	5.80	**0.00**	0.00
		1-3	4.39	5.56	0.43	1.00
	Tb.Sp (mm/mm^3)	1-2	14.47	4.79	**0.00**	0.01
		2-3	-5.90	5.66	0.22	0.67
		1-3	7.57	5.85	0.26	0.78
	DA fraction	1-2	1.26	4.77	0.79	1.00
		2-3	12.65	5.56	**0.02**	0.07
		1-3	13.91	5.80	**0.02**	0.05
	Conn.D (mm^3)	1-2	-12.78	4.77	**0.01**	0.02
		2-3	8.78	5.56	0.11	0.34
		1-3	-4.00	5.80	0.49	1.00

*1 suspensory; 2 quadrupedal; 3 bipedal.
$\alpha=0.05$

5.1.2 Differences in trabecular parameters between selected taxa

Table 6 presents differences in trabecular parameters between individual taxa within locomotor groups. It shows that volume ratio and anisotropy of capitate and anisotropy of scaphoid are the only non-significant differences among suspensory taxa. Among quadrupedal taxa, the only non-significant differences are in volume ratio and anisotropy of capitate and lunate, and volume ratio of scaphoid.

Specifically, Table 6 shows that suspensory *Ateles* and *Hylobates* have thicker and less connected trabeculae in all three carpal bones. *Pongo* is distinct in those parameters and exhibits a large range of variation in trabecular structure. There is less variability among quadrupedal taxa overall, with fewer significant pairwise differences than in suspensory taxa. Most pairwise differences in the quadrupedal category appear to be related to Gorillas. Overall, the majority of trabecular parameters of the selected carpal bones are significantly different among suspensory and quadrupedal taxa (Tab.7). Fig. 7 also shows the overlap between suspensory and quadrupedal taxa. *Pongo* especially is overlapping in most parameters with quadrupedal genera.

Tab. 6: Differences of trabecular parameters among suspensory and quadrupedal taxa.

	Suspensory taxa					Quadrupedal taxa				
Bone	Trabecular parameter	N	Mean rank	Kruskal-Wallis H	*p*	Trabecular parameter	N	Mean rank	Kruskal-Wallis H	*p*
Capitate	BV/TV (%)	19	9.59	1.11	0.57	BV/TV (%)	23	25.22	4.18	0.12
	Tb.Th (mm/mm^3)		9.29	12.09	**0.00**	Tb.Th (mm/mm^3)		12.19	7.45	**0.02**
	Tb.Sp (mm/mm^3)		10.83	13.20	**0.00**	Tb.Sp (mm/mm^3)		12.00	17.66	**0.00**
	DA		10.20	1.84	0.40	DA fraction		11.95	2.05	0.36
	Conn.D (mm^3)		10.55	13.99	**0.00**	Conn.D (mm^3)		12.00	19.57	**0.00**
Lunate	BV/TV (%)	19	9.74	8.17	**0.02**	BV/TV (%)	25	59.39	0.47	0.79
	Tb.Th (mm/mm^3)		10.33	13.00	**0.00**	Tb.Th (mm/mm^3)		12.67	21.34	**0.00**
	Tb.Sp (mm/mm^3)		10.33	12.70	**0.00**	Tb.Sp (mm/mm^3)		12.68	20.73	**0.00**
	DA		10.15	9.97	**0.01**	DA fraction		12.95	0.40	0.82
	Conn.D (mm^3)		9.67	14.38	**0.00**	Conn.D (mm^3)		12.88	7.50	**0.02**
Scaphoid	BV/TV (%)	18	8.64	8.82	**0.01**	BV/TV (%)	23	12.00	0.04	0.98
	Tb.Th (mm/mm^3)		10.05	12.66	**0.00**	Tb.Th (mm/mm^3)		12.00	19.57	**0.00**
	Tb.Sp (mm/mm^3)		10.05	12.66	**0.00**	Tb.Sp (mm/mm^3)		12.01	19.25	**0.00**
	DA		10.03	4.17	0.12	DA fraction		12.24	7.80	**0.02**
	Conn.D (mm^3)		8.63	9.73	**0.01**	Conn.D (mm^3)		12.19	12.84	**0.00**

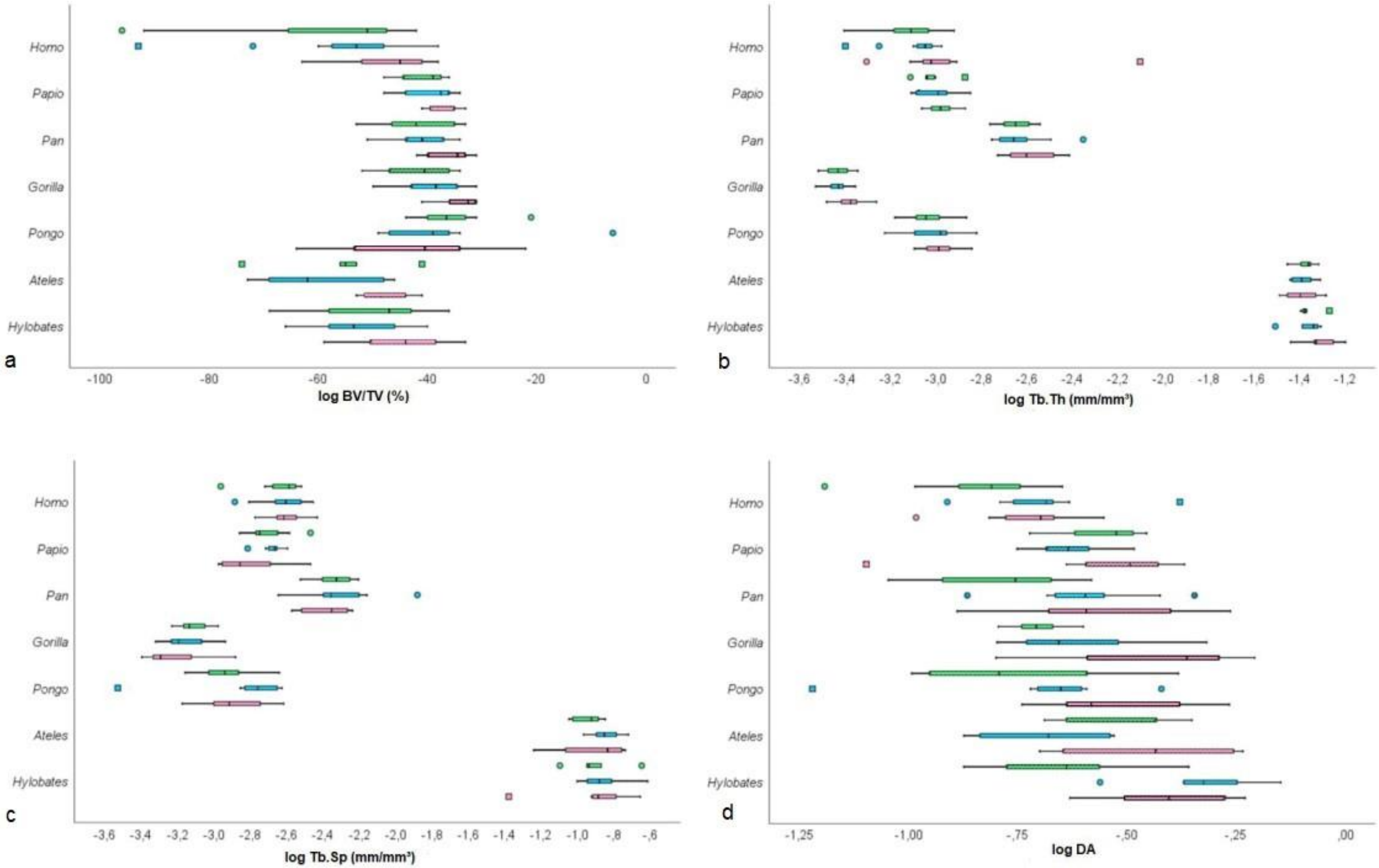
Values of Tb.Th, Tb.Sp and Conn.D were standardized with bone volume by dividing the value of a parameter by bone volume. $\alpha=0.05$

Tab. 7: Pairwise differences in trabecular parameters across suspensory and quadrupedal taxa.

		Suspensory taxa					Quadrupedal taxa				
Bone	Trabecular parameter	Genus*	Mann-Whiteney U	SD	*p*	Bonferroni correction	Species*	Mann-Whitney U	SD	*p*	Bonferroni correction
Capitate	BV/TV (%)	1-3	-3,54	6,35	0,56	1,00	6-5	1,71	6,35	0,27	1,00
		2-3	-9,75	7,51	0,30	1,00	6-4	8,84	6,35	1,39	1,00
		2-1	6,21	7,69	0,81	1,00	5-4	7,13	6,13	1,16	1,00
	Tb.Th (mm/mm^3)	1-3	22,39	6,35	**0,00**	0,01	6-5	11,21	6,35	0,08	1,00
		2-3	19,25	7,51	**0,01**	0,16	6-4	-11,79	6,35	0,06	0,95
		2-1	3,14	7,69	0,68	1,00	5-4	-23,00	6,13	**0,00**	0,00
	Tb.Sp (mm/mm^3)	1-3	22,13	6,13	**0,00**	0,00	6-5	10,13	6,35	0,11	1,00
		2-3	23,96	8,31	**0,00**	0,06	6-4	-11,38	6,35	0,07	1,00
		2-1	-1,83	8,31	0,83	1,00	5-4	-21,50	6,13	**0,00**	0,01
	DA fraction	1-3	9,34	7,99	0,24	1,00	6-5	-2,57	7,99	0,75	1,00
		2-3	5,13	9,46	0,59	1,00	6-4	7,30	7,99	0,36	1,00
		2-1	4,21	9,68	0,66	1,00	5-4	9,88	7,72	0,20	1,00
	Conn.D (mm^3)	1-3	-24,82	7,99	**0,00**	0,04	6-5	-6,09	7,99	0,45	1,00
		2-3	-26,00	9,46	**0,01**	0,13	6-4	-16,21	7,99	**0,04**	0,89
		2-1	1,18	9,68	0,90	1,00	5-4	-10,13	7,72	0,19	1,00
Lunate	BV/TV (%)	1-3	-18,21	8,91	**0,04**	0,86	6-5	-4,15	7,78	0,59	1,00
		2-3	-24,71	8,91	**0,01**	0,12	6-4	-0,75	8,01	0,93	1,00
		2-1	6,50	9,25	0,48	1,00	5-4	3,40	7,78	0,66	1,00
	Tb.Th (mm/mm^3)	1-3	27,36	8,91	0,05	1,00	6-5	15,13	7,78	0,05	1,00
		2-3	25,36	8,91	**0,00**	0,09	6-4	-19,25	8,01	**0,02**	0,34
		2-1	2,00	9,25	0,83	1,00	5-4	-34,38	7,78	**0,00**	0,00
	Tb.Sp (mm/mm^3)	1-3	32,86	8,91	**0,00**	0,00	6-5	17,43	7,78	**0,03**	0,53
		2-3	33,86	8,91	**0,00**	0,00	6-4	-14,63	8,01	0,07	1,00
		2-1	-1,00	9,25	0,91	1,00	5-4	-32,06	7,78	**0,00**	0,00
	DA fraction	1-3	25,29	8,91	**0,00**	0,10	6-5	3,40	7,78	0,66	1,00

		2-3	-2,71	8,91	0,76	1,00	6-4	-1,13	8,01	0,89	1,00
		2-1	28,00	9,25	**0,00**	0,05	5-4	-4,53	7,78	0,56	1,00
	Conn.D (mm³)	1-3	-24,00	8,91	**0,01**	0,15	6-5	-15,83	7,78	**0,04**	0,88
		2-3	-30,67	8,91	**0,00**	0,01	6-4	-14,88	8,01	0,06	1,00
		2-1	6,67	9,25	0,47	1,00	5-4	-15,83	7,78	**0,04**	0,88
Scaphoid	BV/TV (%)	1-3	-20,35	8,64	**0,02**	0,39	6-5	0,07	7,84	0,99	1,00
		2-3	-27,35	8,64	**0,00**	0,03	6-4	-0,55	7,84	0,94	1,00
		2-1	7,00	9,58	0,47	1,00	5-4	-0,63	7,58	0,93	1,00
	Tb.Th (mm/mm³)	1-3	24,03	8,64	**0,01**	0,11	6-5	14,07	7,84	0,07	1,00
		2-3	24,23	8,64	**0,01**	0,11	6-4	-19,68	7,84	**0,01**	0,25
		2-1	-0,20	9,58	0,98	1,00	5-4	-33,75	7,58	**0,00**	0,00
	Tb.Sp (mm/mm³)	1-3	34,35	8,64	**0,00**	0,00	6-5	15,68	7,84	0,05	0,96
		2-3	34,15	8,64	**0,00**	0,00	6-4	-17,07	7,84	0,03	0,62
		2-1	0,20	9,58	0,98	1,00	5-4	-32,75	7,58	**0,00**	0,00
	DA fraction	1-3	10,40	8,64	0,23	1,00	6-5	-18,79	7,84	**0,02**	0,35
		2-3	22,00	8,64	**0,01**	0,23	6-4	-11,54	7,84	0,14	1,00
		2-1	-11,60	9,58	0,23	1,00	5-4	7,25	7,58	0,34	1,00
	Conn.D (mm³)	1-3	-23,63	8,64	**0,01**	0,13	6-5	-3,68	7,84	0,64	1,00
		2-3	-25,43	8,64	**0,00**	0,07	6-4	-24,05	7,84	**0,00**	0,05
		2-1	1,80	9,58	0,85	1,00	5-4	-20,38	7,58	**0,01**	0,15

*1 *Hylobates*; 2 *Ateles*; 3 *Pongo*; 4 *Gorilla*; 5 *Pan*; 6 *Papio*; 7 *Homo*.
α=0.05


a
Homo
Papio
Pan
Gorilla
Pongo
Ateles
Hylobates
-100
-80
-60
-40
-20
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log BV/TV (%)
b
Homo
Papio
Pan
Gorilla
Pongo
Ateles
Hylobates
-3,6
-3,4
-3,2
-3,0
-2,8
-2,6
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log Tb.Th (mm/mm³)
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Homo
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-,50
-,25
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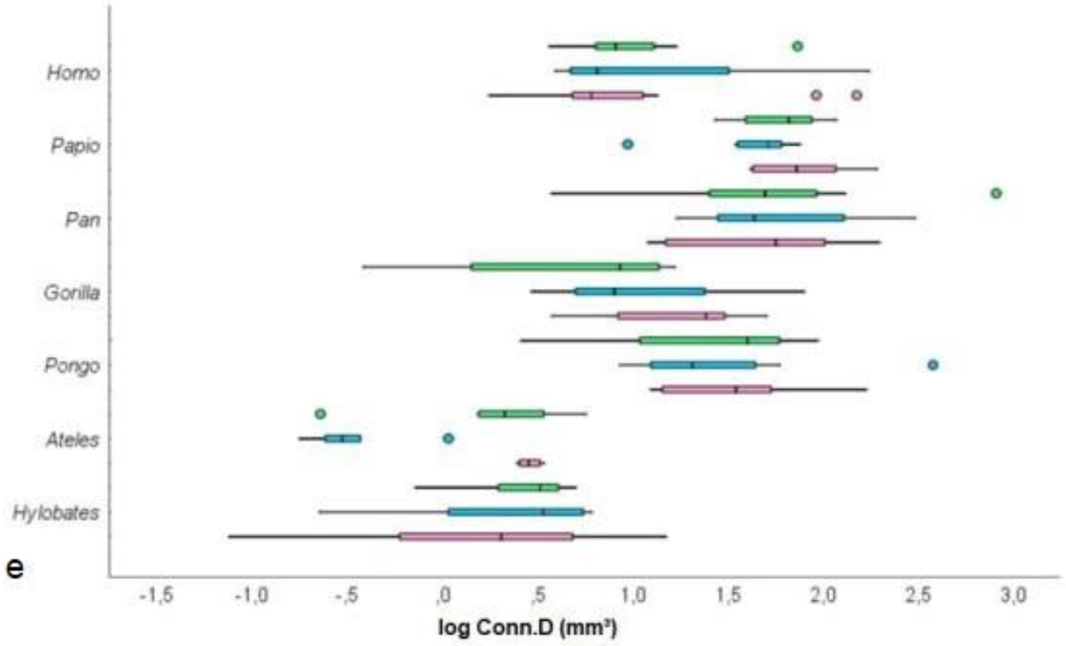

Fig. 7: Trabecular parameters for selected genera. Measured parameters are: a) trabecular spacing (Tb.Sp), b) anisotropy (DA fraction), c) trabecular thickness (Tb.Th.), d) volume ratio (BV/TV), and e) connectivity (Conn.D). The Tb.Th, Tb.Sp, and Conn.D were scaled with body mass and log transformed (log10), to bring the values to similar scale.. The box represents the 25th and 75th percentiles, centre line is the median, points represent outliers and squares are the extreme outliers. Blue colour represents lunate, pink capitate, and green scaphoid.

6 DISCUSSION

Extant primates (except bipedal *Homo*) engage their hands during a wide range of locomotor and postural behaviors. Some of our ancestors bear mosaic morphology of hands with primitive characteristics also referring to the use of hands during locomotion in these ancient hominins. Therefore, the issues related to locomotion and postural behaviors of extant primates are widely discussed. Investigation of trabecular structure of the hand bones can offer a unique insight into these topics.

This thesis has been based on the assumption that trabecular structure responds to mechanical loading. Thus, we should see gradual decline in the amount of trabecular tissue in places where mechanical stress is low and gradual increase in places where mechanical stress is high. Hence, we assume that the trabecular structure reflects the actual individual locomotor biomechanics of hands. There are differences in how and where the carpal bones are loaded between different types of locomotion and therefore, these differences may be able to distinguish suspensory, quadrupedal, and bipedal taxa.

Study of trabecular structure has a relatively long tradition in biological anthropology (e.g. Fajardo and Müller, 2001; MacLatchy and Müller, 2002; Fajardo et al., 2007; Scherf and Hublin, 2013; Lazenby et al., 2008a; 2008b; Scherf et al., 2009; Schilling et al., 2014). Generally, there is a prevalent idea that bone reacts dynamically and adapts to mechanical loading created by locomotor behavior (e.g. Fajardo and Müller, 2001; MacLatchy and Müller, 2002; Fajardo et al., 2007; Scherf and Hublin, 2013; Scherf et al., 2009; Schilling et al., 2014), and manipulative and instrumental behaviors (Lazenby et al., 2008a; 2008b). These studies are based on functional interpretation of extant and fossil primate morphology of skeletal elements.

However, those studies provide a number of methodological challenges to analyses of trabecular structure across anatomical areas among different primates. Fajardo and Müller (2001) raised some challenges of comparing trabecular structure across extant primates. The first challenge is to overcome the issue of different body masses that creates allometric effects possibly affecting trabecular structure remodelling. This is a quite common problem that needs to be addressed since most comparative studies include primates with different body masses (e.g. Ryan and Ketcham, 2005; Maga et al., 2006; Fajardo et al., 2007). For example, in this study, the trabecular thickness (Tb.Th) and trabecular spacing (Tb.Sp) have been scaled negatively while connectivity (Conn.D) has been scaled positively with body mass. Therefore, the trabecular struts are relatively much larger in taxa with lower body mass than in taxa with higher body mass but relatively much less connected in taxa with lower body mass than in taxa with higher body mass.

The next issue with analysing trabecular structure may be in the standardized VOI size. Lazenby at al. (2011) showed that some trabecular parameters might change when VOI size is scaled to a dimension of bone size (Conn.D is particularly sensitive). Therefore, rather than standardized VOI size, the scaled VOI size should be used since placing a same size VOI in both large and small animals may result in having a higher number of trabeculae for analysis in smaller taxa than in larger taxa.

The third issue brought up by Fajardo and Müller (2001) is the location of VOI. Whitehouse and Dyson (1974) concluded that, depending on the VOI position, the relative bone volume (BV/TV), trabecular thickness (Tb.Th), trabecular spacing (Tb.Sp), and degree of anisotropy (DA) may be changed by 1 to 13%. Nägele et al. (2004) showed the trabecular number (Tb.N), trabecular thickness (Tb.Th), and trabecular spacing (Tb.Sp) may significantly change in some anatomical regions when VOI is moved for more than four millimetres.

This is especially true if bones with more complex anatomy and with more heterogenous trabecular structure are analysed, which is the case of hand and feet bones (Maga et al., 2006; Griffin et al., 2010). Hence, the knowledge of morphology of studied bones and the understanding of morphological function of those bones are necessary. (e.g. Tocheri et al., 2007; Maga et al., 2006). In the case of hands, it is important to understand the mechanical relationships between the substrate and hand bones but also between the hand and the rest of the skeleton during locomotion or manipulative or instrumental behavior in general.

This raises the fourth issue whether it is realistic to study trabecular structure of these bones at all. Often (e.g. Kivell et al., 2011; Schilling et al., 2014; Stephens et al., 2018; Williams-Hatala et al., 2018), it is discussed whether it is possible to successfully solve all the methodological challenges mentioned above in such small and complex bones as carpals are. Specifically, the differences in some trabecular parameters can be found but it is unclear if they represent real biological differences or just methodological decisions.

As a response to these challenges, Kivell et al. (2011) investigated the potential influence of VOI size and location on trabecular parameters in the capitate and third metacarpal across primates that vary in body mass and external morphology of those bones. They found that changes in VOI location have an effect on the trabecular structure, particularly on the degree of anisotropy (DA) and connectivity (Conn.D) but they do not affect the volume ratio (BV/TV), trabecular number (Tb.N), trabecular thickness (Tb.Th), and trabecular spacing (Tb.Sp) as much. In their study, most trabecular parameters were more resistant to changes in VOI size than to changes in VOI location (except connectivity that was strongly affected by both). Also, they concluded that some trabecular parameters (particularly trabecular thickness and degree of anisotropy) could be sensitive to changes in scan resolution. Moreover, they pointed out that even among taxa with similar locomotion such as *Gorilla* and *Pan* or *Hylobates* and *Ateles,* we can see differences 1) in trabecular parameter values, and 2) how the trabecular parameters are influenced by changes in VOI location and VOI size. Their results show that we must be cautious in interpreting the data from trabecular structural analyses in general and specifically from comparative studies where methodological approaches could have been different.

6.1 Locomotor signals based on results of this study

In this study, we investigated how variation in trabecular structure of the capitate, lunate, and scaphoid reflects differences in locomotor behavior and body mass of seven taxa (*Ateles*, *Hylobates*, *Pongo*, *Gorilla*, *Pan*, *Papio*, and *Homo*). We first grouped our sample into three broad locomotor categories: “suspensory”, “quadrupedal”, and “bipedal”, based on their hand engagement during the most frequent locomotion and postural behavior.

During the suspensory locomotion (including brachiation), the hand grasps the substrate with body below the hand. In contrast, the hand is in contact with the substrate through dorsal surface of the middle phalanges during the quadrupedal locomotion (including knuckle-walking and digitigrade) with body above the hand. Lastly, the human hand is not used during locomotion at all but it is used during manipulative and instrumental behaviors, in which power and precision grips are employed.

Secondly, we expected the correlation between trabecular parameters (trabecular thickness, spacing, and connectivity) with bone volume. Therefore, we tested this expectation based on prediction that the trabecular structure of wrist bones would vary in the same allometric pattern as it has been observed in other trabecular analyses of other bones (e.g. Doube et al., 2011; Barak et al., 2013; Fajardo et al., 2013; Ryan and Shaw, 2013), and further, we standardized those trabecular parameters for subsequent analysis.

Results from allometric analysis found some support for the expectation that remodelling of trabecular bone structure is also affected by body mass. We found that the connectivity indicates positive allometric relationship with bone volume, and trabecular thickness and spacing indicate negative allometric relationship with bone volume. Connectivity has the highest correlation with bone volume in lunate and the lowest in capitate, trabecular thickness has the highest correlation with bone volume in scaphoid and the lowest in lunate, and trabecular spacing has the highest in scaphoid and the lowest in capitate (Tab. 3).

We can see similar scaling patterns of trabecular structure of humeral and femoral head across primates (Ryan and Shaw, 2013) and in all skeletal elements across mammals (Barak et al., 2013). However, some studies (Fajardo et al., 2013; Schilling et al., 2014) show isometric scaling. This variation may reflect differences in the “size” variable used across studies. Specifically, the bone volume (this study), the mean of body mass (e.g. Fajardo et al., 2013), the geometric mean of carpal dimensions (e.g. Schilling et al., 2014), and femoral head height (e.g. Doube et al., 2011; Ryan and Shawn, 2013) can be used as “size” variables.

Therefore, the variation of trabecular parameters among primates that engage in similar locomotion and yet vary in body mass (e.g. *Gorilla* and *Pan*, or *Ateles* and *Pongo*) may be partly explained by variation in body mass (Tab. 1). Specifically, *Gorilla* has thicker and more widely separated trabeculae compared to smaller *Pan*. Similarly, we can see this tendency also in *Pongo* compared to smaller *Ateles* and *Hylobates*. Furthermore, the variation of trabecular parameters among primates may be partly explained by variation in mechanical loading of the wrist bones or potential differences in remodelling of trabecular structure within each carpal bone.

Finally, we measured five trabecular parameters within the VOI for each carpal bone of each individual. We hypothesized that there would be a significant difference between locomotor groups and no significant difference within the groups (i.e. suspensory and quadrupedal). Specifically, we expected that the volume ratio and trabecular thickness would be lower in suspensory taxa because the selected bones are loaded mostly in tension, than in quadrupedal taxa, in which the selected bones are loaded mostly in compression. We expected the lowest values in *Homo* because the hands are rarely used during the locomotor behavior. Thus, we expected that trabecular spacing would be the highest in *Homo*, lower in suspensory taxa, and the lowest in quadrupedal taxa because it is in negative correlation with trabecular thickness.

We did not predict the distribution for other parameters because they are not directly reflecting the loading. More precisely, mechanical loading influences the anisotropy but it mostly reflects the direction of loading, not the magnitude. Connectivity reflects the number of connected struts but it is not simply related to the volume fraction. Lastly, we hypothesized that there would not be a significant difference among suspensory and among quadrupedal taxa in most trabecular parameters.

Analysis of trabecular parameters reveals some differences in trabecular structure between locomotor groups but also some unexpected similarities. When testing our first hypothesis, we found support for our expectation that volume ratio would be distinct between suspensory and quadrupedal taxa in all carpal bones. Also, the mean rank is lower in

Homo and higher in quadrupedal taxa in all carpal bones as we expected. This result is consistent with the hypothesis that loading during manipulative behavior is much lower than during locomotion (Zeininger et al., 2011). This result is consistent with the other studies about the lower trabecular distribution in *Homo* compared to other primates in the third metacarpal (Zeininger et al., 2001; Tsegai et al., 2013), humerus (Shaw and Ryan, 2011), metatarsals (Griffin et al., 2010), calcalneus (Maga et al., 2006), or thoracic vertebrae (Cotter et al., 2009). All of these bones are involved during locomotion.

The expectation that the volume ratio would be lower in suspensory taxa than in quadrupedal taxa and the lowest in *Homo* has been confirmed. However, we can see the highest value of trabecular thickness in suspensory taxa and the lowest in *Homo* in all carpal bones, a result that does not conform to our expectations. The highest value of trabecular spacing is in suspensory taxa and the lowest in *Homo* in capitate and lunate but there is no significant difference in scaphoid. As we also expected, we found a significant difference in connectivity in all carpal bones and in the degree of anisotropy of capitate and scaphoid but not in the lunate (Tab. 4-5; Fig. 6). In summary, there is some level of variability in trabecular structure with overlaps within each locomotor group but we were able to identify a pattern that separates suspensory from quadrupedal taxa (see below).

Overlaps between locomotor groups could be due to some level of intraspecific variation or phylogeny (see below) or due to the variation in locomotor postures, which can affect trabecular remodelling. For example, Patel (2010) showed that the size and shape of metacarpal heads do not significantly correlate with hand posture during locomotion. There are some differences between suspensory and quadrupedal taxa but similarities also exist. However, those similarities likely exist because the taxa did not adopt just one type of locomotion, e.g. quadrupedal taxa exhibit a substantial amount of vertical climbing, which itself might have left a signal in their trabecular anatomy. In the end, the problem with overlapping values might be more related to creating specific categories (in this case locomotor groups) than that loading and locomotion would not inscribe into the trabecular structure.

Analyses of trabecular parameters among suspensory and quadrupedal taxa reveal mostly expected results. We found moderate support for our hypothesis that there would be no difference in trabecular parameters among suspensory and among quadrupedal taxa across all three carpal bones. However, there are some significant exceptions. The vast majority of significant differences in the suspensory category are caused by *Pongo* being more similar to quadrupedal taxa. In the quadrupedal category, Gorillas cause the majority of significant differences (Tab.5; Fig.7).

Altogether, variation in carpal trabecular structure within suspensory taxa shows a similar pattern in *Ateles* and *Hylobates.* However, *Pongo* is distinct in connectivity, trabecular thickness, and spacing in all the carpal bones from the other suspensory taxa (*Ateles* and *Hylobates*). Figure 7 shows that Pongo exhibits a large range of variation in trabecular structure. Some parameters are more similar in trabecular structure to African apes (*Gorilla* and *Pan*) than to the other suspensory taxa. This variation may reflect more frequent use of hook grips in *Ateles* and *Hylobates* than in *Pongo* or more terrestrial behavior in *Pongo* compared to the others (for example males are more terrestrial than females) or by phylogenetic relationships.

Tsegai et al. (2013) showed that there is a decrease in trabecular thickness, volume ratio, and degree of anisotropy in *Hylobates* and *Ateles* between the last common ancestor of hominoids and the last common ancestor of the hylobatids in metacarpal heads. However, there is an increase in those parameters in *Pongo* between the last common ancestor of great apes and extant *Pongo*. Also, quadrupedal taxa show different evolutionary patterns. There is an increase in trabecular thickness and anisotropy and a decrease in volume ratio in *Gorilla*. *Pan* shows a similar pattern but with lower values than *Gorilla*, which could be caused by different body mass. *Homo* shows reduction in trabecular thickness and volume ratio since the last common ancestor with *Pan*. However, *Homo* also shows an increase in body mass that can explain a reduction rather than an increase in those parameters compared to *Pan*. Tsegai et al. (2013) concluded that the changes in trabecular structure might be due rather to specific trabecular patterning or to mechanical loading than to phylogenetic relatedness. However, the authors allow a certain degree of correlation with phylogenetic relatedness, especially in suspensory taxa (*Pongo* compared to *Hylobates* and *Ateles*).

Variation in carpal trabecular structure within quadrupedal taxa shows a similar pattern in all parameters of all carpal bones except for connectivity, in which *Gorilla* is distinct from *Pan* and *Papio*. Furthermore, it is important to note, that African apes vary in frequency of knuckle-walking with *Gorilla* engaging mostly in terrestrial knuckle-walking (Doran, 1996; 1997) but *Pan* engaging more in arboreal knuckle-walking and climbing (Hunt, 1992; Doran, 1992; 1993; 1997; Susman et al., 1980). Therefore, it is not surprising that *Pan* has its trabecular structure intermediate between quadrupedal and suspensory taxa.

Furthermore, all trabecular parameters of all carpal bones are the lowest in *Homo* compared with suspensory and quadrupedal taxa. These results were expected because of the prediction that human hand is most often used during manipulative and instrumental behavior rather than during locomotion. The trabecular values in *Homo* are most similar to *Gorilla* but still significantly different.

Our results suggest that a higher volume ratio, connectivity, and degree of anisotropy are associated with quadrupedal taxa compared to non-quadrupedal taxa (suspensory and bipedal), and higher trabecular thickness and spacing are associated with suspensory taxa rather than with non-suspensory taxa (quadrupedal and bipedal) in the capitate, lunate, and scaphoid.

In general, higher volume ratio is associated with resisting higher compression in carpal bones during quadrupedal locomotion (Ryan and Walker, 2010). Higher degree of anisotropy has been discussed in previous studies but the inconsistent results for the correlation between quadrupedal and suspensory locomotion, leaping, and bipedalism have been found (Ryan and Ketcham, 2002; Fajardo et al., 2007; Griffin et al., 2010; Ryan and Walker, 2010; Ryan and Shawn, 2012; Shaw and Ryan, 2012). However, the studies of the foot bones (e.g. Maga et al., 2006; Griffin et al., 2010) found a higher anisotropy in *Homo* compared with non-bipedal taxa.

Relatively few studies connected connectivity with mechanical loading. Instead, connectivity is mostly associated with bone loss or porosity of the bone (Shen et al., 1993). However, McCalden et al. (1997) attributed connectivity to the strength of trabecular structure and thus, higher connectivity can be associated with higher modulus of elasticity (Ladd et al., 1997; 1998; Ladd and Kinney, 1997). It is debated because some studies show no functional relationship between connectivity and elasticity (e.g. Kinney and Ladd, 1998). This difference in results may be explained by the fact that the mechanical loading transfers differently based on the contact area. Also, it is important to note that out of all trabecular parameters, connectivity is most affected by body mass, VOI location and shape.

Finally, higher trabecular thickness and thus lesser trabecular spacing provide the information on higher volume of bone that is associated with mechanical loading during suspensory locomotion (Schilling et al., 2014).

The main intention of this study was to identify a relationship between trabecular structure of the capitate, lunate, and scaphoid and locomotor behavior. Such analysis of trabecular structure faces some methodological challenges (see above). In this study, we tried to cope with those methodological problems in several ways: 1) we tested the allometry in trabecular thickness, spacing, and connectivity to see if they are affected by bone volume (as a proxy to body mass) and we standardised those values for subsequent analysis; 2) we placed VOI based on the recommendation by Kivell et al. (2011) in the centre of the body of lunate, between the radial and capitate/centrale articular surface of scaphoid, and centrally under the proximal articular surface of capitate; 3) we also tested differences among suspensory and quadrupedal taxa to see if the locomotor groups were categorized effectively.

Even with those precautions, the results could have been adversely affected. First, the relationship between groups and locomotor signals may have resulted from the methodology itself. Specifically, we did not use scaled VOI size as some authors recommend. Instead, we used standardized VOI size for all the selected primates across different bone sizes. Also, larger samples for particular species could explain some intrageneric variability (e.g. *Pongo*).

Furthermore, it was challenging to place the VOI because of the small size and irregular shapes of carpal bones across selected taxa. It would be helpful to measure the repeatability of the VOI location but unfortunately this was not possible due to time constraints. Fortunately, the intraobserver error has been reported as low in some studies (e.g.

Schilling et al., 2014). Some authors (e.g. Pahr and Zysset, 2009; Tsegai et al., 2013) suggested that it would be ideal to analyse trabecular structure within the entire bone in cases of such irregular and small bones.

Second, the lack of significant differences in some trabecular parameters between locomotor groups and some significant differences among suspensory and among quadrupedal taxa may be due to more diverse ways of locomotion across taxa, i.e., the locomotor categories may be too broad. As we mentioned above, there are differences among suspensory (e.g. Mittermeier and Fleagle, 1976; Cant et al., 2001) and quadrupedal (e.g. Hunt, 1991; Doran, 1996) taxa in frequency and type of locomotion and that may be reflected in trabecular structure.

Third, Currey (2002) suggested that trabecular structure could be less able to respond to mechanical loading and stress in bones, which developed from a single ossification centre, such as carpal bones. Thus, the trabecular structure of carpal bones could actually be resistant to more loading than trabecular structure of bones with more than one ossification centre. Also, the wrist is very complex and includes more bones. Therefore, the loading can spread across those bones avoiding higher impact on each individual bone of the carpus (Dias et al., 2008; Macho et al., 2010; Kersh et al., 2013).

For future study, we would suggest scaling the VOI size based on differences in body mass across selected species and measure the repeatability of VOI location. Particularly, we would suggest exploring the scaling relationships of trabecular structure, the influence of phylogenetic relationships and intraspecific variation. This is a huge methodological challenge for all the studies of the hand bones across extant primates, especially due to difficulties in obtaining appropriate data on individual body sizes. Larger sample sizes resulting from higher availability of microCT scanning would also help to solve some of these issues.

7 CONCLUSIONS

The first aim of this thesis was to test the assumption that variability in carpal bone trabecular structure correlates with locomotor type, regardless of the evolutionary trajectory of selected species. The second aim of the thesis was to explore how the internal structure of the wrist bones differs among the selected taxa, especially with regards to differences in wrist size. We analysed trabecular structure in three carpal bones (capitate, lunate, scaphoid) in a sample of extant primates and *H. sapiens* relative to the dominant type of their locomotion. We conclude that there are significant differences between locomotor groups. Our results suggest that suspensory taxa are associated with higher trabecular thickness and spacing than non-suspensory taxa, while quadrupedal taxa are associated with higher volume ratio, connectivity, and degree of anisotropy compared to non-quadrupedal taxa. However, our results also suggest some significant differences among suspensory and among quadrupedal taxa, especially in *Pongo* compared to *Hylobates* and *Ateles*. Those differences may be due to differences in body size, phylogenetic relationships, or due to the combination of several modes of postural behaviour and locomotion.

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9 RESUME

The first aim of this thesis was to test the assumption that variability in carpal bone trabecular structure correlates with locomotor type, regardless of the evolutionary trajectory of selected species. The second aim of the thesis was to explore how the internal structure of the wrist bones differs among the selected taxa, especially with regards to differences in wrist size. We analysed trabecular structure in three carpal bones (capitate, lunate, scaphoid) in a sample of extant primates and *H. sapiens* relative to the dominant type of their locomotion. We conclude that there are significant differences between locomotor groups. Our results suggest that suspensory taxa are associated with higher trabecular thickness and spacing than non-suspensory taxa, while quadrupedal taxa are associated with higher volume ratio, connectivity, and degree of anisotropy compared to non-quadrupedal taxa. However, our results also suggest some significant differences among suspensory and among quadrupedal taxa, especially in *Pongo* compared to *Hylobates* and *Ateles*. Those differences may be due to differences in body size, phylogenetic relationships, or due to the combination of several modes of postural behaviour and locomotion.

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10.1 Figures

Fig. 1: The radiocarpal joint of the right upper limb; (A) Old World monkeys (*Cercopithecus nictitans*), (B) gibbons (*Hylobates lar*), and (C) chimpanzees (*Pan troglodytes*). (R) radius; (U) ulna; (P) pisiform; (t) triangular disc; (m) intraarticular disc; (l) lunula; (r) palmar radiocarpal ligament; (u) palmar ulnocarpal ligament; (s) styloid process of ulna; (c) spot where the pisotriquetral and radiocarpal joints are connected. The figure was taken from Hamshere and Bucknill (1970) and modified.

Fig. 2: The dorsal view of the left wrist of Old World monkeys (*Papio hamadryas*). (h) hamate; (ca) capitate; (t) trapezoid; (tr) trapezium; (ce) centrale; (ti) triquetral; (l) lunate; (s) scaphoid.

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Fig. 7: Trabecular parameters for selected genera. Measured parameters are: trabecular spacing (Tb.Sp), anisotropy (DA fraction), trabecular thickness (Tb.Th.), volume ratio (BV/TV), and connectivity (Conn.D). The Tb.Th, Tb.Sp, and Conn.D were scaled with body mass and log transformed (log10), to bring the values to similar scale.. The box represents the 25th and 75th percentiles, centre line is the median, points represent outliers and squares are the extreme outliers. Blue colour represents lunate, pink capitate, and green scaphoid. Filled boxes represent significant difference and hatched boxes represent no significant difference across locomotor groups.

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