A COMPARATIVE ANALYSIS OF CARPOMETACARPAL JOINTS FOUR AND FIVE IN VARIOUS HOMINOID AND CERCOPITHECOID SPECIES

A thesis submitted

to Kent State University in partial

fulfillment of the requirements for the

degree of Master of Arts

by

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August 2017

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ACKNOWLEDGEMENTS

I would like to acknowledge the members of my thesis committee. I thank my advisor, Dr. C. Owen Lovejoy, for introducing me to this project and to the topics discussed in the project. He has taught me how to critically approach the field of physical anthropology, and I am a better researcher and thinker for my experiences in his classes and working under his advisement. I thank Dr. Richard S. Meindl for his eagerness to aid in students' understanding of the principles of statistics, even outside of regular working hours. His ceaseless patience as I continue to understand the intricacies of bivariate and multivariate statistics has been invaluable. I thank Dr. Mary Ann Raghanti for her unending guidance and encouragement, especially during times when I was most in need.

I thank my fellow graduate students, especially the efforts of Dexter Zirkle and Dr. Aidan Ruth, for sharing materials and ideas. Thanks to Dr. Linda Spurlock for introducing me to the staff and collections at the Cleveland Museum of Natural History. Thanks to Lyman Jellema for allowing me to access the skeletal collections housed in the Cleveland Museum of Natural History, and for always accommodating my busy schedule.

I would like to give a special thanks to Professor John Reeves at the University of Akron for introducing me to the field of physical anthropology. His efforts have inspired in me an unquenchable thirst for knowledge, for which I am immensely grateful. Completion of this project would not have been possible without his everlasting friendship and support, and also the support of my parents, Mark Lawrentz and JoAnne Waters, grandmother, Leah Musarra, and friend, Dr. Nicole Kline.

CHAPTER 1

Introduction

History of Debate

Charles Darwin and Thomas Huxley were among the first to recognize our relationship to the great apes based on shared physical attributes (Straus 1949). It was their contention that humans evolved from a similar anthropoid form (Straus 1949). Bipedalism is a unique form of locomotion among primates and is considered a hallmark of humankind. Understanding the form of locomotion preceding bipedalism is crucial to understanding how and why bipedalism evolved, and there has been no shortage of hypotheses. Since the time of Darwin and Huxley, the debate over what the ancestral, anthropoid form might have been has raged, with the main candidates being: brachiators, climbers, and knuckle-walkers (Corruccini 1978; Corruccini and McHenry 2001; Gebo 1996; Gregory 1930; Richmond and Strait 2000; Richmond et al. 2001; Stern 1975; Stern and Susman 1981; Tuttle 1981; Washburn 1967).

Years after the publication of Huxley's *Evidence as to Man's Place in Nature (1863)* and Darwin's *The Descent of Man (1871),* Sir Arthur Keith was the first to propose a specific type of locomotion preceding bipedalism (Straus 1949, Tuttle 1969, Tuttle et al. 1974). Keith believed that the upright posture assumed by extant brachiators was a necessary preadaptation for human bipedality (Straus 1949, Tuttle 1969, Tuttle et al. 1974). According to Keith's model, human ancestors passed through three distinct phases. The hylobatian stage was characterized by small-bodied brachiators, much like extant gibbons and siamangs (Straus 1949, Tuttle 1969, Tuttle et al. 1974). In the troglodytian phase, small-bodied brachiators were replaced by larger-bodied ones (Straus 1949, Tuttle 1969, Tuttle et al. 1974). Lastly, our ancestors entered the plantigrade phase, when they ultimately adopted permanent upright posture (Straus 1949, Tuttle 1969, Tuttle et al. 1974).

Many observers originally concurred with Keith. According to Gregory (1930), our brachiating ancestry was clearly evidenced by features of the hand, wrist, limbs, and shoulder girdle that are very similar to chimpanzees and gorillas – both of which occasionally brachiate. However, this theory later fell out of favor, even with Keith himself (Straus 1949). The amount to which extant apes practice brachiation has been overstated; chimpanzees and gorillas spend considerable time on the ground (Tuttle 1969). Also, Straus (1949) argued that brachiation demands some irreversible specializations, and yet many human features remain relatively primitive and unspecialized, more similar to those of monkeys and prosimians.

After the brachiating hypothesis was generally discarded (or at least substantially modified), the debate focused on theories of strict vertical climbing (including suspensory postures) versus a locomotor repertoire comprised of both arboreal and knuckle-walking aspects (Richmond et al. 2001). Proponents of the hypothesis of a climbing predecessor cite biomechanical similarities between vertical climbing and bipedalism as evidence for their theory; similar muscles are employed during both behaviors (Richmond et al. 2001; Stern and Susman 1981). Similar to the vertical climbing model is Tuttle's (1981) hylobatian model. The two differ mainly in predictions of body size and limb proportions (Richmond et al. 2001). Tuttle (1981) postulated that our ancestors stood bipedally to forage in trees, that they were small-bodied, and had powerful gluteals, anterior thighs, and calf muscles. This type of vertical climbing and arboreal feeding preadapted our ancestors to the upright posture assumed during bipedality (Tuttle 1981). Despite anatomical and biomechanical similarities between extant climbers and modern humans, it is unclear whether the arboreal adaptations in humans and known fossil hominids have been retained from the immediate predecessors of bipedality, or if they have been retained from an earlier stage of our ancestry (Richmond et al. 2001).

The other major candidate for the type of locomotion preceding bipedalism is that which is employed by our closest living relatives, the great apes. Tuttle, although not a proponent of the theory himself, studied the anatomy of knuckle-walking and defines the posture as such: “the distal and middle segments of the fingers are flexed and the proximal segments are hyperextended. The palm is elevated and aligned with the wrist and forearm. Thus, in knuckle-walkers, only the backs of middle segments of the fingers come into contact with the substratum” (Tuttle 1969:954). Washburn (1967) was the first major supporter of a knuckle-walking ancestor. He addressed the long-lived assumption that human bipedality evolved in response to selective pressures requiring the use of the hands to manipulate and carry objects. Washburn (1967) proposed that a knuckle-walking phase of human evolution provided the circumstance for bipedalism to evolve. By allowing our ancestors to carry objects during locomotion, it serves as an appropriate intermediate form of locomotion (Washburn 1967).

During the same decade that Washburn proposed this theory, biomolecular studies revealed humans’ close genetic relationship to the great apes, specifically to the chimpanzee (Richmond et al. 2001). The coupling of these two events resulted in much attention and support for the knuckle-walking theory in the following years, and it continues to be popular in the field today.

A Knuckle-Walking Ancestor

It was once thought that bipedalism evolved in congruence with the reduction of tropical forests (Washburn 1967). As trees became scarcer, our ancestors were forced to the forest floors and, as it was assumed, up on their hind limbs. It was later recognized that the absence of trees does not demand bipedal locomotion, because our closest living relatives are large bodied terrestrial quadrupeds (Tuttle 1974, Washburn 1967, Zihlman et al. 1978). It then became a popular premise that humans must have passed through a chimpanzee-like, knuckle-walking phase (Washburn 1967). In current years, the field has become “chimpocentric”, as the chimpanzee model has received the most attention (Beck 1982; Sayers and Lovejoy 2008). Referential models of human evolution focus on the chimpanzee based on our many presumed shared behaviors and hypothesized anatomical parallels (Goodall and Hamburg 1974; Sayers and Lovejoy 2008). One of the most important factors contributing to the popularization of this theory is that chimpanzees occasionally adopt bipedal postures while feeding, and may even travel bipedally for short distances (Goodall and Hamburg 1974; Sayers and Lovejoy 2008). As a result, the chimpanzee has been used as the template from which humans evolved (Sayers and Lovejoy 2008).

During locomotion, chimpanzees “bear their weight on the backs of their middle phalanges (middle segments of their fingers), which involves strongly flexed proximal interphalangeal joints, and extended metacarpophalangeal joints” (Richmond et al. 2001:76). The only anatomical evidence Washburn (1967) originally cited for his theory is the lack of hair on the dorsal aspect of ape and human intermediate phalanges (Richmond et al. 2001). Since the debut of this hypothesis innumerable supposed knuckle-walking traits have been identified by many researchers. Many comparative studies have been performed on the hand, wrist, shoulder, and elbow in search of similarities between humans and chimpanzees that would “prove” a similar function in the last common ancestor (Corruccini 1978, 1991; Patel 2005; Richmond and Strait 2000, 2001; Young et al. 2015; Williams 2006).

With an understanding of the genetic affinity between the great apes and humans, debates now focus on where, temporally, the evolution of knuckle-walking falls on the hominoid family tree. Arguments based on parsimony claim that the uniqueness of knuckle-walking coupled with the distribution of supposed knuckle-walking traits among great apes, humans and human ancestors demands a single evolutionary lineage (Corruccini 1978; Corruccini and McHenry 2001; Gebo 1996; Richmond and Strait 2000; Richmond et al. 2001; Williams 2010); whereas others note the differences between knuckle-walking behaviors and postures among extant hominoid genera and argue for it’s independent evolution (Dainton and Macho 1999; Inouye 1994; Kivell and Schmitt 2009; Lovejoy et al. 2009). Any traits indicative of knuckle-walking or otherwise shared between the three genera are likely to have been present in the last common ancestor (Richmond et al. 2001). If knuckle-walking features are not shared among extant apes and humans, then it is likely that knuckle-walking traits evolved independently in both chimpanzees and gorillas while humans evolved traits suitable for bipedalism (Richmond et al. 2001).

Analysis of the distribution of traits across extinct and extant hominoid taxa would shed light on the origins of bipedalism in relation to knuckle-walking, although another great debate involves identifying true knuckle-walking adaptations. According to Richmond et al. (2001) the two main functions of any “knuckle-walking” trait in the hand or wrist is 1) to lessen compressive loads by enlarging and redirecting joint surfaces (though there is debate over what constitutes a weight bearing adaptation), and 2) to stabilize the wrist via bony “locking mechanisms" that limit mobility of the carpal joints during stance phase. Many examples of these traits have been proposed and debated in the literature.

The present study is concerned with supposed locking mechanisms said to limit flexion and extension of the hominoid wrist. For example, Richmond and Strait (2000) address one such locking mechanism facilitated by the radiocarpal joint. "Locking" is achieved when the projection of the dorsal aspect of the distal end of the radius contacts a corresponding concavity on the dorsal aspect of the scaphoid during wrist extension, creating a close-packed position and limiting further extension at this location (Richmond and Strait 2000). Although not the subject of their analysis, they reference another "locking mechanism," that presumably promotes stability at the metacarpophalangeal joints: the dorsal ridges on the metacarpal heads are met by the dorsal aspect of the base of the proximal phalanges during extension (Richmond and Strait 2000). "Keeling" morphology of the hamate and capitate has likewise been considered (Kivell and Schmitt 2009; Richmond et al. 2001).

Richmond and Strait (2000) claim to have found evidence of the radio-scaphoid locking mechanism in *Australopithecus anamensis* and *Australopithecus afarensis*. Furthermore, they claim that all African apes have this locking mechanism. However, the evaluation of such traits by other researchers yields different results and conclusions (Dainton and Macho 1999; Dainton 2001; Kivell and Schmitt 2009). A large percentage of gorillas, and some chimpanzees, do not share these extension-limiting traits (Kivell and Schmitt 2009). Specifically, the described radio-scaphoid morphology is found in high percentages in chimpanzees (96%) as well as other arboreal palmigrade monkeys (80%) and terrestrial palmigrade monkeys (73%), but found at a very low frequency in gorillas (6%) (Kivell and Schmitt 2009:14242). The ridges on the metacarpal heads are variably present in extant knuckle-walkers (Kivell and Schmitt 2009).

Moreover, Kivell and Schmitt (2009) found that a large percentage of gorillas do not share the extension-limiting morphology of the capitate and hamate. Keeling and dorsal ridges of the distal carpals are found at a frequency of 81%-100% in chimpanzees, but found as low as 39% in gorillas (Kivell and Schmitt 2009:14242).

More importantly, joints are composed of two “almost frictionless surfaces” (Selby et al. 2016:598; Burstein and Wright 1994) moving relative to one another. Synovial fluid within the joint capsule and the hyaline cartilage covering the joint surfaces facilitate their relative motion, and do not restrict it (Lovejoy et al. 2001). Rather, joints are stabilized by surrounding muscles and ligaments (Burstein and Wright 1994; El-shennawy et al. 2001; Gebo 2014; Kapandji 2007; Lovejoy et al. 2001; Selby et al. 2016). Intra-articular ligaments especially play an important role in stabilizing the carpometacarpal joints. Nakamura et al. (2001) found that when dorsal and volar ligaments were severed in human wrists, the intra-articular ligaments alone prevented dislocation of the carpometacarpal joints (when manual pressure was applied).

The articulating surfaces of a synovial joint maintain contact throughout the joint’s range of motion, and “edge loading” does not occur in normal joints (Burstein and Wright 1994; Lovejoy et al. 2001; Selby et al. 2016). Said “locking” of any joint via bony morphology would be detrimental to the underlying articular cartilage and bone (Selby et al. 2016). Interestingly, when wrist and digit flexors are severed in deceased chimpanzees, the wrist can be dorsiflexed 45-55 degrees (Straus 1940). The “extension-limiting” morphology described by Richmond and Strait (2000) is most likely the result of adaptive chondrogenesis occurring at the epiphyseal plates of the distal radius and metacarpal heads as well as at the articular surfaces of the joint (Lovejoy et al. 2001). (The process of chondral modeling will be discussed in detail below).

The present study is concerned with supposed bony “locking mechanisms” achieved via hamate-metacarpal joint morphology and organization of the distal carpal row. This morphology is described more specifically in Chapter 2. This study proceeds while bearing in mind that traits commonly noted as “knuckle-walking traits” have not been found universally in all great apes, and not all primates that have “knuckle-walking traits” are knuckle-walkers (Kivell and Schmitt 2009). Therefore, these traits may not be reliably used to diagnose a specific behavior, and should not be considered further in this context. Explanations alternative to adaptation should be considered when interpreting the origins of any trait.

Alternative Trait Types

It is a common, yet misguided, practice in the field of physical anthropology to reduce the skeleton, or a single bone, to innumerable individual characters, and subsequently assign to each some functional value (Gould and Lewontin 1979, Lovejoy et al. 1999, Lovejoy et al. 2003). To assume functional significance, in the evolutionary perspective, is to assume a genetic basis, for in order for a feature of bone to be an adaptation it must be heritable. Researchers can isolate and define traits, but this is not indicative of heritability (Lovejoy et al. 1999; Lovejoy et al. 2003). We now know adult bony morphology is the result of numerous complex processes, rather than being a simple “read-out” of the “blueprint” from the genome (Carter and Beaupre 2001; Lovejoy et al. 1999). A comprehensive understanding of how bones are formed, from the early embryonic stages through epiphyseal closure in the adult will shed light on the issue of distinguishing between functional and nonfunctional traits, between traits indicative of phylogeny and those that are simply by-products of developmental processes (Lovejoy et al. 1999).

Adult bony morphology is the result of the coaction of several complex processes: the assignment of cells' positional information during early embryogenesis, and the realization of these instructions through various systemic assembly mechanisms (Lovejoy et al. 1999, 2003). Positional information is first assigned via different mechanisms for each of the three axes (Gilbert 2003; Lovejoy et al 1999, 2003). Along the posterior margin of the limb bud, cells within the Zone of Polarizing Activity express the morphogen Sonic hedgehog (*Shh*) (Gilbert 2003; Lovejoy et al 1999, 2003). The gradient of this signaling molecule "tells" cells their anteroposterior address. The dorsoventral axis is specified by ectodermal cells' expression of a number of signaling molecules including *Wnta7* or *En1*. Although not fully understood, it is thought that a cell's proximodistal address is determined by the amount of time spent in the Progress Zone, lying just proximal to the Apical Ectodermal Ridge (Lovejoy et al. 2003). A positive feedback loop between the PZ and the AER established by the expression and reception of different fibroblast growth factors maintains PZ cells in a proliferative state (Gilbert 2003; Lovejoy et al. 2003). These three processes constitute each cell's three-dimensional coordinate system (Lovejoy et al. 1999).

These instructions are communicated early in embryogenesis, and are later refined and carried out by two distinct processes. One takes place via systemic assembly mechanisms. SAMs perform basic "housekeeping" functions, such as maintaining the function of growth plates and regulating mechanotransduction (Lovejoy et al. 1999). These are sustained throughout the musculoskeletal system. Positional information can also be later refined through *cis*-regulation of Hox genes, which can "directly affect both size and shape of presumptive bones" (Lovejoy et al. 1999:13248) by altering downstream genes for bone morphogenetic proteins, fibroblast growth factors, etc. (Lovejoy et al. 2003). Therefore, any hypotheses regarding anatomic adaptation must consider selection in terms of how PI is assigned and implemented (Lovejoy et al. 1999).

The practice of itemizing bones within the adaptationist paradigm can be phylogenetically misleading (Gould and Lewontin 1979). Phylogenetic relationships of extinct taxa can only be based on the assessment of bony characters. Therefore, precise analysis of these characters and their ontogenesis is crucial to the interpretation of extinct lineages. Given what we now understand about skeletogenesis, it would be prudent to consider, in addition to adaptation, the effects of developmental processes and the interaction of these processes with the environment when deciphering the phylogenetic meaning of extinct morphology. In order to accomplish this, Lovejoy et al. (1999, 2002) have proposed five types of morphological traits, including adaptation and four alternative types.

Type 1 traits are heritable and confer, to those that possess them, a reproductive advantage. These traits are the direct result of natural selection, and, thus, are true adaptations. Type 2 traits can be further split into Type 2A or Type 2B categories (Lovejoy et al. 2002). Type 2A traits are genetically linked to Type 1 traits, but serve little to no functional purpose (Lovejoy et al. 1999, Lovejoy et al. 2002). Conversely, Type 2B traits are linked to others that have not been selected, but arise in significant frequency in a population through other evolutionary forces, such as through genetic drift. Type 2B traits also serve little to no functional purpose. Type 3 traits arise as a result of a change to a systemic growth factor that controls several different components, such as body size. Type 4 traits arise from environmental effects during growth and development. They cannot be used to make phylogenetic distinctions; however, they can be useful in making behavioral analyses. Lastly, Type 5 traits are similar to Type 4 in that they are the result of the environment interacting with developmental processes, but Type 5 traits cannot be used to distinguish a specific behavior, as they are not expressed equally in all individuals.

Of particular importance to this study are Type 4 traits and one process by which they originate (Lovejoy et al. 2002, Hamrick 1999). Chondral modeling is involved in both initial joint formation and postnatal cartilage growth.

Early Development of Articular Surface Geometry

Aforementioned studies of joints of the hand and wrist itemize features of carpal and metacarpal joints in minute detail. Bearing in mind that joint surfaces must be perfectly congruent, as well as concordant with all surrounding muscles and ligaments in order to maintain normal joint motion and avoid damaging articular cartilage, the notion that the anatomical synchronicity of all of these structures is strictly genetic, and therefore subject to recombination, is unlikely (Lovejoy et al. 1999). Rather, the genetic influence extends to the mechanisms controlling the plasticity of the tissues preceding the adult bone (Lovejoy et al. 1999). Both genetics and mechanobiology guide the growth and development of articular surfaces.

All limb structures start out as condensations of undifferentiated cells, usually without clear distinctions between what will later be separate bones (Carter and Beaupre 2001). Chondrogensis begins simultaneously in different areas of the blastema, and as the growing cartilage regions expand toward each other, the space between them decreases. This becomes the homogenous interzone. Temporally, interzones appear proximal to distal. Early muscles, tendons and ligaments have already formed when the interzones are established and contractions begin. The interzones separate in response to the muscle contractions, marking the beginning stages of the development of the joint capsule. The two cartilage condensations that have been separated begin to move with respect to each other, “and true joint rotation is realized” (Carter and Beaupre 2001:63). These muscle contractions are required for proper growth and development of the joint. Continuous movement of the joint, “helps to control and guide the contouring of the joint surface so that it develops a kinematically efficient shape” (Carter and Beaupre 2001:65). Paralysis of surrounding joint musculature can lead to joint growth retardation, improper form, or even synostosis (Carter and Beaupre 2001; Plochocki et al. 2006).

Some joints, such as the ball and socket joint of the hip, are predisposed to cleave and result in one concave side and one convex one. Although, not all are endowed with this predisposition. R. Fick (1890) (as cited in Carter and Beaupre 2001) attempted to understand the development of such surfaces. Gypsum blocks were used to represent the two sides of the developing joint surfaces and rubber tubes connected the blocks, acting as muscles. The tubes were attached close to the mock joint surface on one block, and farther away on the other. When the blocks began to move relative to one another, the gypsum was worn away in specific regions, decreasing friction and, thus, increasing efficiency. Fick (1890) found that a concavity was formed on the side of the joint closer to the muscle attachment; on bones where the muscle attachment was further away from the joint the convex side was formed. Actual bones do not “wear away” in this fashion; however, because cartilage growth can be altered in response to mechanotransduction, the forces experienced by the developing joint surfaces can affect growth patterns in a similar way (Carter and Beaupre 2001).

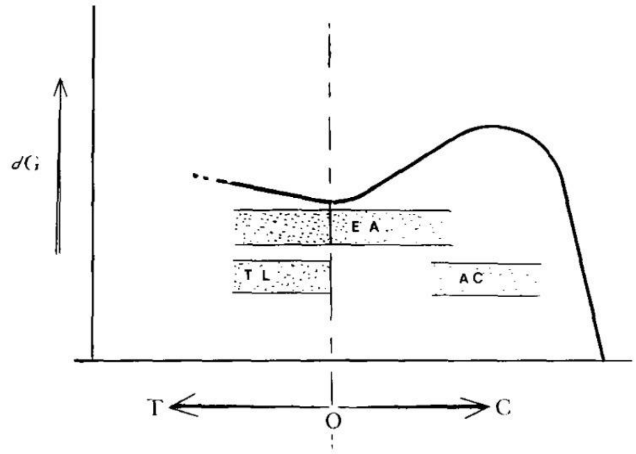
In humans, the homogenous interzones appear in the developing hand at about 6 weeks in utero. At the time of birth, the ends of the phalanges and metacarpals have not yet ossified, and the carpal bones are still completely composed of cartilage (Carter and Beaupre 2001). Unlike most long bones in the body, the metacarpals have only one secondary center of ossification, and it is located near the heads (Carter and Beaupre 2001; Walker et al. 2002). The primary center of ossification proceeds proximally towards the metacarpal bases and eventually ceases, leaving a thin layer of articular cartilage, which protects the joint and facilitates movement (Carter and Beaupre 2001). The rate of growth is genetically determined, although while the bones are still partially composed of cartilage, growth is also influenced by mechanotransduction (Carter and Beaupre 2001; Frost 1979). The hydrostatic and shear stresses generated by the "differential contact distribution patterns" on either side of the joint affect the growth and ossification of cartilage, and therefore the ultimate shape of the joint (Carter and Beaupre 2001). I will present a discussion of the validity of the chondral modeling theory and the processes by which it is achieved below.

Adaptive Chondrogenesis

Among the alternative trait types previously discussed, those deemed Type 4 are of particular importance to this study. One process responsible for the origin of Type 4 traits is chondral modeling. The original cartilage foundation, or anlagen, determines the ultimate shape of a bone (Frost 1994, 1999). Before ossification, the cartilage is somewhat "malleable" when subjected to mechanical forces. H. M. Frost (1979) laid the original framework for the chondral modeling theory, but the processes by which modeling was executed were not well understood at that time. He proposed that the growth of hyaline cartilage is responsive to mechanical forces for the purpose of improving the distribution of weight and protecting the integrity of the joint, and thus, ultimately avoiding arthrosis (Frost 1979, 1994). He formulated the basic components of the theory based on clinical experience, and concluded that there must exist natural physiological ranges of both compression and tension which are necessary to stimulate cartilage growth (Frost 1979). If tensile or compressive forces either fall below or exceed this range, cartilage growth ceases; however, as forces approach the maximum, growth is accelerated, that is until it crosses the biological threshold (Frost 1979). He also hypothesized that cartilage grows faster under compressive loads than under tensile loads (Frost 1979).

The chondral growth-force response characteristic curve (CGFRC) summarizes the laws governing adaptive chondrogenesis (Frost 1979, 1994, 1999). The curve represents the amount of force required to initiate growth of cartilage. The steeper slope on the right side of the curve, compared to the slope on the left, represents faster cartilage growth under compression than under tension. The trough, labeled “O”, represents a point at which neither compression nor tension is affecting growth; growth is under the influence of growth hormone (Frost 1979, Hamrick 1999). When either compression or tension exceeds the normal physiological range, growth slows and eventually stops, and this is represented by the drop-offs on either side of the curve (Frost 1979).

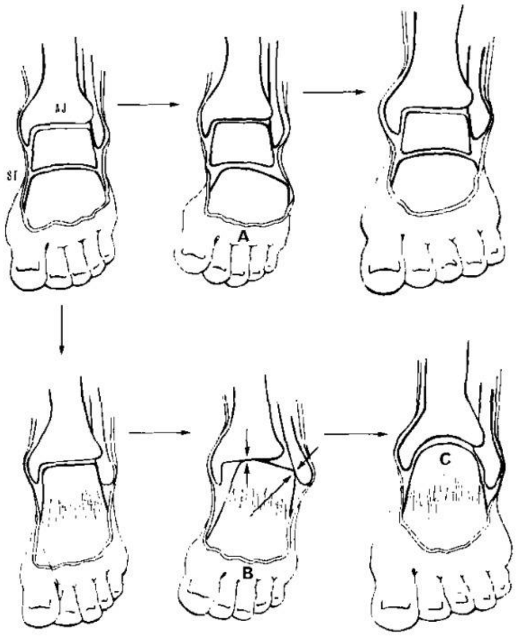
Figure 1. Chondral Growth-Force Response Characteristic (CGFRC) Curve, Frost (1979)



Frost (1979)

Chondral modeling acts to maintain articular congruence (Frost 1979). This theory is based on the assumption that articular cartilage is loaded on the peak of the compression line of the CGFRC curve (Frost 1979). Any incongruence on one side of the joint will be met on the other, increasing compression at that point. Because articular cartilage is already loaded on the peak of the CGFRC curve, this increase would place the amount of compression too high for cartilage growth to occur (Frost 1979). However, growth in the surrounding areas would continue until compressive forces were equalized over the articular surface (Frost 1979).

Figure 2. Inversion and Eversion of the Subtalar Joint, Frost (1979)



Frost (1979)

For example, when the human foot inverts or everts, the mobility at the subtalar joint "relieves the ankle of the resulting tilting force while the strap muscles absorb the energy and impact forces" (Frost 1979:187). In cases of ankylosis of the subtalar joint, inversion and eversion of the foot cause the corners of the talus to press into the articular surfaces of the tibia and fibula, transmitting high compressive loads exceeding the normal physiological range, and thus halting growth in these areas (Frost 1979). Growth continues in the surrounding areas until the “time-averaged load” is equalized across the joint (Frost 1979). Once the load has been equalized, growth continues under the control of genetic growth factors (Frost 1979; Hamrick 1999). The ultimate form of the articular surface is the result of habitual loads, or what Frost calls “time-averaged loads”; infrequent loading positions are not recorded (Frost 1979, 1994, 1999). Once an individual has reached maturity, the adult bone takes the shape of the original cartilage, and any further cartilage modeling is prohibited (Frost 1994, 1999; Hammond 2010).

Since the debut of the chondral modeling theory, advancements have been made in understanding the cellular processes governing cartilage growth, and how these processes are altered by mechanical stimulation. Hydrostatic pressure within the ECM facilitates load-induced cartilage growth via mechanotransduction (Hamrick 1999; Wang and Mao 2001; Wu and Chen 2000). Wu and Chen (2000) placed chondrocytes in a simulated natural environment and studied the effects of matrix deformation on cartilage growth. They found that loading affects chondrocytes differently depending on the level of cellular maturity (Wu and Chen 2000). Stimulation greatly increased proliferation of immature chondrocytes, but had little effect on proliferation of more mature, hypertrophied cells (Wu and Chen 2000). Instead, mature prehypertrophied cells increased synthesis of cartilage matrix protein, and hypertrophied cells increased synthesis of collagen X (Wu and Chen 2000). Hammond et al. (2010) found evidence that mechanical stress causes immature chondrocytes to increase in size. Other studies confirm that cartilage growth is stimulated when subjected to hydrostatic pressure between 1MPa and 10MPa, but growth ceases when forces exceed 10 MPa or fall below 1 MPa, in congruence with Frost’s original CGRFC curve (Hamrick 1999; Frost 1979). Chondrocytes are more greatly stimulated by fluctuating levels of stimulation (Hamrick 1999; Wang and Mao 2002; Wu and Chen 2000; Wu et al. 2001). Wang and Mao (2002) found that in cranial base cartilage of immature rabbits chondrocytes increased proliferation under both static and cyclic stresses, with subjects in the cyclic group increasing most. This is also congruent with Frost's original theory that supposed frequent, recurring loading histories were recorded (Frost 1979).

Although in vitro studies like these have borne positive results, animal studies examining articular cartilage thickness and volume (Eckstein et al. 2002; Hammond et al. 2010; Kiviranta et al. 1992; Muhlbauer et al. 2000; Plochocki et al. 2006), articular surface area of subchondral bone (Eckstein 2002; Lieberman et al. 2001; Plochocki et al. 2006), and articular surface shape (Hammond et al. 2010; Plochocki et al. 2006) in exercised versus sedentary groups of different species have yielded mixed results. Hammond et al. (2010) studied the effects of exercise on groups of active versus sedentary immature pigs, and found no difference in articular cartilage thickness between groups. Kiviranta et al. (1992) found a decrease in articular cartilage thickness on the medial femoral condyle in canines, in response to an exercise program. Although in some cases, there was an increase in patellar and tibial cartilage thickness. Muhlbauer et al. (2000) examined cartilage thickness and volume in triathletes versus sedentary adult males. Triathletes had trained >10 hours/week for three years prior to the study and reportedly had active childhoods, whereas the control group exercised <1 hour of exercise per week and did not participate in sports during childhood and adolescence. There were no differences of cartilage thickness between groups (Muhlbauer et al. 2000).

A similar study was conducted later by some of the same researchers. Likewise, Eckstein et al. (2002) did not find differences in articular cartilage thickness or volume, although using MRI they were able to conclude that both male and female triathletes exhibited larger articular surface areas (ASA) than the sedentary group. The results of this study are in contrast to another by Lieberman et al. (2001). Researchers tested the effects of an exercise program on articular surface areas of sheep of three distinct age groups (juvenile, subadult, and adult). They found slight differences in ASA between exercised and sedentary groups, although these results did not reach statistical significance. Rather, they concluded that joint size was more likely genetically constrained and followed an allometric growth pattern, as both exercised and sedentary subadults had larger ASAs (when corrected for body size) than both juveniles and adults, and adults had smaller ASAs than juveniles (Lieberman et al. 2001). Additionally, Hammond et al. (2010) found that when a discriminant function analysis was run on thirteen metrics representing articular surface area and shape of the femoral head of exercised versus sedentary pigs, the DFA successfully classified the specimens 100% of the time. The exercised group had overall larger dimensions and flatter joint surfaces, consistent with the chondral modeling theory (Hammond et al. 2001). Plochocki et al. (2006, 2009) found overwhelming evidence supporting the chondral modeling theory in several studies. In studies on femoral dimensions of juvenile mice researchers found thicker articular cartilage, larger subchondral articular areas, reduced subchondral and chondral curvature, and greater articular cartilage cellularity in exercised groups versus the sedentary controls (Plochocki et al. 2006).

A pattern emerges from these diverse results: mechanical stimuli have little to no effect on how much cartilage remains on the joint surface after the bone has already matured, as many of these studies found no differences in articular cartilage thickness or volume in exercised versus sedentary groups. Thicker articular cartilage may actually be maladaptive, as it is possible that it inhibits chondrocyte metabolism due to its avascular nature (Eckstein et al. 2002). Also, “optimal load transmission and tissue integrity are guaranteed by hydrostatic pressurization of the interstitial fluid … With thicker cartilage, the ability of the fluid to build up hydrostatic pressure may be impaired since there is more space for it to displace radially from the site of instant contact" (Eckstein et al. 2002:48). However, most of the studies reviewed above reported larger articular surface areas and changes in shape of the mature joint at statistically significant rates indicating that increased mechanical stimuli affects cartilage growth in this respect.

Research Goals

The present study combines aspects of all research previously reviewed including anthropological history, locomotion, development, and adaptive chondrogenesis. The quantitative and qualitative analyses target variation of shape and size of carpometacarpal joints four and five across several genera for the purpose of determining if this variation in joint structure is developmentally related to patterns of use during ontogeny, and if so, the degree to which activity reflects structure. The ultimate objective of this examination is to clarify the relationship between form and function in fossil hominoid wrists, and elucidate the origins of the corresponding morphology.

One tenet of the chondral modeling theory is that joints experiencing heavier loads will grow to be bigger than joints experiencing lesser loads in order to distribute the force over a greater surface area (Frost 1979, 1994, 1999). The present study couples this theory with knowledge of postural and biomechanical differences assumed during knuckle-walking in chimpanzees and gorillas. Gorillas typically hold their wrists in a columnar posture, angled perpendicularly to the line of travel, with their weight balanced across all four knuckles (Matarazzo 2009; Wunderlich and Jungers 2009). Conversely, chimpanzees adopt a more extended wrist posture during the weight-bearing phase of knuckle-walking, and hold their wrist at a variety of angles to the line of travel (perpendicular, oblique, or parallel) (Matarazzo 2009; Wunderlich and Jungers 2009). Also they tend to bear most of their weight on knuckles two through four, and less on five (Matarazzo 2009; Wunderlich and Jungers 2009). One hypothesis is that if adaptive chondrogenesis is affecting growth and development of the carpus and metacarpus, then it would be expected for gorillas to have similarly sized carpometacarpal joints two through five, whereas chimpanzees would be expected to have smaller fifth carpometacarpal joints compared to joints two through four. An alternative hypothesis is that selection has increased the size of MC4 at the expense of MC5 in chimpanzees due to greater use of the former. Although the present study does not test the effects of pure genomics.

If this relationship between joint size and posture is found to exist, it will be used as further evidence that adaptive chondrogenesis is taking place at these locations (for it is already known that modeling affects the contouring of joints during early development [Carter and Beaupre 2001]). The supposition will then be extended that chondral modeling is affecting not only size of the joint but also the shape. The aim is to determine the etiology of wrist morphology (in the region of the hamate, metacarpal four, and metacarpal five) in order to clarify hominoid phylogeny. Characteristics included in the qualitative assessment are not intended to represent distinct adaptations (although some may be); rather, these features were selected by the author to exemplify shape that would illustrate capabilities of flexion, extension, adduction and abduction of the wrist. These data, applied to the fossil record, might further support one or more of the previously discussed hypotheses of pre-bipedal locomotion.

CHAPTER 2

Materials and Methods

Sample

Skeletal specimens used in this study were obtained through the Cleveland Museum of Natural History. The sample consisted of hominoids and cercopithecoids including: *Homo sapiens, Gorilla gorilla, Pan troglodytes, Pongo pygmaeus, Papio hamadryas, Papio cynocephalus,* and *Papio ursinus* (Total N=110). Specimens were chosen to represent a range of primate locomotion including different types of terrestrial quadrupedalism (e.g. *Pan, Gorilla,* and *Papio*) and brachiation/suspension (e.g. *Pongo*). The sample consisted of adult specimens of both sexes.

Table 1. Taxa and Sample Sizes

Taxa	**N**	**Male**	**Female**	**Unknown Sex**
Homo sapiens	31	15	16	0
Gorilla gorilla	33	19	11	3
Pan troglodytes	32	11	15	6
Pongo pygmaeus	8	1	3	4
Papio hamadryas	3	2	1	0
Papio cynocephalus	1	1	0	0
Papio ursinus	1	0	0	1
Total	**109**	**49**	**46**	**14**

Methods

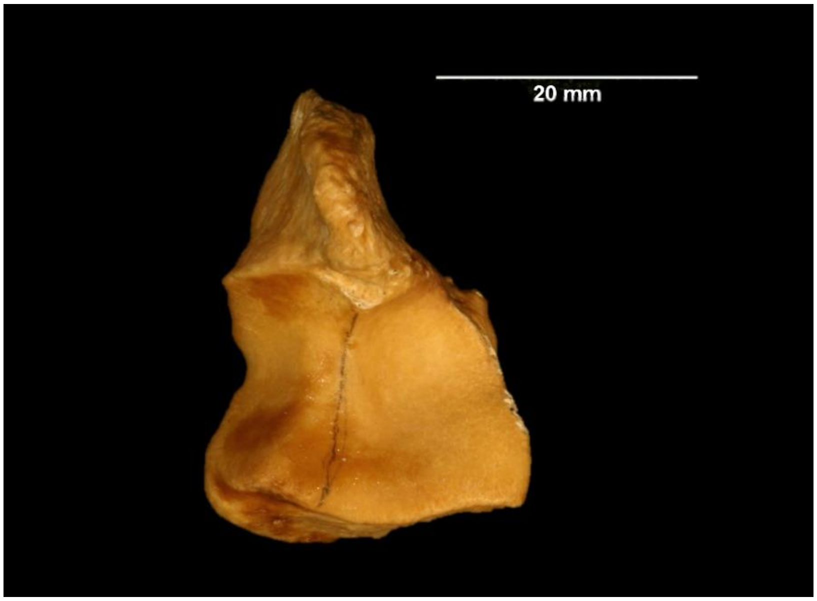
My quantitative and qualitative analyses targeted variation of shape and size of carpometacarpal joints four and five across the above genera to determine if variation in joint structure is developmentally related to patterns of use during growth. The sizes of the joint surfaces are considered in relation to known wrist postures in extant apes. The hypothesis tested here is that chimpanzees have smaller articular facets for the fifth metacarpal than the fourth on the hamate because they bear little/no weight on their fifth digit during knuckle-walking; in contrast, gorillas have relatively equal articular facets on their hamates because they typically distribute weight evenly across all four knuckles (Matarazzo 2013, Wunderlich and Jungers 2009). If this relationship is found to exist, it can be reasonably assumed that adaptive chondrogenesis is taking place at these locations, based on the central tenets of the chondral modeling theory. The supposition is then extended that chondral modeling is affecting not only the size of the joint but also its shape, representing an accurate reflection of how the joint was used during life. These data could potentially alter some of our current notions of hominoid phylogeny based on wrist morphology.

Measurements

Due to the irregular nature of the hamate joint surface shapes and heights, a rough measurement of joint size was obtained via 2-dimensional imaging. Each hamate was manually articulated with the fifth metacarpal of the same individual using maximum joint congruence in full extension of the joint as a guide. A pencil line was drawn across the joint surface indicating the termination of the articulation between the hamate and fifth metacarpal. The same procedure was then repeated with the fourth metacarpal. The purpose of repeating the process twice, once with each metacarpal, was to ensure the accuracy of the placement of the line. Other lines were drawn on the hamate, as needed, where other joint margins were ambiguous in the photographs. These specimens were then photographed a second time.

Once an accurate line was drawn demarcating the separate joint surfaces, the hamate was then placed in a box of black sand. Photographs were taken normal to the joint surface. Figure 3 demonstrates the type of photographs used. Photographs were scaled and measured using ImageJ software (version 1.48v). Articular surface areas for carpometacarpal joints four and five were traced and measured both independently and combined. The purpose of measuring the total articular surface area of the hamate and each facet independently was to calculate researcher error. Average error for the entire sample was 0.77 mm^2, and this was deemed acceptable. Individual specimens yielding >2mm error were measured a second time. A ratio of articular surface areas (MC5:MC4) was calculated in order assess the size of the fifth metacarpal facet in relation to the fourth, regardless of the overall size of the hamate.

Figure 3. Male *Gorilla gorilla* Hamate, Left



Qualitative Assessment

Shape and orientation of articular surfaces can be used to determine the range of motion a joint engages during life. Due to the irregular shape and variable surface topography of the carpometacarpal joints in question, the current study utilizes a qualitative assessment of joint anatomy to determine patterns of use. Different characteristics of the hamate, metacarpal IV and metacarpal V analyzed here were defined in the literature or by the current author in the context of their relationship to wrist mobility and/or stability.

The distal row of carpal bones in African apes is said to display keeling which, in the hamate, separates the facets for the fourth and fifth metacarpals (Kivell and Schmitt 2009; Marzke 1983; Richmond et al. 2001). Keeling is claimed to be present in all African apes and also in some fossil hominids (Richmond et al. 2001). It is argued that this hamate morphology, as well as the reciprocal notches on the fourth and fifth metacarpals, "contribute to a transversely 'jagged' carpometacarpal joint that is probably related to resistance to movement at these joints, such as would be generated during the stance phase of knuckle-walking" (Richmond et al. 2001:94).

In contrast, the human hamate lacks keeling morphology, and consequently permits more flexion/extension of the carpometacarpal joints four and five. CMC5 is the most mobile of the human carpometacarpal joints (dependent on the mobility of MC4) (Buffi et al. 2013; El-shennawy et al. 2001; Kapandji 2007; Selby et al. 2016). The articular facet for the fifth metacarpal is saddle shaped, permitting roughly 25 degrees of palmarflexion and dorsiflexion (Kapandji 2007; Nakamura et al. 2001). This shape also facilitates the rotation of MC5 about it's long axis during opposition of the fifth ray, as would be employed during a variety of human grips (Buffi et al. 2013; El-shennawy et al. 2001; Marzke 1983; McHenry 1983; Ward et al.

1999). Any motion greater than 15 degrees at MC4 or 30 degrees at MC5 is restricted by the soft tissues (El-shennawy et al. 2001; Nakamura et al. 2001). In the case of the fifth carpometacarpal joint, “the intermetacarpal ligaments tether the proximal portion of the metacarpals to one another and act as important stabilizers of the hamatemetacarpal joint” (El-shennawy et al. 2001:1034). African apes are not capable of this degree of mobility at this location (Marzke 1983; McHenry 1983). Other palmigrade anthropoids, either terrestrial or arboreal, also lack keeling and have more mobile, saddle-shaped hamate facets, enabling conformation of the hand to variable terrain (Selby et al. 2016).

Additionally, length and orientation of the hamulus are argued to limit flexion and extension (Marzke 1983; Ward et al. 1999). In African apes, the hamulus is long and projects distally, intensifying the action of the flexor carpi ulnaris, and thus strengthening adduction capabilities (Marzke 1983; Ward et al. 1999). Although in humans, the hamulus projects palmarly suppressing adduction capabilities of the flexor carpi ulnaris, but facilitating its action as a wrist flexor (Ward et al. 1999). Furthermore, in apes, the basal articular surface of the fifth metacarpal extends palmarly, and this articulates with the base of the hamulus, limiting mobility (Marzke 1983). Conversely, in humans, neither the fifth nor the fourth metacarpal articulate with the hamulus (Ward et al. 1999).

Lack of articulation between MC4 and the capitate is also considered to be a stabilizing mechanism by preventing side to side dislocation of the metacarpals during support phase of knuckle-walking (Marzke et al. 1994). Marzke et al. (1994) found that in 100% of a sample of chimpanzees, the fourth metacarpal did not articulate at all with the capitate, and this was due to the more distal orientation of the hamate’s articular surface. Articulations for MC4 and MC5 on the hamate project more distally than articulations for MC2 and MC3 on the capitate, contributing to the “jagged” distal carpal row. In humans, the distal carpal row is even and the degree of articulation between MC4 and the capitate is variable (El-shennawy et al. 2001). Marzke et al. (1994) found that gorillas also had varying degrees of articulation between MC4 and the capitate, and hypothesized that this is because gorillas typically use one more support than chimpanzees, and their wrists are therefore more stable and lack the need for a jagged carpal row.

In addition to these traits, the current author defines corresponding morphological features on the fourth and fifth metacarpal bases. Characteristics included in the following qualitative assessment are not intended to represent distinct adaptations. It may be the case that specifics of the morphology described here are of any Trait Type discussed in section 1.3. These features were selected by the author to exemplify shape that would illustrate capabilities of flexion and extension of the wrist. The following characteristics and their abbreviations are also listed and described in more detail in Table 2.

Morphological features of the hamate analyzed in this study include shape of the facet for the fifth metacarpal (HAML), robusticity of the hamulus (HAMROB), and the degree to which the metacarpals articulate with the hamulus (HAMART). Morphological features of the metacarpals include: degree of articulation between the fourth metacarpal and the capitate (MC4CAP), topographical variation of the joint surface on the base of the fourth metacarpal (MC4TOP), dorsopalmar curvature of the MC5 base (MC5DPC), mediolateral height variation on the joint surface of the fifth metacarpal (MC5RUG), and the extent to which the joint surface extends onto the dorsal aspect of the base of MC5 (MC5RIG).

The specimens were then graded on a 1-5 scale for each of the characteristics described. Some characters were graded on smaller scales (i.e. 1-3) because they did not display sufficient variation among or within species to warrant five distinct grades. Some specimens have missing values for some characters because they fell outside the “normal” range of variation for that character. Low grades are indicative of primitive morphology, i.e. any characteristics associated with flexible carpometacarpal joints as seen in most monkey taxa (Selby et al. 2016). Conversely, high grades are indicative of derived morphology, i.e. characteristics that increase, “structural integrity during vertical climbing and true (i.e., habitual reliance upon) suspension as well as dissipating bone contact forces that occur during these forms of locomotion” (Selby et al 2016:585). Upon examination of the entire sample, archetypal specimens were chosen to represent each of the grades for every character. Photographs of the archetypal specimens representing each grade of all morphological characters are provided in Figures 4-11. Each photograph is numbered according to the grade it represents.

Statistical Analyses

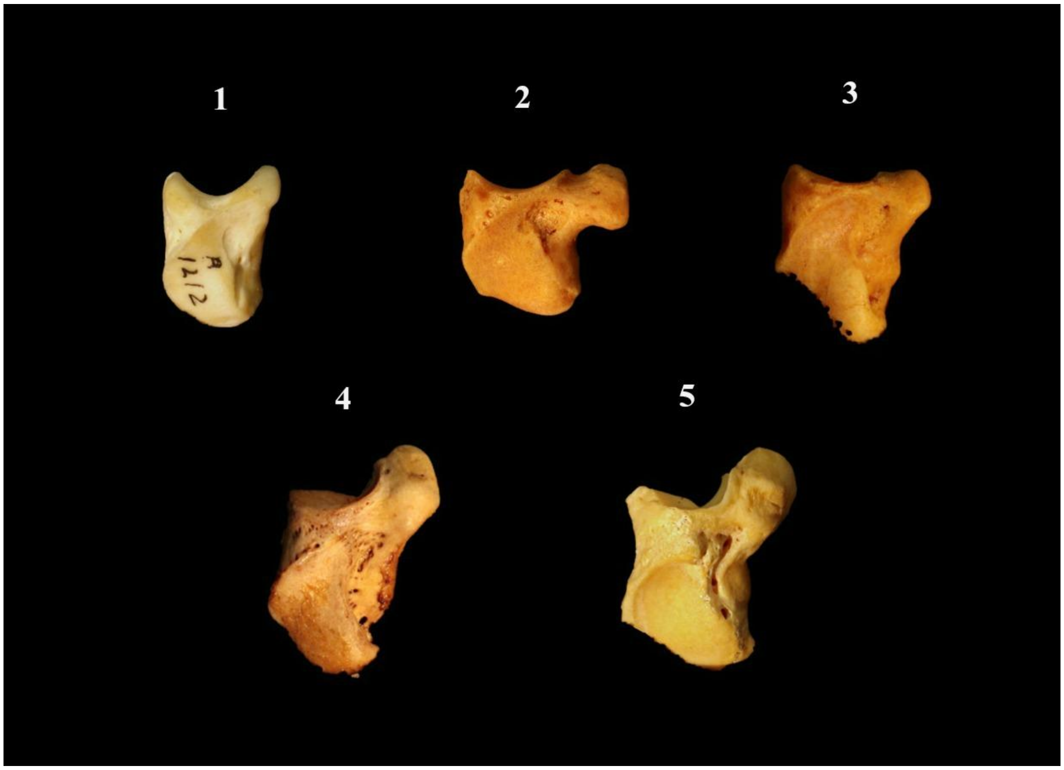
Hamate facet size differences were evaluated using Students t-tests. A principal components analysis (PCA) was used to extract significant sources of variation from the shape variables. All statistics were performed using SPSS software, version 22.

Table 2. Shape Characters

Abbreviation	Description
HAML	Shape of the facet for the fifth metacarpal; Saddle shaped (1) (i.e. simultaneously dorsoventrally convex and mediolaterally concave), versus "L" shaped (5).
HAMROB	Robusticity of the hamulus. Slight (1) versus very robust (4).
HAMART	Articulation between the hamulus and the fifth metacarpal. No articulation (1) versus significant articulation (3).
MC4CAP	Articulation between the fourth metacarpal and the capitate (1) versus no articulation (3).
MC4TOP	Topographical variation in height of the proximal joint surface of the fourth metacarpal. Some specimens are smooth (1), whereas others are characterized by a central concavity, or depression (3).
MC5DPC	Dorsopalmar curvature of the proximal joint surface of the fifth metacarpal. Some specimens show extreme dorsopalmar convexity (1), whereas others are planar (5).
MC5RUG	Mediolateral rugosity of the basal articular surface of MC5. Some specimens are flat (1), whereas others are characterized by a central valley running dorsopalmarly, resulting in medial and lateral ridges (4). Note: pronounced rugosity accompanies the keel on the hamate, running dorsopalmarly.
MC5RIG	Rigidity of the fifth carpometacarpal joint. Some specimens had significant extension of the joint surface onto the dorsal aspect of the metacarpal base (1), indicating flexion capabilities, whereas others had no extension of the joint surface (5).

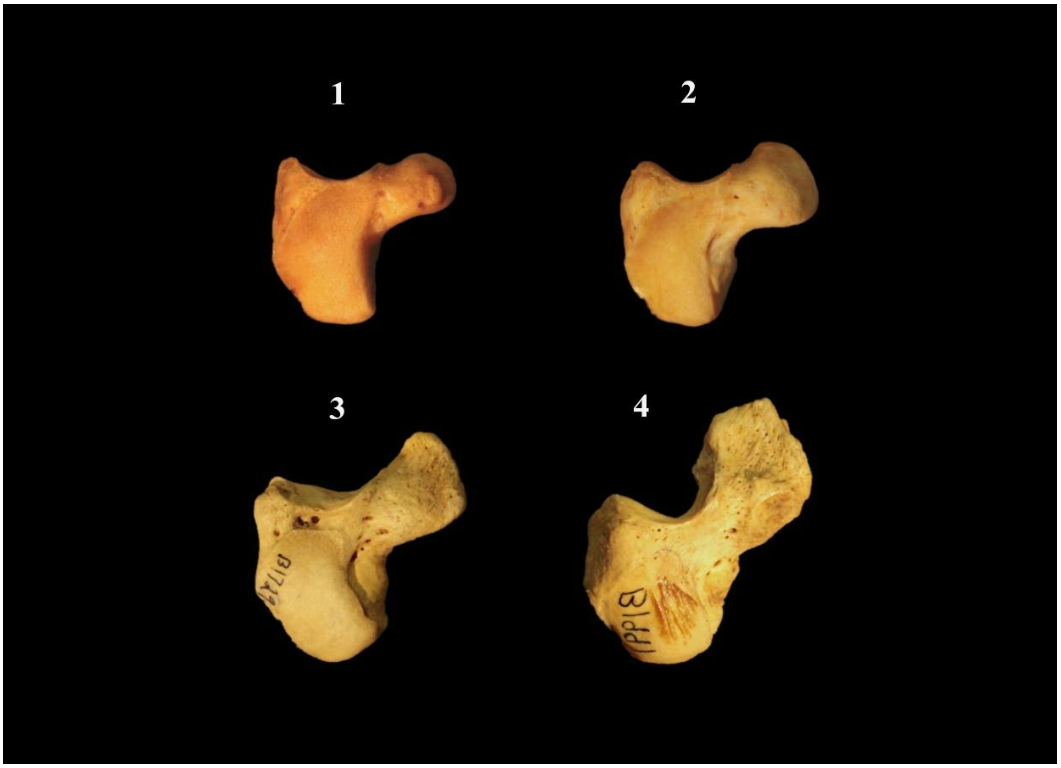
* The numbers in parentheses indicate which grade was assigned to each character description.

Figure 4. Archetypal Specimens for Variable HAML



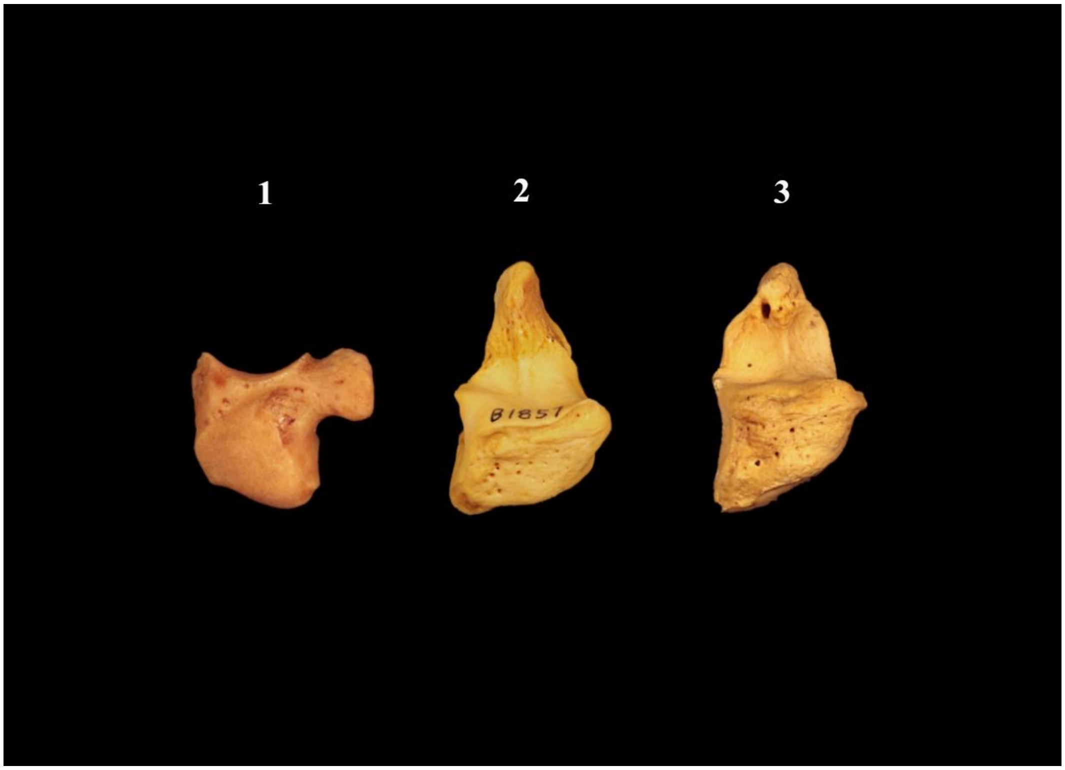
Right hamates, medial sides. Top row, left to right: *Papio cynocephalus*, *Homo sapiens*, *Homo sapiens*. Bottom row, left to right: *Pan troglodytes*, *Pan troglodytes*. Numbers indicate grades assigned to each specimen.

Figure 5. Archetypal Specimens for Variable HAMROB



Right hamates, medial sides. Top row, left to right: *Homo sapiens*, *Homo sapiens*. Bottom row, left to right: *Gorilla gorilla*, *Gorilla gorilla.*

Figure 6. Archetypal Specimens for Variable HAMART

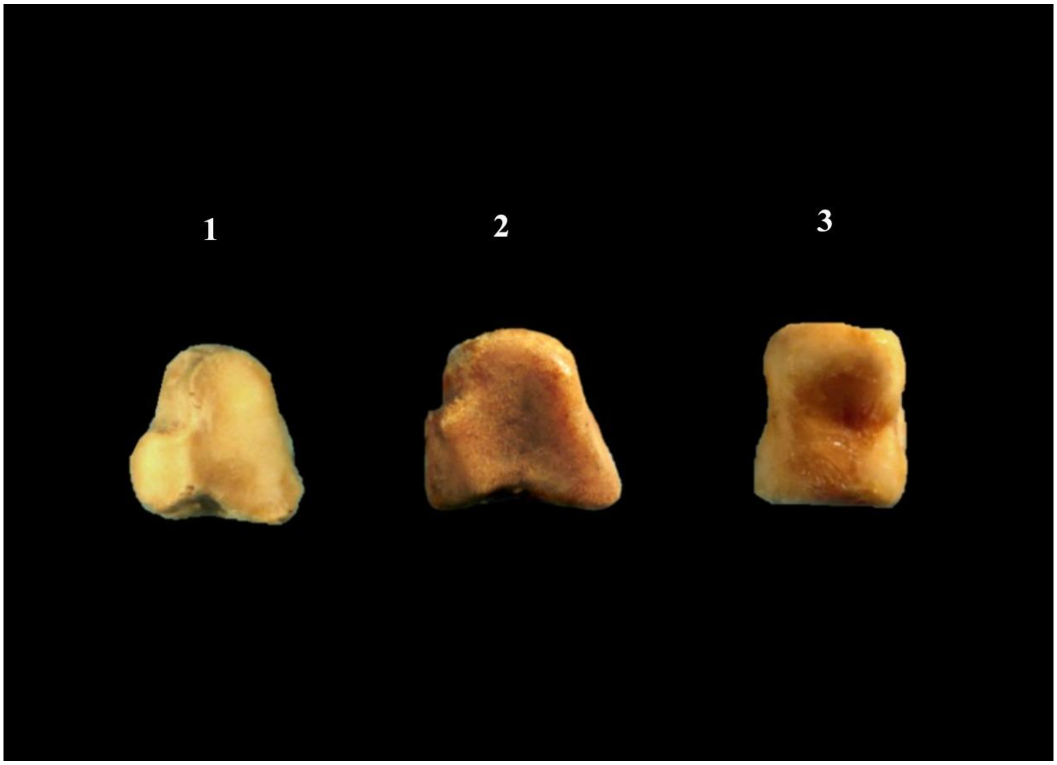


Left: right hamate, medial view, *Homo* sapiens, representing grade 1. Middle and right: Right hamates, dorsal view, both *Gorilla gorilla*, representing grades 2-3.

Figure 7. Archetypal Specimens for Variable MC4CAP

Right hand, carpometacarpal joints 4 and 5. Left to right: *Homo sapiens, Pan troglodytes, Pan troglodytes.*

Figure 8. Archetypal Specimens for Variable MC4TOP



Left, fourth metacarpals, inferior view. Left to right: *Homo sapiens, Gorilla gorilla, Pan troglodytes*.

Figure 9. Archetypal Specimens for Variable MC5DPC

Fifth metacarpals, lateral side. From top to bottom: *Papio ursinus*, *Homo sapiens*, *Homo sapiens, Gorilla gorilla, Pan troglodytes.*

Figure 10. Archetypal Specimens for Variable MC5RUG

Fifth metacarpals, dorsal view. Left to right: *Gorilla gorilla*, *Pan troglodytes*, *Homo sapiens, Gorilla gorilla.*

Figure 11. Archetypal Specimens for Variable MC5RIG

Fifth metacarpals, dorsal view. Left to right: *Papio cynocephalus*, *Homo sapiens, Homo sapiens, Pan troglodytes, Pan troglodytes.*

CHAPTER 3

Results

Hamate Articular Facet Size

Manual pressure applied to digit four is constant across all quadrupedal genera examined; the use of the fifth digit is variable. Consequently, a ratio of the articular facets (MC5:MC4) was taken to assess the size of the fifth metacarpal facet in relation to the fourth, in order to observe any changes in response to differences of body size, locomotion or phylogeny. Averages and standard deviations are listed in Table 3. Student's t-tests were conducted between all genera, and the results are summarized in Table 4. There are no significant differences of the hamate facet ratio between sexes of any genus.

Table 3. MC5/MC4 Ratio Averages and Standard Deviations

	Mean	Standard Deviation
Homo	1.21	0.20
Gorilla	0.84	0.14
Pan	0.71	0.10
Papio	0.69	0.17
Pongo	0.89	0.20

The MC5 facet is larger than the MC4 facet in 87% of the Homo sample, with an average ratio of 1.21 (SD=0.20), which is significantly different ($p<.001$, $\alpha=.05$) than all other genera. The Gorilla ratio is significantly larger than both Pan and Papio, but not significantly larger than Pongo. Conversely, Pan ratios are statistically similar to Papio, but they are smaller than Pongo. Papio and Pongo do not differ from each other; however it should be noted that sample sizes for these genera are small (see Table 2).

Table 4. MC5/MC4 Ratio T-Test Results

$\alpha=.05$	*Homo*	*Gorilla*	*Pan*	*Papio*	*Pongo*
Homo		***	***	***	***
Gorilla	***		***	*	-
Pan	***	***		-	*
Papio	***	*	-		-
Pongo	***	-	*	-	

- = not significant, *p<.05, **p<.01, ***p<.001

Figure 12 plots the MC5/MC4 ratio against the hamate's total articular surface, using the combined facet size as a rough correlate for body size. According to this figure, there is no ascending linear relationship between the facet ratio and combined facet size; therefore variation in hamate facet ratios is unaffected by body size.

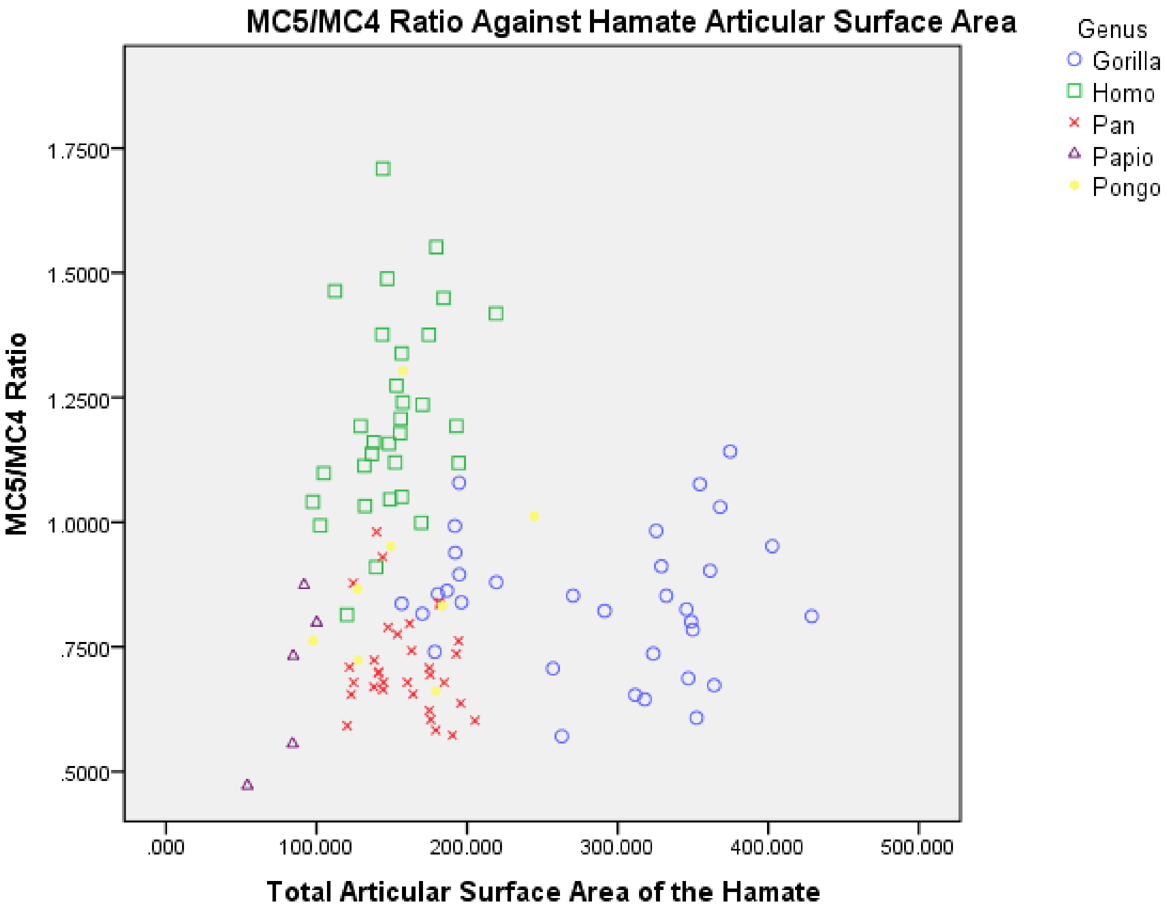
This metric distinguishes *Homo* from cercopithecoids and other hominoids. It differentiates between types of knuckle-walking (*Pan* v. *Gorilla*), but does not fully differentiate between knuckle-walking and terrestrial palmigrade locomotion (*Gorilla* and *Papio* are significantly different, but not *Pan* and *Papio*). Only *Homo* and *Pan* differ significantly from brachiating/fist-walking (*Pongo*). Although the t-tests yield significant results among most groups, measures of association are low to moderate between all genera, excluding pairs involving *Homo*. Strength of association coefficients are given in Table 5. Therefore, while group means are significantly different, the effect size is small. This discrepancy is likely an effect of the large sample sizes of *Homo, Pan,* and *Gorilla*.

Table 5. Strength of Association*

	Homo	*Gorilla*	*Pan*	*Papio*	*Pongo*
Homo		2.16	2.74	2.94	1.61
Gorilla	2.16		1.05	1.09	-
Pan	2.74	1.05		-	1.40
Papio	2.94	1.09	-		-
Pongo	1.61	-	1.40	-	

* d = $\frac{|\bar{x}-\bar{y}|}{\sqrt{Sp^2}}$

Figure 12. Facet Ratios



Carpometacarpal Joint Shape Analysis

A principal components analysis (PCA) was conducted on the shape character scores. A Varimax rotation was performed in order to maximize the expression of a few variables, and simplify each component's description. Component loadings are listed in Table 5. Averages and standard deviations of factor scores for each genus are listed in Table 6. *Papio* and most *Pongo* were excluded from the PCA. *Papio* received no scores for variables HAMART and HAMROB, as they have no true hamulus. *Pongo* was almost entirely excluded as they had missing values because 1) the morphology fell outside the "normal" range of variation examined in this study, and 2) some specimens had missing or broken bones. In the absence of factor scores, averages and standard deviations of individual trait scores are provided in Tables 7 and 8, detailed descriptions of these specimens are provided in the Appendix, and an analysis of the morphology is given in Chapter 4.

The first component accounts for 34.5% of the variation within the sample. Component 1 loads most heavily on variables MC5DPC, HAML, and MC5RIG, and can be defined as mobility of CMC5. Individuals scoring high on Component 1 are characterized by planar MC5 bases, no extension of the joint surface onto the dorsum of the base, and corresponding "L" shaped hamate facets. Therefore, individuals scoring high on Component 1 have little/no mobility at the fifth carpometacarpal joint. Specimens with a negative score have more mobile joints, and are characterized by dorsopalmarly curved MC5 bases, with the joint surface extending onto the dorsum, and saddle-shaped hamate facets. *Homo* scores the lowest on Component 1 (mean= -0.42, SD=0.42); *Pan* has the highest average score (mean=0.89, SD=0.55); *Gorilla* scores intermediate, and also with the highest standard deviation (mean= -0.16, SD=1.06). According to Figure 3.2, *Gorilla* factor scores span the entire primate sample, occupying both extremes of the continuum.

Table 6. Component Loadings

	1	2	3
Percent of Variance	34.51%	32.28%	13.15%
HAML	.865	.294	.036
HAMROB	.393	.819	.109
HAMART	.348	.853	.111
MC4CAP	.120	.765	-.191
MC4TOP	.522	.603	.137
MC5DPC	.898	.220	-.065
MC5RUG	.034	.005	.979
MC5RIG	.801	.318	.097

Component 2 accounts for roughly 32% of the variation within the sample. This component loads most heavily on variables HAMART and HAMROB. The second highest loadings are MC4CAP and MC4TOP. This component can be defined as both hamulus morphology and mobility of MC4. A high factor score for this component indicates a robust hamulus that extends distally and articulates with the fifth metacarpal base, no articulation between MC4 and the capitate (although this variable is not a direct indication of a jagged distal carpal row), and topographical complexity of the proximal joint surface of MC4. As expected, *Homo* scores the lowest (mean= -1.33, SD=0.38); *Pan* (mean=0.51, SD=0.46) and *Gorilla* (mean=0.55, SD=0.69) score similarly to each other, but again, *Gorilla* is the most variable.

Component 3 is strictly related to the variable MC5RUG, as all other loadings are negligible, and accounts for 13% of the variation. *Gorilla* scores the highest on Component 3 (mean=0.74) but, again, has the highest standard deviation (SD=1.18) and factor scores span almost the entire sample (Figure 3.3). *Pan* has the lowest scores for Component 3 (mean= -.51, SD=0.79). Their MC5 bases are angled ulnarly, but the joint surfaces themselves are mostly flat. *Homo* scores intermediate (mean= -.025, SD=0.73), as they have slight mediolateral rugosity of the MC5 base.

Component 1 discriminates between humans and chimpanzees, but gorillas span the entire sample. Some *Gorilla* CMC5 joints are planar, whereas few score within the *Homo* range of Component 1. The two *Pongo* included in the PCA fall within *Pan/Gorilla* range. African and Asian apes have larger hamuli than humans, and this is relayed by Component 2 factor scores plotted in Figures 13 and 15. Component 3, when plotted, does not clearly distinguish between genera or locomotion; although it does separate some gorillas, who are suspected to display extreme rugosity accompanied by marked "keeling" of the hamate.

Table 7. Factor Scores: Averages and Standard Deviations

	Comp 1	Comp 2	Comp 3	
Homo	-0.41755	-1.32719	-0.25452	Average
	0.41872286	0.38034498	0.73464149	SD
Gorilla	-0.16186	0.54586	0.74448	Average
	1.05598498	0.69280301	1.17611984	SD
Pan	0.89338	0.51213	-0.50512	Average
	0.54564027	0.45922288	0.78658276	SD
*Papio**	Insufficient Data			
*Pongo**	Insufficient Data			

* *Papio* and *Pongo* were almost entirely excluded from the PCA due to missing values. Trait scores, averages and standard deviations are listed in Tables 3.5 and 3.6. Detailed descriptions of morphology are provided in the Appendix.

Figure 13. PCA:Components 1 and 2 Factor Scores

Figure 14. PCA: Components 1 and 3 Factor Scores

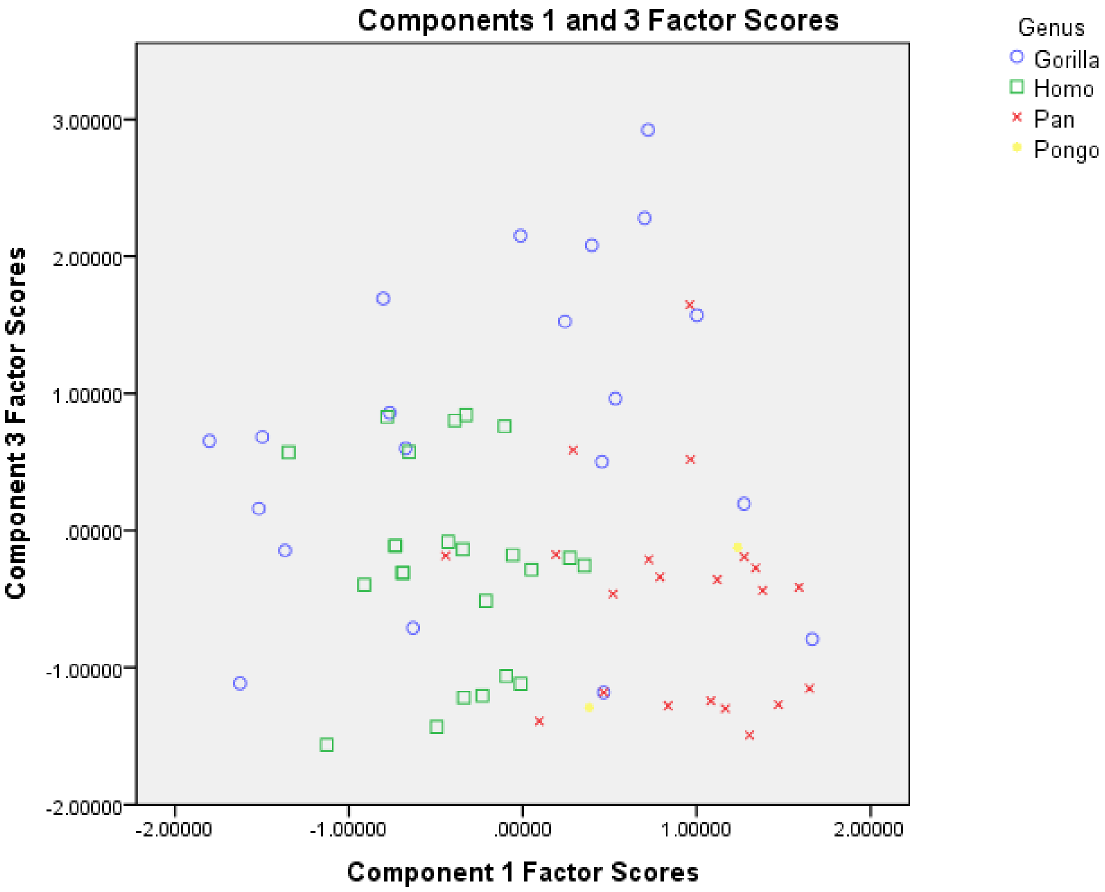


Figure 15. PCA: Components 2 and 3 Factor Scores

Table 8. *Papio* Averages and Standard Deviations

	HAML	HAMROB	HAMART	MC4CAP	MC4TOP	MC5DPC	MC5RUG	MC5RIG
Mean	1	-	-	2	1.4	1	1.8	1
SD	0	-	-	0.71	0.55	0	0.84	0

Table 9. *Pongo* Averages and Standard Deviations

	HAML	HAMROB	HAMART	MC4CAP	MC4TOP	MC5DPC	MC5RUG	MC5RIG
Mean	3.25	3.43	2.5	2.33	2.43	3.71	1.6	3.57
SD	1.39	1.13	0.53	0.82	0.79	1.25	0.89	0.98

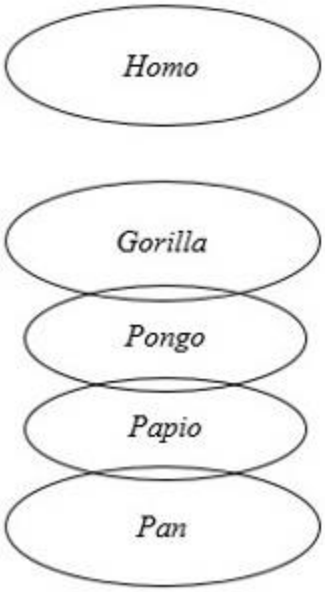
CHAPTER 4

Discussion, Conclusions and Further Research

Discussion: Hamate Facet Ratios

The t-test results indicate that there are no significant differences of hamate facet ratios between sexes of any genus. Therefore, this metric is not likely affected by sex-related body size differences. *Homo* is the only genus that is significantly different (larger) than all others. In addition to *Homo*, *Gorilla* is significantly different (larger) than both *Pan* and *Papio*. Only *Homo* and *Pan* differ significantly from *Pongo*. Figure 16 provides a visual summary of the t-test results. Again, it is noted that the effect size is small to moderate between all genera, excluding *Homo*.

Figure 16. Facet Ratio Visual Aid



Homo is distinguished from all others because it is the only genus in which the fifth metacarpal facet is consistently larger than the fourth (87% of the sample displayed larger MC5 facets). One possible explanation for this derivative morphology is a response to unique human gripping capabilities. Metacarpal two and, to a lesser degree, metacarpal three are relatively fixed and provide a stable central axis around which metacarpals four and five can rotate (El-shennawy 2001). Metacarpal five rotates more than metacarpal four because it is further away from the central axis of the hand. Greater rotation of the base requires more space (mediolaterally) on the opposing joint surface in order to achieve this motion (El-shennawy et al. 2001; Kapandji 2007).

Based on postural data and weight distribution patterns recorded by Matarazzo (2013) and Wunderlich and Jungers (2009), *Pan* and *Gorilla* exhibit the expected differences between facet ratios ($p<.001$ at $\alpha=.05$), although the effect size is small ($d=1.05$). On average, *Gorilla* have a larger fifth metacarpal facet (when compared to the fourth) than *Pan*. One likely explanation for this distinction is differential cartilage growth in response to greater mechanical stress experienced at the location of the *Gorilla* CMC5 than *Pan* CMC5, due to the fact that gorillas typically distribute weight across all four knuckles, whereas chimpanzees typically utilize knuckles 2-4. Inouye (1994) suggests that the more robust (albeit shorter) fifth metacarpal in *Gorilla* compared to *Pan* could be an adaptation to reduce the increased bending stresses experienced as a result of a larger body size in the former; however, genomics are not tested in the present study.

Papio is primarily terrestrial, and adopts a digitigrade posture when walking, but becomes more palmigrade when traveling at higher speeds (Patel and Wunderlich 2010). Baboons flex their proximal interphalangeal joints while extending the metacarpophalangeal joints. Regardless of speed, the distal phalanges always make first contact with the substrate, and the heads of metacarpals II-V make contact thereafter. During digitigrade walking, the highest pressure is distributed across digits three and four, with peak pressure culminating specifically near the head of metacarpal four (see Figure 17). During palmigrade running, pressure is distributed across the distal metacarpus, with peak pressure culminating at the medial and lateral areas. Pressure decreases proximally. In the current study, *Papio* had the lowest average MC5:MC4 ratio, and overall, fell within the *Pan* range. These data coupled with pressure distribution data from Patel and Wunderlich (2010) are not entirely conducive of the hypothesis that carpometacarpal joint size is affected by chondral modeling. Although, cartilage growth is unresponsive to infrequent loadings, ergo it is possible that facet size in *Papio* is a reflection of weight distribution patterns experienced while walking, if walking is performed more frequently than running.

Figure 17. Peak Pressure Distribution Patterns in *Papio* (Patel & Wunderlich 2010)

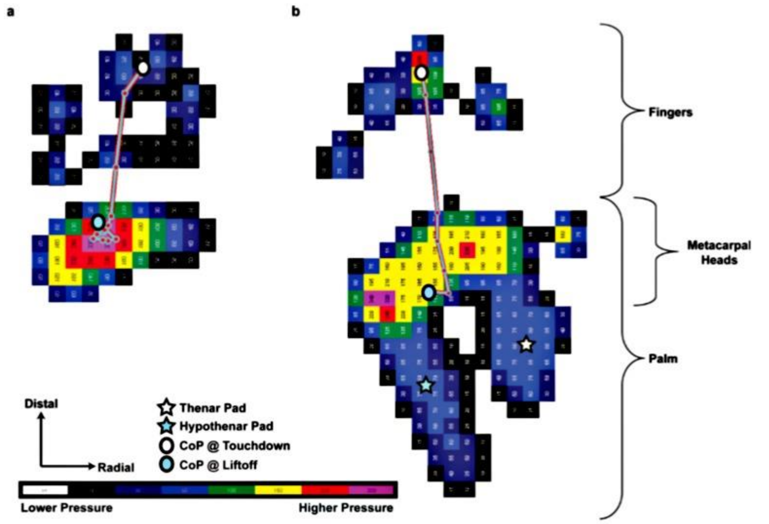


Fig. 2. Representative pressure diagrams illustrating peak pressure over one entire step. **a**) Slow female baboon (2.1 m/s) using a digitigrade hand posture. **b**) Fast male baboon (4.0 m/s) using a palmigrade-like hand posture. At slow speeds, peak pressures are located under the metacarpal heads of the palm. At fast speeds, peak pressures are located under the metacarpal heads of the palm, but contact area also increases to include the thenar and hypothenar regions of the palm. Across all speeds, peak pressure is greater in the palm region compared to the finger region. Also across all speeds, there is minimal contact between the ground and the area underlying the proximal interphalangeal joint (i.e., white space between the finger and palm regions). Center of pressure (CoP) migrates from the fingertips at touchdown to the metacarpal heads at lift-off across all speeds.

Pongo is a facultative terrestrial quadruped that uses a variety of postures when traveling on the ground. In the absence of pressure distribution data similar to that from Patel and Wunderlich (2010) and Wunderlich and Jungers (2009), behavioral observations provide the only evidence for locomotor patterns of orangutans. Tuttle (1969) observed that *Pongo* uses a range of terrestrial locomotor postures, from fist-walking (with weight borne on the dorsal aspect of the proximal phalanges) to palmigrade locomotion (as cited in Susman 1974). Although Susman's (1974) study of orangutan locomotion found that they rarely use palmigrade postures. In addition to fist walking, they also occasionally knuckle-walk, and when doing so, Susman (1974) reports that they bear weight on intermediate phalanges II-V. In the present study, *Pongo* facet ratios and standard deviations (mean = 0.86; SD = 0.14) are very similar to *Gorilla* (mean = 0.84; SD = 0.14). If chondral modeling is affecting joint size, one possible explanation for this likeness is due similar weight distribution patterns when travelling terrestrially. Although, it should be reiterated that orangutans are primarily arboreal, and thus facet ratios are not likely affected by infrequent terrestrial excursions (Ashbury 2015; Loken et al. 2013; Manduell et al. 2011). To render the chondral modeling hypothesis applicable, inter-joint stress during brachiation and other arboreal travel would need to be evaluated.

The results of the tested hypothesis, that hamate facet size is affected by differential cartilage growth in response to mechanical forces, are inconclusive. *Homo* is substantially different from all other tested genera, but there are small to moderate differences of means between *Gorilla, Pan, Pongo* and *Papio*. Patel and Wunderlich (2010) found that in the hands of *Papio anubis*, pressure is highest near the fourth metacarpal head during digitigrade walking; although during palmigrade running, pressure is distributed more evenly across the distal metacarpus. In the absence of manual pressure distribution data for fist-walking, it is uncertain whether comparable facet ratios between *Gorilla* and *Pongo* are related to ground reaction forces similar in orientation and magnitude. Also, terrestrial quadrupedalism is facultative, not obligatory, for orangutans. Thus, the pressure distributions during such behavior may not warrant an adaptive chondrogenic response, as infrequent loadings are not recorded (Frost 1979, 1994, 1999). Even if joint size is genetically constrained (Lieberman et al. 2001), joint geometry can still be affected by chondral modeling (Carter and Beaupre 2001; Hammond et al. 2010, Lieberman et al. 2001). The adaptive response of growing cartilage, "may depend on joint type and mobility requirements, and include adaptive shape changes rather than global increases in size." (Hammond et al. 2010:667). In the case of the carpal bones, "the shape of each bone is moulded by its movements, which are directed by the interosseous ligaments" (Kapandji 2007:176).

Discussion: Carpometacarpal Shape Analysis

Component 1 is defined as mobility of the fifth carpometacarpal joint, with high factor scores attributed to less flexible joints and low scores attributed to mobile joints. Component 2 is characterized by restrictive hamulus morphology and rigidity of the fourth carpometacarpal joint. Component 3 loads solely on variable MC5RUG, and is defined as mediolateral rugosity of the MC5 proximal joint surface. Together, the variables discussed heretofore are intended to give an indication of the degree of mobility of carpometacarpal joints four and five; and the subsequent component loadings and factor scores convey the distribution of this morphology among extant hominoids.

Homo has the lowest average factor score for Component 1 (mean= -0.42). They have saddle-shaped hamate facets and fifth metacarpal bases that are dorsopalmarly curved, with extension of the joint surface onto the dorsal aspect of the base, an indication of flexion-extension capabilities. *Homo* also has the lowest average score for Component 2 (mean= -1.33), indicating that they have slight hamuli that do not articulate with the metacarpals, also enabling movement of the metacarpals. They have varying degrees of articulation between MC4 and the capitate (although it should be noted that lack of articulation between the two is not directly indicative of a jagged distal carpal row), and the base of MC4 is smooth. *Homo* scores intermediate to *Pan* and *Gorilla* on Component 3 (although still negatively). They have slight mediolateral concavity of the fifth metacarpal proximal joint surface. This mediolateral concavity coupled with the dorsopalmar curvature creates a saddle-shaped MC5 base that articulates opposite the saddle-shaped hamate facet. The inverse saddle morphology of the fifth carpometacarpal joint facilitates the rotation of MC5 about it's long axis (Kapandji 2007). These findings are congruent with what is cited in the literature. Humans maintain flexible wrists. Specifically metacarpals IV and V are the most mobile of the medial metacarpals (El-shennawy 2001).

The *Gorilla* sample is the most diverse. They have the highest standard deviations for all components. Some individuals displayed planar MC5 bases and corresponding "L" shaped hamate morphology, whereas others had dorsopalmar curvature of the MC5 base, with the joint surface extending dorsally, and slight saddling of the hamate. However, overall, they maintain large hamuli (averages for HAMART and HAMROB are high), a condition characteristic of the African great apes. *Gorilla* scores highest on Component 3, but again, with the highest standard deviation. Some individuals display extreme mediolateral rugosity of the MC5 joint surface, which is accompanied by pronounced keeling of the hamate. Unlike the slight mediolateral concavity of the human MC5, the interlocking of this morphology with the keeled hamate in *Gorilla* indicates no possible rotation of the MC5 about it's long axis.

Pan scores the highest on Component 1, compared to *Homo* and *Gorilla*, indicating that they have planar CMC5 joints with little or no flexion/extension capabilities at this location. They score similarly to *Gorilla* on Component 2 (although they were not as variable as *Gorilla*) indicating that they have robust hamuli that articulate with the fifth metacarpal; again, limiting flexion and extension. *Pan* scores lowest on Component 3, signifying their mediolaterally flat MC5 bases.

The *Papio* specimens exhibit somewhat uniform morphology. All individuals display extreme dorsopalmar curvature and MC5 joint surface extension, accompanied by hook-shaped hamate facets, enabling a high degree of dorsiflexion. Some specimens had slight mediolateral rugosity, but the genus average was still low for variable MC5RUG (mean=1.8). There is little/no topographical variation of the joint surface of MC4, and scores for MC4CAP are variable. Although joint surface extension of MC5 has been the subject of this analysis, it should be noted that *Papio* specimens also have joint surface extension of MC4, again indicating mobility of the carpometacarpal joints.

Pongo specimens are much more diverse. A small sample size may exaggerate variation; however, given a larger sample, I hypothesize that *Pongo* will be similar to *Gorilla* in degree of variation. Some specimens have planar MC5 bases (dorsopalmarly), whereas few others have some curvature. The accompanying hamate facets are also variable. Some individuals have a deep, wide groove running mediolaterally on the palmar aspect of the hamate facet. Dorsally, the joint surfaces are markedly convex, creating a “shelf-like” appearance. Other *Pongo* hamate facets are smooth and condyloid. The hamuli are not as robust as the African apes, yet *Pongo* has high averages for variables HAMART and MC4TOP, and varying degrees of articulation between MC4 and the capitate. They display little/no mediolateral rugosity of MC5. The two *Pongo* specimens that receive factor scores fall within the *Pan*/*Gorilla* range for Components 1 and 2, and within the *Pan* range of Component 3.

Fossil Anthropoid Metacarpals and Hamates

The hand of *Ardipithecus ramidus* represents the oldest hominid carpus and metacarpus found to date. Overall, the metacarpals are short and lack knuckle-walking grooves on the heads (Lovejoy et al. 2009). The base of the fifth metacarpal is dorsopalmarly curved, and the joint surface extends onto the dorsal aspect of the base, unlike the "planar" bases of *Pan troglodytes* and, in the case of this study, some *Gorilla gorilla* (Lovejoy et al. 2009). The basal joint extension is similar to the condition observed in *Australopithecus afarensis, Homo sapiens,* and *Papio* (Lovejoy et al. 2009). There appears to be no mediolateral rugosity of the joint surface. Several fifth metacarpals attributed to *Australopithecus afarensis* have proximal articular facets that also display varying degrees of dorsopalmar convexity (Bush et al. 1982). Some specimens exhibit mediolateral concavity (Bush et al. 1982). Based on descriptions provided in the literature, the MC5 basal morphologies of *Ar. ramidus* and *Au. afarensis* are similar, not only to each other, but also to what was observed in *Homo* and *Papio* specimens examined in the present study. The dorsopalmar convexity of the base coupled with dorsal extension of the joint surface is indicative of a mobile fifth carpometacarpal joint.

The distal hamate facet of *Ar. ramidus* lacks the distopalmar angulation that is common in great apes, which is further evidence that it retained mobility at these joints (Lovejoy et al. 2009). The fifth metacarpal facet on the hamate of *Au. afarensis* is ovoid and dorsopalmarly concave (Bush et al. 1982). The fourth metacarpal facet is larger, and is palmarly concave and dorsally convex (Bush et al. 1982). Extinct and extant hominids all exhibit primitive, slight hamuli, as do *Sivapithecus, Oreopithecus, Proconsul, Equatorius,* and many monkeys, further enabling dorsiflexion of MC5 (Beard et al. 1986; Lovejoy et al. 2009; Spoor et al. 1991). It is likely that the more distally projecting hamuli and rigid CMC5 of the *Pan, Gorilla* and *Pongo* evolved in parallel, in response to suspensory locomotion (Lovejoy et al. 2009). Alternatively, small hamuli and greater mobility at the hamate-metacarpal joints enable conformation of the palm to various terrain and/or arboreal substrate (Beard et al. 1986; Lovejoy et al. 2009; Spoor et al. 1991), and later permits the hominid hand to perform human-like grips.

Conclusions

The t-test results are inconclusive; the expected differences between *Pan* and *Gorilla* are statistically significant, although the effect size it too small to be of much relevance. Additionally, *Papio* facet sizes may be inconsistent with weight distribution during terrestrial locomotion. The succeeding question is whether palmigrade running is performed at a frequency that would initiate an adaptive chondrogenic response. The null hypothesis, that joint size is genetically conserved, has not been definitively rejected. The studies previously reviewed (see Chapter 1; Hammond et al. 2010, Lieberman et al. 2001, Plochocki et al. 2006, Plochocki et al. 2009) also bore variable results, suggesting that the adaptive chondrogenic relationship between joint size and weight distribution varies according to age of the individual, location of the joint, and species (Lieberman et al. 2001). However, joint contour remains, to some degree, plastic during development (Carter and Beaupre 2001). Opposing surface geometries (as well as surrounding muscles, ligaments and tendons) must be precisely congruent in order to maintain normal joint motion (Carter and Beaupre 2001; Lovejoy et al. 1999). It is unlikely that the intricacies of joint anatomy are subject to genetic recombination while maintaining proper function and form (Lovejoy et al. 1999).

The PCA results for *Homo* and *Pan* indicate morphology that coincides with patterns of use reported in the literature. *Homo* maintains carpometacarpal joints capable of flexion, extension and rotation. *Pan* scores highest on the first two components, indicating a lack of significant mobility. The qualitative assessment of *Papio* carpometacarpal joints confirms the extreme dorsiflexion capabilities, as employed during palmigrade locomotion. *Pongo* requires a larger, more complete sample to make an effective evaluation of the relationship between joint shape and use. I hypothesize that the degree of variation will be similar to that seen in *Gorilla*, although the morphological pattern may deviate due to the fact that *Pongo* uses a wider variety of hand postures, both arboreally and terrestrially.

Gorilla displays a peculiar degree of variability in carpometacarpal joint structure. Although some *Gorilla* specimens score within the *Homo* range on Component 1, these same specimens score from neutral to very high on Component 2. These few individuals have dorsopalmarly curved fifth metacarpal bases, dorsally extended joint surfaces, and corresponding saddle-shaped facets; yet, they maintain large hamuli that articulate with the fifth metacarpals. The third and fourth most loaded variables on Component 2 are MC4CAP and MC4TOP, indicating that these *Gorilla* specimens also have limited mobility of CMC4.

The discrepancy between component scores for these few *Gorilla* specimens emphasizes the importance of examining a total morphological pattern rather than relying on a single trait to determine phylogeny, locomotion, etc. (Le Gros Clark 1955). No single feature examined in the present study is a quintessential indicator of mobility or rigidity. Although if any one trait would be a contender, articulation between MC5 and the hamulus prohibits any flexion, extension, and/or rotation without cavitation of the joint. It is likely that these few *Gorilla* specimens maintain minimal mobility of CMC 4 and 5; and subsequently, any contradictory morphology (i.e. saddling of the hamate and MC5 curvature) has been misinterpreted in the present classificatory system. Intraspecific variation in *Gorilla* carpometacarpal joint geometry can be attributed to Type 5 origins.

Selection for large, distally projecting hamuli in the great apes, in response to vertical climbing and suspensory locomotion (Lovejoy et. al 2009; Ward 1999), preadapted the hominoid wrist for the stability later engaged during knuckle-walking. The function of joints is to facilitate motion, and not restrict it (Lovejoy and Meindl 2001, Selby et al 2016), therefore the geometric features of the rigid carpometacarpal joints in question must not be the direct result of adaptation (Type 1). The specific contours of the carpometacarpal joints are guided by chondral modeling in response to the surrounding stabilizing musculature. Hominids, as well as modern humans, have retained primitive, slight hamuli as seen in *Sivapithecus*, *Oreopithecus*, *Proconsul*, *Equatorius,* and many monkeys (Beard et al. 1986; Lovejoy et al. 2009; Spoor et al. 1991). Slight hamuli permit mobility, and chondral modeling further guides development of joint shapes according to individual patterns of use.

Future Research

Larger sample sizes of better quality (for all genera) are needed for an effective analysis of morphological variance among anthropoid wrists. Due to the scarcity of materials and quality of present specimens, *Papio* and *Pongo* were excluded from the principal components analysis, and this hindered statistical evaluation. Likewise, more genera representing a greater range of primate locomotion would be ideal for comparison. Furthermore, comparisons with non-primate taxa could elucidate origins of traits (e.g. parallel evolution, convergence, and adaptive chondrogenesis) by controlling for phylogeny, as attempted by Orr (2005).

An examination of articular cartilage, especially comparisons of adults to juveniles within and among species, would illuminate the relationship, if any, between joint form/size and patterns of use. Unfortunately, most juvenile hominoid hands at the Cleveland Museum of Nature History were articulated, and examination of articular surfaces was not possible.

REFERENCES

Ashbury, A M.; Posa, M. R. C.; Dunkel, L. P.; Spillmann, B.; Atmoko, S. S. U.; Van Schaik, C. P.; Van Noordwijk, M. A. (2015) Why Do Orangutans Leave the Trees? Terrestrial Behavior Among Wild Bornean Orangutans (*Pongo pygmaeus wurmbii*) at Tuanan Central Kalimantan. *American Journal of Primatology*. 77:1216-1229.

Beard, C. W., Teaford, M. F., Walker, A. (1986) New Wrist Bones of *Proconcul africanus* and *P. nyanzae* from Rusinga Island, Kenya. *Folia Primatologica*. 47(2-3):97-118.

Beck, B. B. (1982). Chimpocentrism: Bias in cognitive ethology. *Journal of Human Evolution, 11*, 3.

Buffi, J. H., Crisco, J. J., & Murray, W. M. (2013). A method for defining carpometacarpal joint kinematics from three-dimensional rotations of metacarpal bones captured in vivo using computed tomography. *Journal of Biomechanics, 46*, 2104.

Burstein, A. H. & Wright, T. M. (1994). *Fundamentals of Orthopaedic Biomechanics*. Baltimore, Maryland, USA: Williams and Wilkins.

Bush, M. E.; Lovejoy, C. O.; Johanson, D. C.; Coppens, Y. (1982). Hominid Carpal, Metacarpal, and Phalangeal Bones Recovered From the Hadar Formation: 1974-1977 Collections. *American Journal of Physical Anthropology*. 57:651-677.

Carter, D. R., & Beaupre, G. S. (2001). *Skeletal function and form: Mechanobiology of skeletal development, aging, and regeneration*. Cambridge, UK: Cambridge University Press.

Corruccini, R. S. (1978). Comparative osteometrics of the hominoid wrist joint, with special reference to knuckle-walking. *Journal of Human Evolution, 7*, 307.

Corruccini, R. S., & McHenry, M. H. (2001). Knuckle-walking hominid ancestors. *Journal of Human Evolution, 40*, 507.

Dainton, M. (2001). Paleoanthropology: Did our ancestors knuckle-walk? *Nature, 410*(6826), 324.

Dainton, M., & Macho, G. A. (1999). Did knuckle-walking evolve twice? *Journal of Human Evolution, 36*, 171.

Day, M. H.; Scheuer, J. L. (1973) SK14147: A New Hominid Metacarpal from Swartkrans. *Journal of Human Evolution*. 2:429-438.

Ecktein, F., Faber, S., Muhlbauer, R., Hohe, J., Englmeier, K.-H., Reiser, M., Putz, R. (2002) Functional adaptation of human joints to mechanical stimuli. *Osteoarthritis and Cartilage, 10*, 44-50.

El-shennawy, M., Nakamura, K., Patterson, R. M., & Viegas, S. F. (2001). Three-dimensional kinematic analysis of the second through fifth carpometacarpal joints. *The Journal of Hand Surgery, 26A*(6), 1030.

Fick, R. (1890). Ueber die form der gelenkflaechen. *Arch Anat Physiol Anat Abt Supp,* , 391.

Frost, H. M. (1979). A chondral modeling theory. *Calcified Tissue International, 28,* 181.

Frost, H. M. (1994). Perspectives: A vital biomechanical model of synovial joint design. *The Anatomical Record, 240,* 1-18.

Frost, H. M. (1999). Joint anatomy, design, and arthroses: Insights of the Utah paradigm. *The Anatomical Record, 255,* 162-174.

Gebo, D. L. (1996). Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. *American Journal of Physical Anthropology, 101,* 55.

Goodall, J., & Hamburg, D. A. (1974). Chimpanzee behavior as a model for the behavior of early man. new evidence on possible origins of human behavior. *Am.Handb.Psychiat, 6,* 14-43.

Gebo, D. L. (2014). *Primate comparative anatomy*. Baltimore, MD: Johns Hopkins University.

Gilbert, S. F. (2003). *Developmental biology* (Seventh ed.). Sunderland, Massachusetts: Sinaur Publishers Inc.Press.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London B: Biological Sciences, 205*(1161), 581.

Gregory, W. K. (1930). The origin of man from a brachiating anthropoid stock. *Science, 71*(1852), 645.

Hammond, A. S., Ning, J., Ward, C. V., & Ravosa, M. J. (2010). Mammalian limb loading and chondral modeling during ontogeny. *The Anatomical Record, 293,* 658.

Hamrick, M. W. (1999). A chondral modeling theory revisited. *Journal of Theoretical Biology, 201,* 201.

Inouye, S. E. (1994). Ontogeny of knuckle-walking hand postures in African apes. *Journal of Human Evolution, 26,* 459

Kapandji, A, I. Physiology of the Joints. Volume 1: Upper Limb. Sixth ed. 2007. Churchill, Livingston, Elsevier.

Kivell, T. L., Schmitt, D., & Walker, A. (2009). Independent evolution of knuckle-walking in african apes shows that humans did not evolve from a knuckle-walking ancestor. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(34), 14241.

Kivell, T.L.; Deane, A. S.; Tocheri, M.W.; Orr, C. M.; Schmid, P.; Hawks, J.; Berger, L. R.; Churchill, S. E. (2015). The hand of *Homo naledi*. *Nature Communications*. 6 (8431):1-9.

Kiviranta, I., Tammi, M., Jurvelin, J., Arokoski, J., Saamanen, A., & Helminen, H. J. (1992). Articular cartilage thickness and glycosaminoglycan distribution in the canine knee joint after strenuous running exercise. *Clincal Orthopaedics and Related Research*, *283*, 302.

Le Gros Clark, W. E. (1955) The Fossil Evidence for Human Evolution: An Introduction to the Study of Paleoanthropology. The University of Chicago Press. Chicago, IL.

Lieberman, D. E., Devlin, M. J., & Pearson, O. M. (2001). Articular area responses to mechanical loading: Effects of exercise, age and skeletal location. *American Journal of Physical Anthropology, 116*, 266-277.

Loken, B.; Spehar, S.; Rayadin, Y. (2013) Terrestriality in the Bornean Orangutan (*Pongo pygmaeus morio*) and Implications for Their Ecology and Conservation. *American Journal of Primatology*. 75:1129-1138.

Lovejoy, C. O., Cohn, M. J., & White, T. D. (1999). Morphological analysis of the mammalian postcranium: A developmental perspective. *Proceedings of the National Academy of Sciences of the United States of America, 96*(23), 13247.

Lovejoy, C. O., Heiple, K. G., & Meindl, R. S. (2001). Paleoanthropology: Did our ancestors knuckle-walk?. *Nature, 410*(6826), 325-326

Lovejoy, C. O., Meindl, R. S., Ohman, J. C., Heiple, K. G., White, T. D. (2002). The Maka femur and its bearing on the antiquity of human walking: Applying contemporary concepts of morphogenesis to the human fossil record. *American Journal of Physical Anthropology, 119*, 97.

Lovejoy, C. O., McCollum, M. A., Reno, P. L., & Rosenman, B. A. (2003). Developmental biology and human evolution. *Annual Review of Anthropology*, *32*, 85.

Lovejoy, C.O., Simpson, S., White, T. D., Asfaw, B. & Suwa, G. (2009). Careful Climbing in the Miocene: The Forelimbs of *Ar. ramidus* and Humans Are Primitive. *Science, 326*, 70.

Manduell, K. L.; Morrogh-Berbard, H. C.; Thorpe, S. K. S. (2011) Locomotor Behavior of Wild Orangutans (*Pongo pygmaeus wurmbii*) in Disturbed Peat Swamp Forest, Sabangau, Central Kalimantan, Indonesia. *American Journal of Physical Anthropology*. 145:348-359.

Marzke, M. W. (1983). Joint functions and grips of the *Australopithecus afarensis* hand, with special reference to the region of the capitate. *Journal of Human Evolution, 12*, 197.

Marzke, M. W., Wullstein, K. L., & Viegas, S. F. (1994). Variability at the carpometacarpal and midcarpal joints involving the fourth metacarpal, hamate, and lunate in Catarrhini. *American Journal of Physical Anthropology, 93*, 229.

Matarazzo, S. (2013) Manual Pressure Distribution Patterns of Knuckle-Walking Apes. *American Journal of Physical Anthropology*. 152:44-50.

McHenry, H. M. (1983). The capitate of *Australopithecus afarensis and A. africanus*. *American Journal of Physical Anthropology, 62*, 187.

Muhlbauer, R.; Lukasz, S.; Faber, S.; Stammberger, T.; Eckstein, F. (2000) Comparison of Knee Joint Cartilage Thickness in Triathletes and Physically Inactive Volunteers Based on Magnetic Resonance Imaging and Three-Dimensional Analysis. *The American Journal of Sports Medicine*. 28(4): 541-546.

Nakamura, K.; Patterson, R. M.; & Viegas, S. F. (2001) Ligament and Skeletal Anatomy of the Second Through Fifth Carpometacarpal Joints and Adjacent Structures. *The Journal of Hand Surgery*. 26A(6): 1016-1029.

Orr, C. M. (2005) Knuckle-Walking Anteater: A Convergence Test of Adaptation for Purported Knuckle-Walking Features of African Hominidae. *American Journal of Physical Anthropology*. 128:639-658.

Patel, B. A. (2005). The hominoid proximal radius: Re-interpreting locomotor behaviors of early hominins. *Journal of Human Evolution, 48*, 417.

Patel, B. A.; Wunderlich, R. E. (2010) Dynamic Pressure Patterns in the Hands of Olive Baboons (*Papio anubis*) During Terrestrial Locomotion: Implications for Cercopithecoid Primate Hand Morphology. *The Anatomical Record*. 293:710-718.

Plochocki, J. H.; Riscigno, C. J.; Garcia, M. (2006) Functional Adaptation of the Femoral Head to Voluntary Exercise. *The Anatomical Record Part A*. 288A:776-781.

Plochocki, J. H.; Ward, C. V.; Smith, D. E. (2009) Evaluation of the Chondral Modeling Theory Using fe-Simulation and Numeric Shape Optimization. *Journal of Anatomy*. 214:768-777.

Richmond, B. G., & Strait, D. S. (2000). Evidence that humans evolved from a knuckle-walking ancestor. *Nature, 404*, 382.

Richmond, B. G., Begun, D. R., & Strait, D. S. (2001). Origin of human bipedalism: The knuckle-walking hypothesis revisited. *Yearbook of Physical Anthropology, 44*, 70.

Sayers, K., & Lovejoy, C. O. (2008). The chimpanzee has no clothes: A critical examination of Pan troglodytes in models of human evolution. *Current Anthropology, 49*(1), 87.

Selby, M. S.; Simpson, S. W.; Lovejoy C.O. (2016) Functional Anatomy of the Carpometacarpal Complex in Anthropoids and Its Implications for the Evolution of the Hominoid Hand. *Anatomical Record*. 299(5): 583-600.

Spoor, F. C.; Sondaar, P. Y.; Hussain, S. T. (1991) A new hominoid hamate and first metacarpal from the Late Miocene Nagri Formation of Pakistan. *Journal of Human Evolution, 21*, 413.

Stern, J. T. (1975). Before bipedality. *Yearbook of Physical Anthropology, 19,* 59.

Stern, J. T., & Susman, R., L. (1981). Electromyography of the gluteal muscles in *Hylobates, Pongo*, and *Pan*: Implications for the evolution of hominid bipedality. *American Journal of Physical Anthropology, 55*, 153.

Straus, W. L. (1940). The posture of the great ape hand in locomotion, and its phylogenetic implications. *American Journal of Physical Anthropology, 27*(2), 199.

Straus, W. L. (1949). The riddle of man's ancestry. *The Quarterly Review of Biology*, *24*(3),200.

Susman, R. L. (1974) Facultative Terrestrial Hand Postures in an Orangutan (*Pongo pygmaeus*) and Pongid Evolution. *American Journal of Physical Anthropology.* 40:27-38.

Tuttle, R. H. (1969). Knuckle-walking and the problem of human origins. *Science, 166*(3908),953.

Tuttle, R. H., Butzer, K. W., & Blumenberg, B. (1974). Darwin's apes, dental apes, and the descent of man: Normal science in evolutionary anthropology. *Current Anthropology, 15*(4), 389.

Tuttle, R. H. (1981). Evolution of hominid bipedalism and prehensile capabilities. *Philosophical Transactions of the Royal Society of London, B292*, 89.

Walker, R. A., Lovejoy, C. O., Bedford, M. E., & Yee, W. (2007). *Skeletal and developmental anatomy for students of chiropractic* (2nd ed.) Linus Publications, Inc.

Wang, X.; Mao, J.J. (2002) Chondrocyte Proliferation of the Cranial Base Cartilage Upon *in vivo* Mechanical Stresses. *J Dent Res.* 81(10):701-705

Ward, C. V., Leakey, M. G., Brown, B., Harris, J., & Walker, A. (1999). South Turkwel: A new Pliocene hominid site in Kenya. *Journal of Human Evolution, 36*, 69.

Washburn, S. L. (1967). Behaviour and the origin of man. *Proceedings of the Royal Anthropological Institute of Great Britain and Ireland*, *1967*, 21.

Williams, S. A. (2010). Morphological integration and the evolution of knuckle-walking. *Journal of Human Evolution*, *58*, 432.

Wu, Q., & Chen, Q. (2000). Mechanoregulation of chondrocyte proliferation, maturation, and hypertrophy: Ion-channel dependent transduction of matrix deformation signals. *Experimental Cell Research, 256,* 383.

Wu, Q.; Zhang, Y.; Chen, Q. (2001) Indian Hedgehog Is an Essential Component of Mechanotransduction Complex to Stimulate Chondorcyte Proliferation. *Journal of Biological Chemistry*. 276(38):35290-35296.

Wunderlich, R.E.; Jungers, W. L. (2009) Manual Digital Pressures During Knuckle-Walking in Chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*. 139:394-403.

Young, N. M., Capellini, T. D., Roach, N. T., & Alemseged, Z. (2015). Fossil hominin shoulders support an african ape-like last common ancestor of humans and chimpanzees. *Pnas, 112*(38), 11829.

Zihlman, A. L., Cronin, J. E., Cramer, D. L., & Sarich, V. M. (1978). Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas. *Nature*, *275*, 74.

APPENDICES

APPENDIX A

Morphological Descriptions of *Papio*

Missing or broken bones exclude most *Pongo* specimens from the PCA. Also, if a specimen's morphology fell outside the described range of variation associated with a specific trait, then the specimen received no score for that trait. Tables 7 and 8 list individual trait scores for each *Papio* and *Pongo* specimen. Detailed descriptions of the morphology of each of these specimens are given below.

HTB 0828 - Papio ursinus

The proximal articular surface of MC4 has minimal variation in surface topography, with an overall dorsal angle of the joint surface. The fifth metacarpal base has extreme dorsopalmar curvature, with moderate mediolateral rugosity. The articular surface of the hamate is mediolaterally convex, and extrememly dorsopalmarly concave, forming a hook-shaped joint. Joint surfaces are oriented oblique each other.

HTB 0890 – Papio hamadryas

The proximal articular surface of MC4 has little/no variation in surface topography, although the joint surface is angled dorsally and ulnarly. The basal joint surface extends onto the dorsal aspect of the base on the medial side. The fifth metacarpal base has extreme dorsopalmar curvature and the joint surface extends onto the dorsal aspect of the base. There is slight mediolateral rugosity. The distal joint surfaces on the hamate are mediolaterally flat, but are extremely dorsopalmarly concave, resulting, again, in a hook-shaped joint.

HTB 1028 – Papio hamadryas

The proximal joint surface of MC4 has little/no variation in surface topography, and little/no angulation of the joint surface. The proximal joint surface of MC5 is angled radially. Mediolaterally, the joint surface is mostly flat, but extremely dorsopalmarly convex. The joint surface extends onto dorsal aspect of the base. Again, the hamate is mediolaterally convex, and dorsopalmarly concave.

HTB 1043 – Papio hamadryas

The proximal joint surface of MC4 is mostly flat. Joint surface is angled dorsally, but there is no continuation of the joint surface onto the dorsal surface of the base. MC5 has extreme dorsopalmar curvature of the base, with the joint surface continuing onto the dorsal aspect of the bone. The most proximal aspect of the joint surface is mediolaterally flat (thus it scored a "1"), however there is some convexity as the joint surface continues distally on the dorsum of the bone. The hamate is mediolaterally convex and dorsoventrally concave, producing a hook/saddle shape. Again, MC4 and MC5 joint surfaces are oriented opposite each other.

HTB 1212 – Papio cynocephalus

The basal joint surface of MC4 is flat, but angled dorsally. There is some continuation of the joint surface onto the dorsum of the base, on the medial side. There is slight mediolateral rugosity of MC5 coupled with extreme dorsopalmar curvature (convexity). The joint surface extends onto the dorsal aspect of the base. Hamate joint surfaces combined produce a hook/saddle shaped joint, and the articular surfaces for metacarpals four and five are oriented opposite each other.

APPENDIX B

Morphological Descriptions of *Pongo*

HTB 0625 – Pongo pygmaeus

The basal articular surface of the fourth metacarpal exhibits a slight central depression. There is no substantial mediolateral concavity of the proximal articular surface of MC5, but it joint topography falls outside the “normal” range of variation seen in the entire sample. The ulnar side the joint surface is mediolaterally concave, but on the radial side the joint surface is mediolaterally convex. The joint surface continues onto the dorsal aspect of the base. The hamate facets for MC4 and MC5 are smooth. There is no apparent distinction on the hamate between the two facets. Mediolaterally the facets are relatively flat. Dorsopalmarly they are convcave. The joint surface extends partially onto the base of the hamulus; the hook of the hamulus is oriented laterally (similar to morphology seen in *Homo*, as opposed to projecting distally like most other great apes).

HTB 1030 – Pongo pygmaeus

The center of the basal articular surface of MC4 is slightly depressed in relation to the outer margins of the joint. The base of MC5 has minimal dorsopalmar convexity, and the joint surface can does not extend onto the dorsum, but it is mediolaterally concave. The distal articular surface of the hamate displays a slight keel, distinguishing the separation of the two joint surfaces. The hamulus is very slight.

HTB 1055 – Pongo pymaeus

The proximal articular surface of the fourth metacarpal is topographically complex compared to other bases of the same species. There is a deep central groove running dorsopalmarly resulting in mediolateral ridges, much like the morphology described for trait MC5RUG. The ulnar margin of the joint surface is convex palmarly, and concave dorsally. MC5 joint surface is angled ulnarly. There is little variation in surface topography, mediolaterally, no dorsopalmar curvature or continuation of the joint surface onto the dorsum. The hamulus is moderate in size and extends distally. Joint surfaces on the hamulus are mostly flat, with some extension onto the base of the hamulus, producing a slight "L" shape.

HTB 1443 – Pongo pygmaeus

The basal joint surface of MC4 was irregular, compared to the rest of the sample. Overall, the joint surface was oriented radially. The dorsal margin is mediolaterally concave. There is a deep groove on the ulnar side of the base (accommodating the carpometacarpal ligament in life) contributing to complex proximal articular surface topography. MC5 is markedly concave mediolaterally with moderate joint extension onto the dorsum. The hamate facet for MC5 is dorsopalmarly concave; the facet for MC4 is more variable, accommodating the complexities of MC4 basal topography.

HTB 1444 – Pongo pygmaeus

Morphology of MC4 base is complex. The dorsomedial corner of the joint surface is flat. The dorsolateral margin of the joint protrudes proximally. Palmarly, the joint surface becomes convex. The MC5 proximal joint surface is angled dorsally. It is mediolaterally convex, thereby receiving no score for trait MC5RUG, as it did not fit with the previously defined continuum spanning concave to flat. This specimen has no dorsopalmar curvature and the joint surface does not continue onto the dorsum of the bone. Congruent with the topography of the metacarpal bases, the articular surface of the hamate is elaborate. It is “L” shaped in nature with a deep depression at the base of the hamulus, but moving dorsally becomes shelf-like. There are variable central protrusions that are accommodated by grooves on MC4. The most lateral portion of the hamate joint surface slopes proximally, accommodating the lateral protrusion of the MC4 base.

HTB 1885 – Pongo pygmaeus

Minimal variation in surface topography of MC4. MC5 has some degree of dorsopalmer curvature, and the joint surface extends moderately onto the dorsum of the bone. Mediolaterally, the base of MC5 is flat, but with an ulnar angle. Facets for the fourth and fifth metacarpals on the hamate are separated by a slight ridge. Both facets are mediolaterally and dorsopalmarly concave (condyloid). The hamulus is small, with the MC5 facet extending blending into the base, and the hook extends distally.

HTB 2073 – Pongo pygmaeus

There is marked variation in topography of the MC4 proximal joint surface. No fifth metacarpal was present for this specimen, hence the missing values and exclusion from the PCA. Distal joint surfaces on the hamate are oriented oblique to each other. The dorsal portions of the hamate facets are convex dorsopalmarly; the palmar portion of the combined joint surfaces is concave. Both facets for MC4 and MC5 extend onto the base of a slight hamulus.

HTB 2583 – Pongo pygmaeus

The basal articular surface of MC4 is characterized by a central depression, when compared to the outer margins of the joint. In the mediolateral plane, the basal joint surface morphology of MC5 falls outside the “normal” range of variation observed in this study. There is slight mediolateral concavity on the radial side, but convexity on the ulnar side. The joint surface is dorsopalmarly flat. Any possible extension of the joint surface onto the dorsal aspect of the base is difficult to discern due to poor quality of the bone. The distal joint surface of the hamate was especially irregular in nature. Palmarly, there is a deep, wide groove running mediolaterally; dorsally, the joint surfaces were markedly convex, creating a “shelf-like” appearance.