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Anatomy of a precision grip in human and non-human primates

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ABSTRACT

ANATOMY OF A PRECISION GRIP IN HUMAN AND NON-HUMAN PRIMATES

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Prehensility is a hand activity that applies forces while grasping an object. In the crudest sense, prehensile movements of the hand can be divided into two types based on an actor needing a precision or a power grip. To analyze prehensility more specifically, I suggest that the movements of the hand can be divided into three categories: power, modified precision, and true precision grips. A power grip is when an object is held in one hand with the aid of the palm with fingers buttressing the object, whereas a true precision grip is when an object is picked up using only the tips of the first and second digits in similar fashion as tweezers. The in-between category, a modified precision grip, is defined when using an anatomically restricted hand posture that mimics the forceful pinch biomechanics of true precision grips.

In this project, I study human hand anatomy by assessing hand proportions, finger curvature, and fourth metacarpal articulation in African apes (*Pan troglodytes, Gorilla gorilla*), other living primates (*Papio anubis, Papio papio, Macaca fascicularis,* and *Cebus apella*), and several fossil humans (*Australopithecus sediba, Homo naledi,* and *Homo neanderthalensis*). I assess the evolution of the human hand in association with our evolutionary ability to grasp tools using a true precision grip. Non-human primates with a more generalized functional hand may show enhanced dexterity capabilities that could be quite informative about the evolution of true precision grip in the human fossil record. To compare all of the living primates, humans, and fossils, I expressed averages for inner hand proportions and hand proportions including geometric means. This study also the included angle of phalangeal curvature and the radius of phalangeal curvature for measured specimens. Using a principal component analysis (PCA), this project showed significant similarities between extant and fossil primates to the modern-day humans analyzed. My overall assessment is that a precision grip is possible in other non-human primates and this result suggests that tool use could have been possible before the appearance of stone tools in the human fossil record.

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ANATOMY OF A PRECISION GRIP IN HUMAN AND NON-HUMAN PRIMATES

BY

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CHAPTER 1

INTRODUCTION

The hominid hand has long been the focus of morphological research with a particular interest in the functional and evolutionary implications of wrist anatomy. Although research has been conducted on discrete joint movements during hand function in non-human and human primates, only a few studies have attempted to bridge the gap between fossil and modern human hand anatomy (Marzke & Marzke, 2000; Almecija et al., 2010; Kivell et al., 2013). Furthermore, only a select few have tried to analyze the phylogenetic context of these hand changes (see Sarmiento, 1988; Marzke, 1997; Kivell et al., 2013; Kivell, 2015; Richmond et al., 2016).

General hand movements can be divided into two main groups: *prehensile* and *non-prehensile movements* (Napier, 1956; Napier & Tuttle, 1993). Prehensile movements can be classified as any action in which an object is held partly or wholly with the entire hand. Non-prehensile movements are actions that require no grasping, but the manipulation of objects can be carried out by motions of the hand or digits individually (Napier, 1956; Landsmeer, 1962; Napier & Tuttle, 1993). Prehensile activity is the application of forces while grasping an object. Prehensility can be observed in a variety of mammals besides primates, but “true prehensility”, that is holding an item with one hand without the aid of the palm, is currently thought to only be achieved by humans and their close ancestors (Napier & Tuttle, 1993; Marzke & Marzke, 2000). On the other hand, many clawed mammals are capable of holding food between their two paws to make-up for their lack of single-handed prehensility (Cartmill, 1972; Napier & Tuttle, 1993).

In the crudest sense, prehensile movements of the hand can be divided further into two types based on an actor needing precision or power in one's grip postures (Napier, 1956; Napier & Tuttle, 1993). To analyze prehensility more specifically, I suggest that movements of the hand can be divided into three groups: power, modified precision, and true precision grips. Power grips are used to stabilize an object in the palm of the hand with digits wrapped around as the thumb is placed perpendicular to the other digits, as a buttress for support. Power grips are commonly used for cylindrical objects such as hammers and baseball bats. True precision grips are when an object is picked up using only the tips of the first and second digit in similar fashion as tweezers. Modified precision grips will be defined as anatomically restricted hand postures mimicking the forceful pinch biomechanics of true precision grips. Better definitions and distinctions between these variety of grip postures allow for a more complete and an understandable view of hand function aside from locomotion or body weight support.

The basic five-digit pattern of the human hand is a primitive anatomical trait retained from an ancestral condition for all mammals (Napier, 1956; Forbisch & Riesch, 2009; Richmond et al., 2016). Primate hands diverged from this mammalian ancestral condition with the evolution of two distinct characteristics: possessing nails instead of claws or hoofs, and thumb opposability during grasping (Napier, 1956; Richmond et al., 2016). General hand anatomy comparisons between modern non-primate mammals and early mammals shows adaptability in the hand as a functional organ to support body weight across a variety of body types and locomotor patterns (Napier & Tuttle, 1993; Forbisch & Riesch, 2009; Richmond et al., 2016). Fossil hominins and early hominids practiced a variety of hand postures that aided in a variety of locomotor patterns in both arboreal and terrestrial settings (Stern, 1983; Sarmiento, 1988; Gebo, 1996; Kivell & Schmitt, 2009; Richmond et al., 2016). Due to this wide array of ancestral primate movements and hand postures, most living primates did not require a wholesale anatomical remodeling of their hands and they exhibit functional flexibility with different locomotor patterns depending on the context or environmental situation (Fiex et al., 2015). This functional flexibility can often confuse the phyletic interpretation of morphologically derived characteristics in the human fossil record.

The most substantial changes in functionality of the hominid hand occurred 6-7 Mya after the most recent split of the last common ancestor in the hominid family (Sarmiento, 1988; Forbisch & Riesch, 2009; Kivell et al., 2013; Kivell, 2015). The intensification of hand manipulation is thought to be associated with true precision grips that are essential for tool use, tool making, and more fine-tuned motor skills. Further, the evolution of bipedalism reduced the need for weight-bearing morphology in the wrist and forearms allowing the hand to function in a novel way (Sarmiento, 1988; Marzke & Marzke, 2000; Wolfe et al., 2006; Kivell et al., 2013; White et al., 2015; Richmond et al., 2016). The ability to precisely manipulate objects is an autapomorphic characteristic that separates hominids from other primates (Fiex et al., 2015).

In this project, I studied the evolution of the human hand by assessing hand proportions, finger curvature, and carpal architecture in comparison to the great apes and several fossil hominins (australopithecine and *Homo* species) in association with the evolution of the ability to grasp tools. Support for the hypothesis that enhanced dexterity or specialized precision grip for tool-use is the ancestral condition of hominins is growing (see Marzke & Marzke, 2000; Panger et al., 2003; Kivell et al., 2013; Almecija et al., 2015). Understanding non-human primates expressing palmigrade grasping and finger dexterity is necessary to view human hand development and evolution as well, since these primates do not have specialized locomotor patterns such as African ape knuckle-walking. Given a more general hand use starting point, non-human primates' enhanced dexterity capabilities may be quite informative about the evolution of the precision grip in the human fossil record. The morphological necessities of grasping tools differ from the morphological necessities of branch grasping from above, but both grasps may not be quite as divergent as we have come to believe.

Research Questions

1A: What are the hand proportions in humans relative to non-human primates (*Pan troglodytes*, *Gorilla gorilla*, *Papio anubis*, *Papio papio*, *Mandrillus (Papio) leucophaeus*, *Theropithecus gelada*, *Macaca fascicularis*, *Cebus capucinus*, and *Cebus apella*)?

1B: How are digital proportions of the hand related to a modified precision grip or to a true precision grip found in humans?

1C: What are the hand proportions of fossil hominins (*Australopithecus sediba*, *Homo habilis*, and *Homo neanderthalensis)*; are they similar to those of humans?

2A: What is the average pattern of phalangeal curvature (radius and included angle) in humans relative to non-human primates?

2B: How is phalangeal curvature (radius and included angle) related to a modified precision or to a true precision grip?

3A: Can the carpal architecture characteristics (relative surface area of the joint of the first metacarpal of the first digit and trapezoid carpal bones (Richmond et al., 2016)) that define a true precision grip be found in any extant non-human primate hands?

3B: What is the sequence of anatomical changes that are required to achieve the mechanical requirements for a true precision grip?

CHAPTER 2

BACKGROUND

Factors Influencing Grip Postures

Factors that influence choice of a grip posture to stabilize objects held include shape and size of the object, intended activity, and other factors that may play a minor role (Napier, 1956; Landsmeer, 1962). The shape of objects was used first by Griffiths (1943) to describe similar functions as “power” and “precision” grips in the literature (Napier, 1956; Napier & Tuttle, 1993; Domalain et al., 2008). In these types of hand posture descriptions, the object could be gripped with either the tips of the digits or the flexed fingers and palm (Napier, 1956; Napier & Napier, 1967; Napier & Tuttle, 1993). The descriptive terms that were first used were insufficient as the names lacked any specifications of hand position and the focus was mainly on the object being held (Napier, 1956; Landsmeer, 1962). While these object-based descriptions of hand postures do not allow a complete view of the biomechanics involved in grip postures, the shape of the object does play a part in the type of grip employed while holding a specific object (Napier, 1956; Landsmeer, 1962; Richmond et al., 2016). The currently accepted terms for grip postures (precision and power) are distinct both in the anatomical and functional senses (Napier, 1956; Landsmeer, 1962).

For example, intermediate object sizes allow for either precision or power grips for stabilization, while extreme object sizes require specialized grip posture tactics (Napier, 1956; Napier & Tuttle, 1993). Objects with larger sizes need to be held with both hands with power grips, or if only one hand is available the objects can be held with a precision grip between the tips of all the fingers and thumb (Napier, 1956; Landsmeer, 1962; Domalain et al., 2008). In contrast, small objects are usually held with one hand between the pulp of the index finger and thumb to allow for stability with sensory acuity, instead of focusing on mechanical support (Napier, 1956; Napier & Tuttle, 1993).

The largest factor in specific grip postures is intended activity of the actor (Napier, 1956; Napier & Tuttle, 1993; Domalain et al., 2008). As noted above, objects of intermediate size allow for either power or precision grips to be employed (Napier, 1956; Napier & Tuttle, 1993). While the two grips are not mutually exclusive of each other, meaning that power and precision grips can be employed simultaneously as a composite grip, the intention of the actor affects the nature of the grip (Napier, 1956; Domalain et al., 2008). This composite grip is defined differently than the “modified precision” grip that I am attempting to define. When a hand is photographed in mid-activity, it shows a mixture of posture phases that could be interpreted as either a power or a precision grip (Napier, 1956; Landsmeer, 1962). In most everyday activities, a composite grip is employed (Napier, 1956; Landsmeer, 1962). A poignant example of this composite grip can be observed in expert stone tool knappers who use a variety of both precision and power grips simultaneously when making bifacial tools (Marzke & Marzke, 2000). Other factors that can affect grip postures include weight, texture, temperature, and wetness / dryness of the object, as well as emotional states of the actor including fear, distaste, and hunger (Napier, 1956).

The ability of the hand to stabilize an object is the most fundamental factor in prehensile movements (Napier, 1956; Wolfe et al., 2006). While almost all primates have opposable thumbs, only humans and closely related relatives are thought to be able to employ both power and precision grip postures (Landsmeer, 1962; Wolfe et al., 2006; Richmond et al., 2016).

Hand Postures

Power Grip

A power grip ("clubbing grip" or "forceful grip"; Fig. 1c) is when an object is gripped in the palm with fingers flexed, forming one jaw of the clamp and the palm forming the other jaw (Napier, 1956; RW Young, 2003; Wolfe et al., 2006). The thumb becomes adducted for small adjustments of hand posture that control the direction of force being applied (Napier, 1956; Landsmeer, 1962). Under some conditions of power grip the thumb provides directional control (Napier, 1956; Napier & Tuttle, 1993). Power grip has adduction at both metacarpo-phalangeal and carpo-metacarpal joints (Napier, 1956; Landsmeer, 1962; Marzke & Marzke, 2000). The ability to rotate the 5th metacarpal towards the opposed digits is the most substantial facilitator of this grip (Napier, 1956; Marzke, 1997).

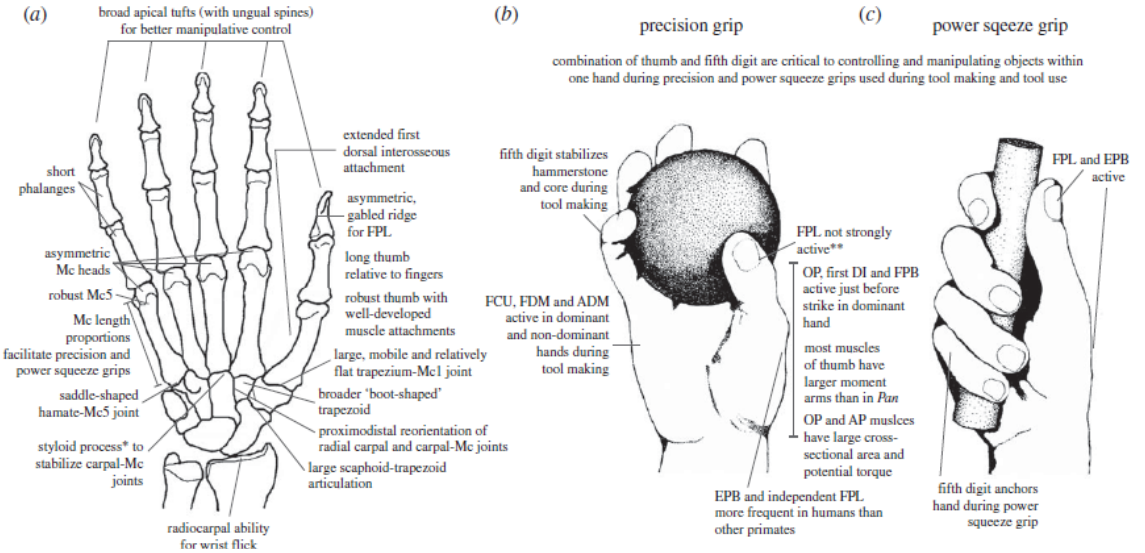

Figure 1: Morphology of the human hand necessary for power and precision grip (Kivell, 2015)

The main function of power grip is to resist forces applied to an object held within the palm. This grip is employed when there is no demand for precision and the thumb can be wrapped over the dorsum of the middle phalanges as a reinforcing mechanism (Napier, 1956; Napier & Tuttle, 1993). The thumb in this grip posture acts as a powerful buttress on the lateral side, which is evident when the thumb is adducted and aligned with the axis of the cylinder, causing the buttress to be lost (Napier, 1956; Landsmeer, 1962; Napier & Tuttle, 1993). This powerful buttress is thought to have facilitated the use of tools in non-human primates and fossil hominins (Napier, 1956; Landsmeer, 1962; Wolfe et al., 2006; Kivell, 2015).

Precision Grip

Generally, a precision grip ("forceful pinch grip"; Fig. 1b) is currently defined as when an object is pinched between the opposing thumb and flexing second digit (Napier & Napier, 1967; Marzke, 2013; Richmond et al., 2016). Although a precision grip could involve more than the first and second digits depending on the size of an object being held (ex: a basketball would require all of the digits to employed to hold with just the finger tips; Napier & Napier, 1967; Napier & Tuttle, 1993). Precision grip involves abduction at both metacarpo-phalangeal and carpo-metacarpal joints (Napier, 1956; Landsmeer, 1962; Richmond et al., 2016). The thumb and part or whole of the flexor surface of the finger forms the jaws of a clamp (Napier, 1956; Napier

& Napier, 1967; Napier & Tuttle, 1993). In this research project, when a grip is employed with these anatomical characteristics it will be designated as a “true precision” grip.

During true precision grip, fingers are flexed and abducted at the metacarpo-phalangeal joints, increasing hand span to produce a degree of axial rotation of the digits (Napier, 1956; Napier & Napier, 1967; Marzke, 2013). The flexion and axial rotation of the fingers depends largely on the size and shape of the object (Napier, 1956; Napier & Napier, 1967). With a decrease in object size the need for precision handling increases. Digital usage involving the tips of the fingers allows for more fine control as the axis of the grip shifts towards the thumb and index finger (Napier, 1956; Napier & Tuttle, 1993). Sensory surfaces of the digits also allow for minute adjustments to postures in response to skin receptors (Napier, 1956; Napier & Napier, 1967). Along with the shift of axial rotation of the digits during precision grip, the third, fourth and fifth digits are free to support the object if size and intention of the actor requires it (Napier, 1956; Marzke, 2013).

During a true precision grip position of the hand, the hand is held midway between radial and ulnar deviation with a dorsiflexed wrist (Napier, 1956; Sarmiento, 1988; Richmond et al., 2016). During the throwing motion associated with precision grip posture, the wrist moves from extension to flexion (RW Young, 2003, Richmond et al., 2016). This wrist extension in chimpanzees is limited by knuckle-walking adaptations for both quadrupedal and arboreal locomotion (Napier, 1962; RW Young, 2003; Kivell & Schmitt, 2009; Zihlman et al., 2011). Adaptations for knuckle-walking include scaphoid dorsal concavity, scaphoid beak, capitate distal concavity, capitate waisting, capitate dorsal ridging, hamate dorsal ridging, and hamate distal concavity (Kivell & Schmitt, 2009). While these features are small, irregularly shaped, and hard to reliably measure, the frequency and expression of these features were assessed qualitatively and consistently appeared in chimpanzees (Kivell & Schmitt, 2009). Enhanced ulnar deviation capabilities in most apes are possible with changes in the pisiform bone and ulnar flexor and extensor muscles (Lewis et al., 1970; Marzke et al., 1992; Zihlman et al., 2011).

The ability to maintain a true precision grip is thought to have influenced the morphology of the modern human hand as it evolved alongside bipedalism, tool use, brain enlargement and language (Wolfe et al., 2006; Marzke, 2013; Fiex et al., 2015; Richmond et al., 2016). Along with kinematic differences between living humans and those that are inferred for extinct hominins, the innovation of stone tools has generally supported the hypothesis that the evolution of a precision grip has influenced hand morphology (Marzke & Marzke, 2000; Wolfe et al., 2006; Marzke, 2013; Fiex et al., 2015).

Hand Anatomy

Hand Proportions

The most significant anatomical requirement of a precision grip is in the proportions of the thumb relative to lateral digit finger lengths (Napier & Napier, 1967; Marzke & Marzke, 2000; Almecija et al., 2010; Fiex et al., 2015; Kivell, 2015; Richmond et al., 2016). A true precision grip requires the rotation of the thumb into a pad-to-pad contact with the other lateral digits (Napier, 1956; Wolfe et al., 2006; Kivell et al., 2011; Richmond et al., 2016). This action requires relatively long thumbs and relatively short fingers for effective opposition. Differences in the lengths of the thumb and fingers limit the degree of pad-to-pad contact, whereas too much difference between thumb and finger lengths completely eliminates the ability of pad-to-pad contact (Napier, 1962; Napier & Napier, 1967; Kivell et al., 2011; Richmond et al., 2016).

Almecija et al. (2015) argue that hominin hands with high thumb-to-digit ratios are in fact the ancestral condition of chimpanzees and humans which convergently evolved with other anthropoids. Current evolutionary ideas explain the differences between extant human and ape hands through natural selection (manipulation vs locomotion) acting on the two clades separately (Napier & Tuttle, 1993; Almecija & Alba., 2014; Almecija et al., 2015). The manipulation vs. locomotion dichotomy means that the human-chimpanzee last common ancestor (LCA) is commonly thought to have similar hand proportions to chimpanzees, assuming knuckle-walking preceded hominin bipedalism (Washburn, 1968, 1971; Gebo, 1996; Almecija et al., 2015; Kivell, 2015). According to Almecija et al. (2015), fossil evidence of early hominins and apes directly challenges this view (Alba et al., 2003; Lovejoy, Suwa et al, 2009; Almecija et al., 2010; Kivell et al., 2011).

A traditional measurement that is used to assess hand proportions is the phalangeal index. The phalangeal index describes the sum length of the three middle finger phalanges as a proportion of total hand length (Napier & Napier, 1967; Napier & Tuttle, 1993). In primates, this index reflects the locomotion adaptations for their niches (Napier & Tuttle, 1993; Marzke & Shackley, 1986; Richmond et al., 2016).

Thumb-to-finger ratios differ from the phalangeal index (Richmond et al., 2016). Napier and Napier (1967) describe a thumb-to-finger ratio as an “opposability index.” The opposability index can be calculated using the total length of the thumb including metacarpal X 100 divided by the total length of the index finger with its metacarpal. Either relatively long thumbs or relatively short fingers in terms of hand proportions have been considered critical features for true precision grips (Wolfe et al., 2006; Kivell et al., 2011; Kivell, 2015; Richmond et al., 2016). Gelada baboons have extreme manual dexterity including the ability to use pad-to-pad precision grips during foraging in the wild despite their small thumbs (Napier & Tuttle, 1993; Richmond et al., 2016). True precision grips of gelada baboons are made possible by the evolution of shorter fingers, instead of the evolution of longer thumbs, the opposite condition that aids modern human prehensility (Marzke & Shackely, 1986; Napier & Tuttle, 1993; Kivell et al., 2011; Richmond et al., 2016). The facilitation of modified and true precision grips in primates can be attributed to many anatomical features, including long thumbs, short index fingers and hyper-extendable distal interphalangeal joints (Etter, 1973; Marzke & Shackley, 1986; Marzke, 1997; Kivell, 2015; Richmond et al., 2016). To better understand the origins of enhanced manual dexterity (including true and modified precision grips), I took hand proportion measurements on a variety of primate taxa that not only exhibit longer thumbs but are also have thought to have shortened finger lengths. If primates with both longer thumbs and shortened fingers have similar hand proportions, then it can be assumed that either evolutionary path would result in the ability to produce true precision grips.

Phalangeal Curvature

Strong longitudinal curvature of proximal and middle phalanges is associated with arboreal suspensory behavior in primate taxa (Napier & Napier, 1967; Napier & Tuttle, 1993; Kivell, 2015; Richmond et al., 2016). This association can be attributed to the opposing forces of palmar-orientated extrinsic flexor tendons that tend to “open” the proximal phalanx and the proximo-distal components of the joint and the reaction forces that tend to “close” the phalanges (Sarmiento, 1988; Richmond, 1998; Zihlman et al., 2011; Richmond et al., 2016). Terrestrial primates exhibit straighter phalanges because palmigrade and knuckle-walking hand postures reduce bending forces (Sarmiento, 1988; Richmond, 1998; Richmond et al., 2016). Longitudinal curvature changes during ontogeny and serves as a strong indicator of arboreal behavior during juvenile stages of individuals (Richmond, 1998; Kivell, 2015; Richmond et al., 2016).

There is no consensus on how to interpret the behavioral implications of phalangeal curvature in fossil hominins (Kivell, 2015; Richmond et al., 2016), as the functional morphology of phalangeal curvature is still not entirely understood (Richmond, 1998; Richmond et al., 2016). Body size-to-support ratio may influence flexed postures of fingers during arboreal locomotion since primates with lower body to branch ratios do not need to grasp branches from underneath (Napier & Tuttle, 1993; Richmond et al., 2016).

Phalangeal curvature is sometimes thought to be a retained primitive characteristic without the persistence of associated behaviors, which complicates our understanding of locomotor patterns in extinct species (Stern, 2000; Kivell et al., 2011; Richmond et al., 2016). Comparison of phalangeal curvature across extant primate taxa coinciding with behavioral observation can aid in the interpretation of anatomical changes due to locomotor patterns in extinct species (Crompton et al., 2008; Kivell et al., 2011; Kivell, 2015). Longitudinal curvature remodeling during a lifetime plays an unknown role in the interpretation of these patterns (Crompton et al., 2008). To test the retained primitive characteristic hypothesis, phalangeal curvature is analyzed across a variety of species that employ different locomotive hand postures. If strong phalangeal curvature occurs in primates that are not considered arboreal in a full-time sense, then phalangeal curvature is most likely a retained primitive characteristic from an ancestral condition.

Carpal Architecture

A true precision grip is not only made possible by finger proportions of the hominin hand, but this grip is also dependent on carpal architecture (Kivell, 2015; Richmond et al., 2016). The most common interpretation of carpal anatomy divides the wrist into two rows (one proximal, one distal) that move independently (Camp, 1926; Wolfe et al., 2006). Kinematic analysis of carpal architecture shows the proximal carpal row in extant humans to be almost stationary during gripping, thereby providing a stable platform for force generation during both precision and power grips (Camp, 1926; Wolfe et al., 2006; Marzke, 2013). These findings are consistent with modern human hands being adapted for effective manipulation of stones, cylindrical pieces of wood, and bone tools for throwing and clubbing (Panger et al., 2003; Wolfe et al., 2006).

In the fossil record, few synapomorphic features are known to occur in the wrist of modern humans and African apes' other than the fusion of the os centrale to the scaphoid (Lewis et al., 1970; Lovejoy et al., 2009; Richmond et al., 2016). In all known hominin fossils to date, including *Ardipithecus ramidus*, the os centrale is fused (Kivell and Schmitt, 2009; White et al., 2016). This is indicative that the above feature did not evolve independently across hominoid lineages (Napier & Napier, 1967; Kivell & Schmitt, 2009; Lovejoy, Simpson et al., 2009; Lovejoy, Suwa et al., 2009; Richmond et al., 2016). Even though the os centrale fusion is a shared feature of all hominins, modern human carpal morphology is distinct from other extant or fossil primates (Lewis et al., 1970; Marzke et al., 2007; Wolfe et al., 2006; Richmond et al., 2016). Most anthropoids have trapezoids that are wedge-shaped with a narrow edge projecting towards the palm of the hand and in so doing this projection limits mobility of the wrist during grasping activities (Lewis et al., 1970; Marzke et al., 2007; Richmond et al., 2016). In contrast, modern humans have expanded the palmar portion of the trapezoid to realign the carpal rows for a more effective supination movement, which is crucial for precision grips that generate forces while throwing (Lewis et al., 1970; Marzke et al., 2007; Wolfe et al., 2006; Richmond et al., 2016). This change in the hominoid wrist has been a research focus with implications for human evolutionary history and it may have an effect on locomotor patterns prior to the emergence of bipedalism, in the degree of arboreality in early hominins, as well as for the evolution of human hand dexterity (Marzke & Shackley, 1986; Kivell et al., 2013; Almecija & Alba, 2014; Almecija et al., 2015; Kivell, 2015).

Fossil Hominins and Tool Use

Historically, the hominoid hand was thought to be a passive part of evolution until a more complex and robust central nervous system developed (Napier, 1962; Wolfe et al., 2006). Since less than 1% of the identified animal genera evolved tool-using behaviors, many researchers believe that it is not only necessary for species to have a robust central nervous system but also enhanced brain function for creativity and innovation (Wolfe et al., 2006; Biro et al., 2013). The hominoid hand was viewed as static until crafted tools were found in association with hands unlike modern humans (Napier, 1956; Napier, 1962; Wolfe et al., 2006). Darwin was first to propose the idea that "freeing" the hands was directly linked to tool use (Darwin, 1871; Kivell, 2015). However, the discovery of bipedal *Au. afarensis,* 1.5 Mya before the appearance of stone tools, made researchers link cranial capacity to the evolution of stone tools (de la Torre, 2011; Fiex et al., 2015; Kivell, 2015;).

The cause-effect relationship of tool-related behaviors and hominin bipedalism is less accepted within paleoanthropology currently (Marzke, 1983; Richmond et al., 2001; Kivell 2015). Enhanced dexterity appears in the fossil record around 3.2 Mya. Some interpretations of the earliest hominins (*Orrorin* and *Ardipithecus ramidus*) suggest potential human-like precision grips almost 4 Mya before the first known modified stone tool appears in association with *Homo habilis* (around 2 to 1.5 Mya; Panger et al., 2003; Almecija et al., 2010; Marzke, 2013; Kivell, 2015). The first appearance of stone tools associated with fossil specimens is still debated, with innovation credit most commonly being given to the aptly named *Homo habilis* (the "handy-man"), although evidence is growing for earlier stone tool manufacturing (Semaw et al., 1997;

Ambrose, 2001; Panger et al., 2003; McPherron et al., 2010; Kivell et al., 2011; Kivell et al., 2013; Kivell, 2015).

The latest evidence of flesh removal from bones or percussion marks for marrow access indicates that the earliest stone tool manufacturing practices date to around 3.42 to 3.24 Mya (McPherron et al., 2010; Harmand et al., 2015). This discovery predates the oldest direct evidence (stone tools being discovered directly associated with fossil specimens) of stone tool manufacturing from Ethiopia (2.6 to 2.5 Mya) by more than 800,000 years (Semaw et al., 1997; McPherron et al., 2010). *Australopithecus afarensis* (3.9 to 2.9 Mya) hand bones show capabilities for power grip postures without the robust fifth metacarpal that is thought to be necessary for modern power grip postures (Marzke et al., 1992; Wolfe et al., 2006; Kivell, 2015). Partial acceptance of morphological capabilities for precision grips earlier in the fossil record than appearance of stone-tools indicates that fossil hominins did not necessarily need to "free" hands from functional requirements of locomotion to increase their dexterity (Clarke, 1999; Kivell, 2015). More likely, early hominins were capable of combining functional requirements of arboreal locomotion and enhanced dexterity (Kivell et al., 2013; Kivell, 2015; Fiex et al., 2015).

Kivell (2015) suggests that the time lag between the appearance of enhanced dexterity and stone tool emergence is due to organic material not preserving in the fossil record or tools not being recognizable to modern notions of tools (Panger et al., 2003; Haslam, 2009). Several extant primate taxa, including New and Old World monkeys and hominoids, have been observed modifying plants for tool use (Panger et al., 2003; Haslam, 2009; Kivell, 2015). The most compelling evidence of tool use in the LCA of *Pan* and *Homo* (8 to 5 Mya) is that our closest relative, chimpanzees, frequently modifies organic materials for tool use (Parker & Gibson, 1977; McGrew, 1992; Panger et al., 2003). Fossil hominins are associated with environments of riparian forests, wooded habitats and grasslands that would have high-energy, difficult-to-acquire foods such as nuts, social insects, and honey (Reed, 1997; Plummer et al., 1999; Panger et al., 2003). Similarly, in chimpanzees' environment, raw materials, such as sticks, grasses, leaves and stones, were available for tool-making to facilitate in obtaining high-energy foods (McGrew, 1992; Panger et al., 2003). Over several million years, grip positions enabled use of our hands in food-gathering, food-processing, and tool making patterns which would make bipedal life easier and more cost-efficient (Marzke et al., 1992; Marzke, 1997; Wolfe et al., 2006).

CHAPTER 3

METHODS

Living primate specimens that were analyzed in this study include *Homo sapiens* (n = 20; 10 male, 10 female), *Pan troglodytes* (n = 20; 11 male, 9 female), *Gorilla gorilla* (n = 20; 10 male, 10 female), *Papio anubis* (n = 3; 2 female), *Papio* (n = 9; 5 male, 3 female, 1 unknown), *Mandrillus leucophaeus* (n = 3; 2 male, 1 unknown), *Cebus apella* (n= 9; 1 female, 8 unknown), *Cebus capucinus* (n = 8; 5 male, 1 female, 2 unknown), and *Macaca fascicularis* (n = 18; 2 male, 16 unknown). Fossil hominins include *Australopithecus sediba* (n = 1), *Homo naledi* (n = 2), and *Homo neanderthalensis* (n = 2). In the collections of Field Museum of Chicago *Mandrillus leucophaeus* is labelled as *Papio leucopheaus*. Available fossil hominins were located at the Cleveland Museum of Natural History; unavailable specimens were located through published photographs in other papers.

Hand Proportions

Hand proportions were measured in two ways according to Almecija et al. (2015): intrinsic hand proportions (IHP) and shape analysis of extrinsic hand proportions (EHP). While

Almecija et al. (2015) use these terms, I use the terms “inner hand proportions” to describe IHPs and “hand proportions including geometric means” to describe EHPs. Inner hand proportions were computed as a ratio between the long bones of the thumb (metacarpal, proximal, and distal phalanges) and the long bones of the fourth ray not including the distal phalanx (Almecija et al., 2015). The distal phalanx of the fourth ray was not be included because it is commonly lost in the fossil record due to its small size. Many specimens did not have the distal phalanx of the first digit associated with their skeleton. Specimens with all phalanges present were analyzed and compared. In addition, all measurements of distal phalanxes of the first digit were omitted and ratios were computed without this variable. Ratios of specimens with distal phalanxes and ratios without distal phalanxes included were compared against each other.

Hand proportion including geometric means were analyzed by standardizing the length (mm) of manual elements (same used in the inner hand proportions analysis) by BM (kg) associated with each individual (finger element / BM; Almecija et al., 2015). For specimens for which body mass was not available, an average body mass was used for species and sex of the specimens (Primate Research Center, University of Wisconsin-Madison). Specimens with no sex specified were compared to lowest known male body mass of their species with anything below being considered female. Human body mass was determined by using averages from the early 18th century (Odgen et al., 2004: Flegal et al., 2012) due to the fact that most of the Hamann-Todd Collection at the Cleveland Natural History Museum was acquired from 1910 – 1940 (Mensforth & Latimer, 1989; Kern, 2006). Body mass was included since previous observations on modern ape thoraces and limbs suggest living apes have similar adaptations to fulfill similar functional demands related to specialized locomotion (Tuttle, 1975; Larson, 1998; Almecija et al., 2013; Almecija et al., 2015). Due to this, similarities in hand length proportions between suspensory taxa, including geometric means of the hand, may account for homoplastic hypotheses (Almecija et al., 2015). This model adapts evolutionary scenarios by using the Ornstien-Ulenbeck (OU) stabilizing selection model (Hansen, 1997; Almecija et al., 2015). OU attempts to identify cases where multiple lineages have convergently evolved similar phenotypes (Hansen, 1997; Almecija et al., 2015). Using this stabilization technique attempts to detect instances of phenotypic convergence in hand proportions across taxa (Almecija et al., 2015). Since tissue density is similar in all terrestrial organisms, mass can be assumed as roughly the same as volume, and the cube root of BM is proportional to linear size (Sneath & Sokal, 1973; Jungers, 1985; Almecija et al., 2015). An ANOVA test was run on hand proportions including geometric means to recognize any significant differences between species measured.

To further investigate similarities between hand evolution and morphology, the proportional composition of each ray measured was graphed for each species. A mean was calculated for each species and compared to see if there was consistency across species in bones of the hands. This allows for further comment on whether hand proportions are homologous in nature or convergently evolved. These relationships could also be used in the future to predict missing data in the fossil record

Phalangeal Curvature

Phalangeal curvature is analyzed using the Jungers et al. (1997) methodology including radius of curvature and the included angle of the phalanges (see Fig. 2). Proximal phalanges were used due to the structure-function feedback expressed in biomechanical theory and experimental evidence (Lanyon, 1980; Stern et al., 1995; Jungers et al., 1997). Through this analysis of phalangeal curvature, photographs of otherwise unavailable specimens can be used to collect data. This analysis will assess the validity of the perceived need to reduce arboreality for enhanced dexterity.

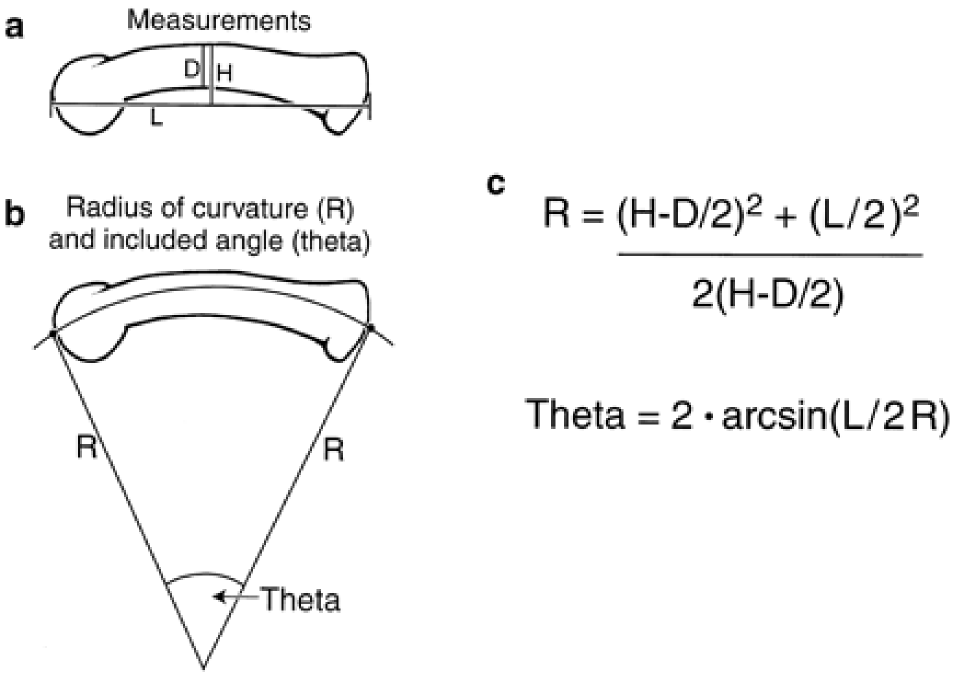

Figure 2: Methodology measurements of phalangeal curvature (Stern et al., 1995)

Carpal Architecture

Currently, only two carpal architecture characteristics are viewed as synapomorphic within the fossil hominin record (Richmond et al., 2016). In humans and African apes, the os centrale/scaphoid fusion is thought to limit mobility and aid in stability during knuckle-walking (Tuttle, 1975; Sarmiento, 1988; Gebo, 1996; Richmond et al., 2016). However, this os centrale/scaphoid fusion is observed in both extant and extinct species that do not exhibit patterns of knuckle-walking: *Indri, Avahi, Lepilemur* and *Babakotia* (Kivell & Begun, 2007; Richmond et al., 2016). As discussed earlier, modern humans have a distinct pattern of their trapezium and trapezoid from other primate species (Richmond et al., 2016). Carpal architecture that is necessary for true precision grip (according to Richmond et al., 2016) is measured through the relative joint surface area of the first metacarpal articulation of the trapezium and the shape of the trapezium.

Relative surface area of the first metacarpal articulation site on the trapezium was measured with the software Image J (Rasband, 2016). Photographs of the distal view of the trapezium were used to create ratios of joint surface to total bone area. Trapezoid morphology was rated based on circularity and solidity across species. Trapezoids were photographed from the distal view. Total circularity and solidity were measured in Image J. Circularity is a measure of an object compared to a perfect circle (with a perfect circle being expressed as 1). Solidity measures the convexity of an object based on a Y and X axis created within the program.

Statistical Analysis

All the statistical analyses were done within RStudio and SPSS (IBM Corp., released, 2013; RStudio Team, 2015). All variables were analyzed by running an ANOVA with a post hoc Tukey test (alpha = .05, CI = .95). ANOVAs were implemented to test for differences of species means across variables for inner hand proportions, hand proportions including surface material, phalangeal curvature (radial and included angle), and carpal architecture (relative trapezium joint surface and shape of the trapezoid). A post hoc Tukey test was chosen to assess differences across species and variables. Since data were non-normally distributed with uneven sample sizes, the Tukey test is appropriate as it is most robust to these characteristics. Finally, PCA (principal component analysis) was used to test for groupings of similar species based on all variables. If overlap does occur in the output of a principal component analysis test with humans, it may suggest that true precision grip is possible in other non-human primates and this result would signify that tool use would have been possible before the appearance of the genus *Homo* in the fossil record.

CHAPTER 4

RESULTS

Hand Proportions

Inner Hand Proportions

Inner hand proportions (IHP) describe the length of the fourth digit in relation to the first digit of the hand. High IHPs demonstrate longer fourth digits relative to the first digit. For example, *Pan troglodytes* has an IHP of 2.78 and this proportion shows that the fourth digit of a chimpanzee is almost three times as long as its first digit. While IHP does measure the general relationship between fourth and first digits, it does not indicate if similarities are homologous or convergent in terms of primate evolution.

In this proportional calculation (IHP), more than 50% of the specimens were missing the distal phalanx of either one or both digits measured. Due to this sampling problem, two methods were used to calculate a species' IHP. The first method used specimens that had all the previously discussed components present, including the distal phalanx, associated with their skeletons. The second method removed the measurements of the distal phalanx from both the first and the fourth digits. IHP values were then compared across the two methods to verify the accuracy of results. While the IHP themselves did change in value, similarities in associated groups stayed the same visually and statistically (Figs. 3, 4).

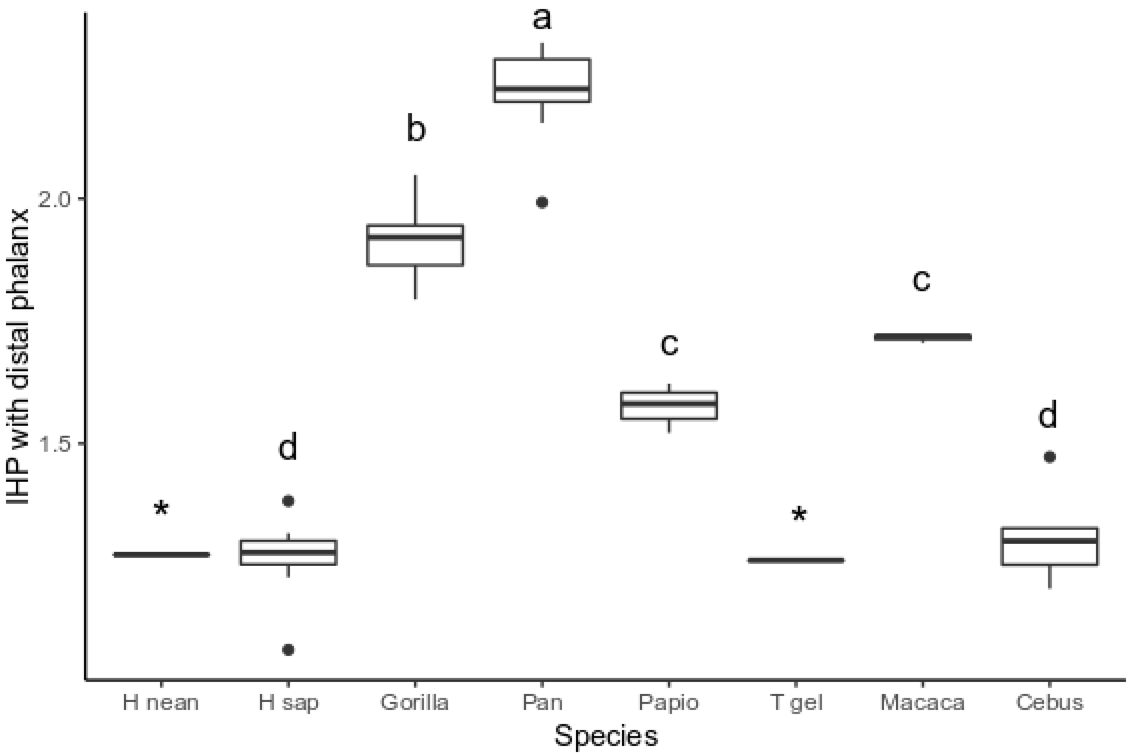

Figure 3: Inner hand proportions (IHP) with distal phalanx across species. Mean IHPs represented by black lines; asterisks represent species without large enough sample sizes to be included in statistical analysis; groups of statistical association marked by lower-case letters described in Table 1.

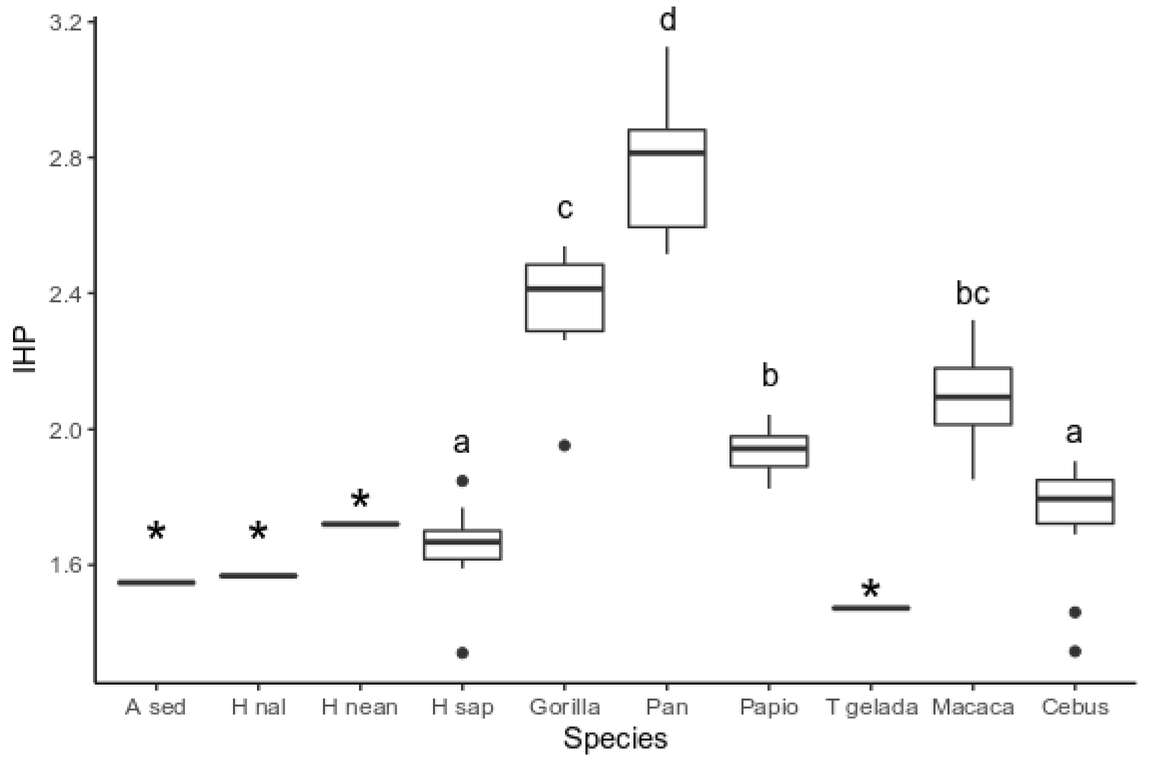

Figure 4: Inner hand proportions (IHP) excluding distal phalanx across species. Mean IHPs represented by black lines; asterisks represent species without large enough sample sizes to be included in statistical analysis; groups of statistical association marked by lower-case letters described by Table 2.

Four groups are present after the statistical analysis of hand proportions (Table 1). This first group (a from Table 1) consists of species with fourth digits less than two times the length of the first digit. In this group, a relationship between *Homo sapiens* and *Cebus* is found as both have either elongated their thumbs or shortened their fingers to create similar inner hand proportions. *Theropithecus gelada* appears visually similar to *Homo sapiens* and *Cebus apella* (see Fig. 3). Since only one specimen was able to be located at the museums visited, gelada baboons were not able to be included in statistical analysis. The second statistical grouping (b from Table 1) shows a link between *Cebus*, *Papio* and *Macaca.* The second group consists of species with fourth digits around two times the length of the first digit. The third statistical grouping (c from Table 1) is between *Macaca* and *Gorilla*, with fourth digits being more than two times as long as first digits, but less than three times as long. The fourth statistical grouping (d from Table 1) consists of only *Pan*. Here *Pan* is considered an outlier and is unlike any of the other primates examined in this ratio comparison as *Pan* has fourth digits almost three times as long as its first digit.

Table 1: Tukey test results of inner hand proportions with distal phalanx of digit 1 between species (associated with Figure 3)

Species	n	IHP
Cebus (d)	7	1.30 (± 0.091)
Macaca (c)	3	1.71 (± 0.009)
Papio (c)	7	1.58 (± 0.039)
T. gelada (d)	1	1.26 (± NA)
Gorilla (b)	5	1.91 (± 0.951)
Pan (a)	8	2.21 (± 0.105)
H. sapiens (d)	19	1.27 (± 0.059)
H. naledi (d)	1	1.25 (± NA)
H. neanderthalensis (d)	1	1.27 (± NA)

Table 2: Tukey test results of inner hand proportions without distal phalanx of digit 1 between species (associated with Figure 4)

Species	n	IHP
Cebus (d)	11	1.74 (± 0.179)
Macaca (c)	15	2.08 (± 0.127)
Papio (c)	12	1.94 (± 0.071)
Gorilla (b)	8	2.36 (± 0.190)
Pan (a)	12	2.77 (± 0.189)
H. sapiens (d)	19	1.66 (± 0.100)

As noted above, similar IHP ratio values do not seem to be tied directly to closest phyletic relative. For example, gorillas show an inner hand value of 2.36 while chimpanzees show a value of 2.78. As expected, IHP value for species that are from the same genus are closely associated with each other. Old World monkey IHP values are statistically similar to one another and fall into the second grouping with fourth digits being about twice as long as their first digit. Both *Papio* and *Macaca* are known to use more generalized hand patterns for a mixture of terrestrial and arboreal locomotion (Patel, 2009a, 2009b). In addition, *Homo sapiens* and *Cebus* show the strongest similarities of inner hand proportions and these two species are not considered to have analogous hand functionality.

Due to small sampling size, *Australopithecus sediba*, *Homo neanderthalensis,* and *Homo naledi* could not be included in the statistical analysis. Visual analysis of these species using the box plot discussed in Figures 3 and 4 shows a close similarity with the inner hand proportions (IHP) of *Homo sapiens.* These results for the taxa in the genus *Homo* were expected due to their close phyletic relation and their unique ability to make stone tools. Kivell et al. (2011) suggested that the hand anatomy of *Australopithecus sediba* should be considered the basal condition associated with stone tool use and production. The similar inner hand proportions (IHP) of *Australopithecus* and *Homo* support her hypothesis.

What are we to make of the inner hand proportions across the taxa examined here? First, *Homo sapiens* does not stand alone as its inner hand proportions are similar to both fossil hominins and the New World monkey *Cebus*. This suggests similar IHP values may not be indicative of similar hand functionality nor may it be associated with a specific locomotor pattern. Napier (1956) had suggested that inner hand proportions could affect a primate’s ability to achieve “true” and “modified” precision grips. Results of this study support Napier’s (1956) hypothesis, although other factors may inhibit a primate’s ability to achieve precision grip postures.

Hand Proportions Including Geometric Means

Hand proportions including the geometric mean data modifications did not produce results different from that of the inner hand proportions noted above. Using body mass to standardize the proportional relationships between each variable in the hand created different values but, in the end, did not create a new result when they were summed together to create a ratio value for hand proportions. In addition, when these new values were analyzed as percentages of the first and fourth digits their values did not differ from the values that are discussed in the phalanx ratios section.

Phalanx Ratios

The proportional contributions of individual hand components to the overall hand length were measured to compare across the species examined in this study. Many ideas have been presented concerning the evolution of precision grips in modern humans (e.g. Napier, 1956; Avis, 1962; Parker, 1973; Marzke & Marzke, 2000; Almecija et al., 2015; Kivell, 2015). For example, Napier (1956) suggests that the elongation of the thumb is a key factor in the employment of "true" precision grips in modern humans whereas Kivell (2015) suggests enhanced dexterity mimicking that of modern humans in *Theropithecus gelada* is only made possible by a shortening of the fingers instead of an elongation of the thumb. This analysis of phalanx ratios allows for more specific comments on these possible evolutionary scenarios.

Ratios of phalanx segments were calculated to aid in the prediction of missing data in the specimens from the fossil record. Distal phalanges are missing from the primate and human fossil record due to their light and easily breakable bone structure (Almecija et al., 2015; Richmond et al., 2016). In this study, there were several missing components of hand anatomy including more than the distal phalanges of a digit. A methodology was developed to predict missing element data, but these mathematical equations were not able to account for variation across species. No extensive research has been performed on phalangeal ratios across extant primates, with a few exceptions including *Carpolestes simpsoni* (Bloch & Boyer, 2002), Scadentia, Dermoptera, and plesiadapiforms (Hamrick, 2001). *Equatorius africanus* (Patel et al., 2009) was analyzed in terms of its phylogenetic relationship based on its hand element ratios in terms of primate origins.

Homo sapiens shows first digits with first metacarpals consisting of almost half the overall digit length while possessing short distal phalanges (first metacarpal = 47%, first distal phalanx = 23%; Fig. 5). Fourth digits of *Homo sapiens* have slightly shorter metacarpals in comparison to their first rays with the largest percentage of the fourth digit consisting of the proximal phalanx. *Homo sapiens* seems to visually differ in lengths of first metacarpal from *Homo neanderthalensis* and *Homo naledi*. Statistical analysis of the *Homo* taxa reveals close association across all components of the hand. Surprisingly, *Pan* and *Gorilla* are similar in digital proportional lengths to *Homo* even though their inner hand proportions (IHP) are significantly different,although a close African ape phylogenetic relationship could explain these digital similarities.

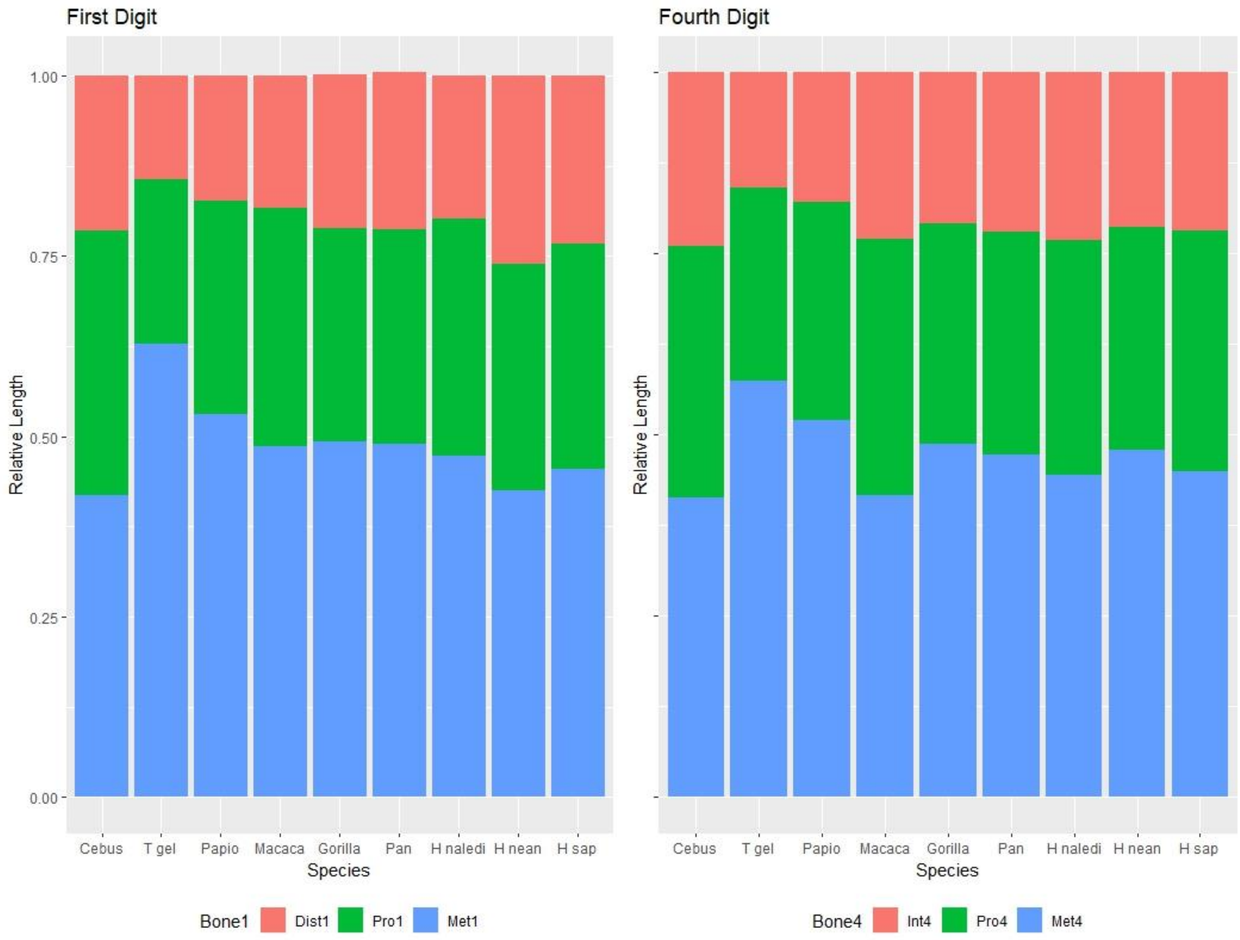

Figure 5: Phalanx ratios of first and fourth rays standardized by body mass- Met1 = First metacarpal, Pro1 = first proximal phalanx, Dist1 = first distal phalanx, Met4 = fourth metacarpal, Pro4 = fourth proximal phalanx, Int4 = fourth intermediate phalanx.

In Figure 5, the smallest proportional contribution of the first and fourth metacarpals is expressed in *Cebus*, meaning a greater proportion of their digit length is due to proximal phalanges. *Macaca* have similar digital ratios with slightly longer first and fourth metacarpals in comparison to *Cebus* (Fig. 5). Unlike the comparison between great apes and modern and fossil humans, this similarity cannot be explained through a close phyletic relationship.

Theropithecus gelada hand proportions differ significantly from other primates (Fig. 5) as noted by Napier (1956), Parker (1973) and Kivell (2015). The first and fourth metacarpals of *Theropithecus* make up more than half the digit's length, with extreme shortening of the proximal, intermediate, and distal phalanges. *Papio* follows a similar pattern of hand element ratios expressed in *Theropithecus*. The proportional contribution of the metacarpals for the first and fourth digits of *Papio* is slightly less than seen in *Theropithecus*. The other phalangeal elements in these digits of *Papio* are similar in proportional contribution to that of gelada baboons. This Old World monkey pattern can be explained through the close phylogenetic relationship of these two taxa similar as noted above for the African apes.

Statistical groupings of the digital elements varied based on the phalanx being assessed (Tables 3, 4, 5, 6, 7, 8). No special relationships were correlated across both the first and fourth rays across these species. While some surprising associations did appear (for example *Homo neanderthalensis* and *Cebus* in the first metacarpal; *Pan* and *Macaca* in the first metacarpal; *Gorilla* and *Cebus* in the first distal phalanx; see Table 3, 5), no consistent pattern emerged across this analysis. The similarities that could be noted in the hand components were outside of any close phyletic relationships, for example in *Homo naledi* and *Cebus* (5 out of 6 ratio values for individual elements).

Table 3: Tukey test analysis of the first metacarpal across species, displaying means across groups

Species	n	Metacarpal (1) Ratio of Digit
Cebus (e)	7	0.42 (± 0.005)
Macaca (c)	3	0.49 (± 0.017)
Papio (b)	7	0.53 (± 0.011)
T. gelada (a)	1	0.62 (± NA)
Pan (c)	7	0.48 (± 0.016)
Gorilla (c)	5	0.49 (± 0.014)
H. sapiens (d)	19	0.45 (± 0.155)
H. naledi (cd)	1	0.47 (± NA)
H. neanderthalensis (de)	1	0.42 (± NA)

Table 4: Tukey test analysis of the first proximal phalanx across species, displaying means across groups

Species	n	Proximal (1) Ratio of Digit
Cebus (a)	7	0.37 (± 0.029)
Macaca (ab)	3	0.33 (± 0.017)
Papio (bc)	7	0.30 (± 0.011)
T. gelada (c)	1	0.22 (± NA)
Gorilla (bc)	7	0.30 (± 0.017)
Pan (bc)	8	0.31 (± 0.024)
H. sapiens (bc)	19	0.31 (± 0.017)
H. naledi (ab)	1	0.33 (± NA)
H. neanderthalensis (abc)	1	0.32 (± NA)

Table 5: Tukey test analysis of the first distal phalanx across species, displaying means across groups

Species	n	Distal (1) Ratio of Digit
Cebus (ab)	7	0.21 (± 0.029)
Macaca (bc)	3	0.18 (± 0.004)
Papio (c)	7	0.17 (± 0.017)
T. gelada (c)	1	0.14 (± NA)
Gorilla (ab)	5	0.21 (± 0.011)
Pan (ab)	8	.22 (± 0.021)
H. sapiens (a)	10	0.23 (± 0.015)
H. naledi (abc)	1	0.19 (± NA)
H. neanderthalensis (a)	1	0.26 (± NA)

Table 6: Tukey test analysis of the fourth metacarpal across species, displaying means across groups

Species	n	Metacarpal (4) Ratio of Digit
Cebus (d)	7	0.41 (± 0.019)
Macaca (cd)	3	0.42 (± 0.020)
Papio (a)	7	0.52 (± 0.019)
T. gelada (a)	1	0.57 (± NA)
Gorilla (b)	5	0.49 (± 0.016)
Pan (bc)	8	0.47 (± 0.023)
H. sapiens (c)	19	0.45 (± 0.010)
H. naledi (cd)	1	0.45 (± NA)
H. neanderthalensis (cd)	1	0.48 (± NA)

Table 7: Tukey test analysis of the fourth proximal phalanx across species, displaying means across groups

Species	n	Proximal (4) Ratio of Digit
Cebus (a)	7	0.35 (± 0.003)
Macaca (ab)	3	0.35 (± 0.015)
Papio (cd)	7	0.30 (± 0.013)
T. gelada (d)	1	0.27 (± NA)
Gorilla (cd)	5	0.31 (± 0.014)
H. sapiens (ab)	19	0.33 (± 0.011)
H. naledi (abc)	1	0.32 (± NA)
H. neanderthalensis (bcd)	1	0.31 (± NA)

Table 8: Tukey test analysis of the fourth intermediate phalanx across species, displaying means across groups

Species	n	Intermediate (4) Ratio of Digit
Cebus (a)	7	0.23 (± 0.022)
Macaca (ab)	3	0.23 (± 0.009)
Papio (b)	7	0.18 (± 0.013)
T. gelada (b)	1	0.16 (± NA)
Gorilla (b)	5	0.21 (± 0.015)
Pan (ab)	8	0.22 (± 0.014)
H. sapiens (ab)	19	0.22 (± 0.016)
H. naledi (ab)	1	0.23 (± NA)
H. neanderthalensis (ab)	1	0.21 (± NA)

Phalangeal Curvature

Radius of Curvature

Phalangeal curvature was analyzed in two different ways. The first analysis used radial curvature which is expressed as a whole number. Radial curvature can be influenced not only by the curvature of a phalanx but by its overall length. If a specimen has a higher radial curvature than the other, it could simply mean that the phalanx is more curved or that the phalanx is significantly longer than the other specimen. Further, curvature values directly correlate with the radius of an enclosed circle if the phalanx extended.

Figures 6 and 7 show African apes and humans to have similar values of radial curvature with values above 7. Other species such as Papio*, Cebus,* and *Macaca,* were closely associated statistically and visually with radial curvature values below 5. As noted above, these values could be due to a close similarity in phalangeal curvature or a similarity in length. To analyze these correlations more specifically, included angle was measured in addition to radial curvature.

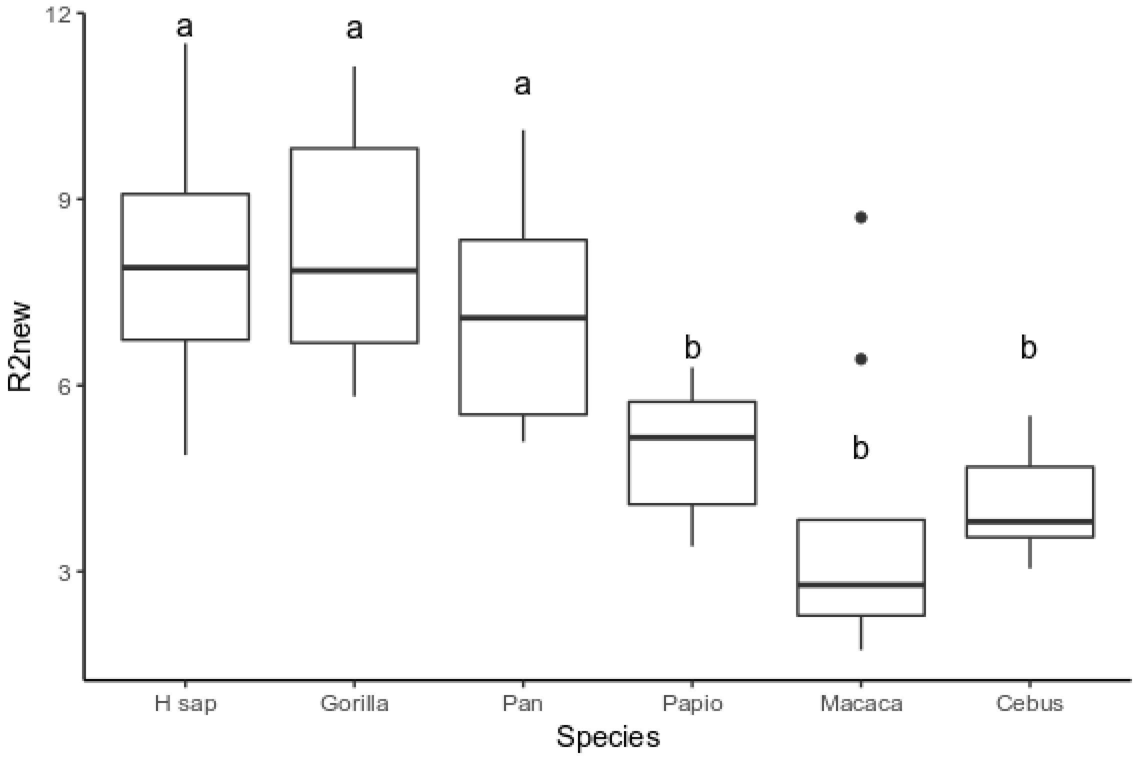

Figure 6: Radius (mm) of the second proximal digit. Mean radial curvature are represented by black lines, groups of statistical association marked by lower-case letters.

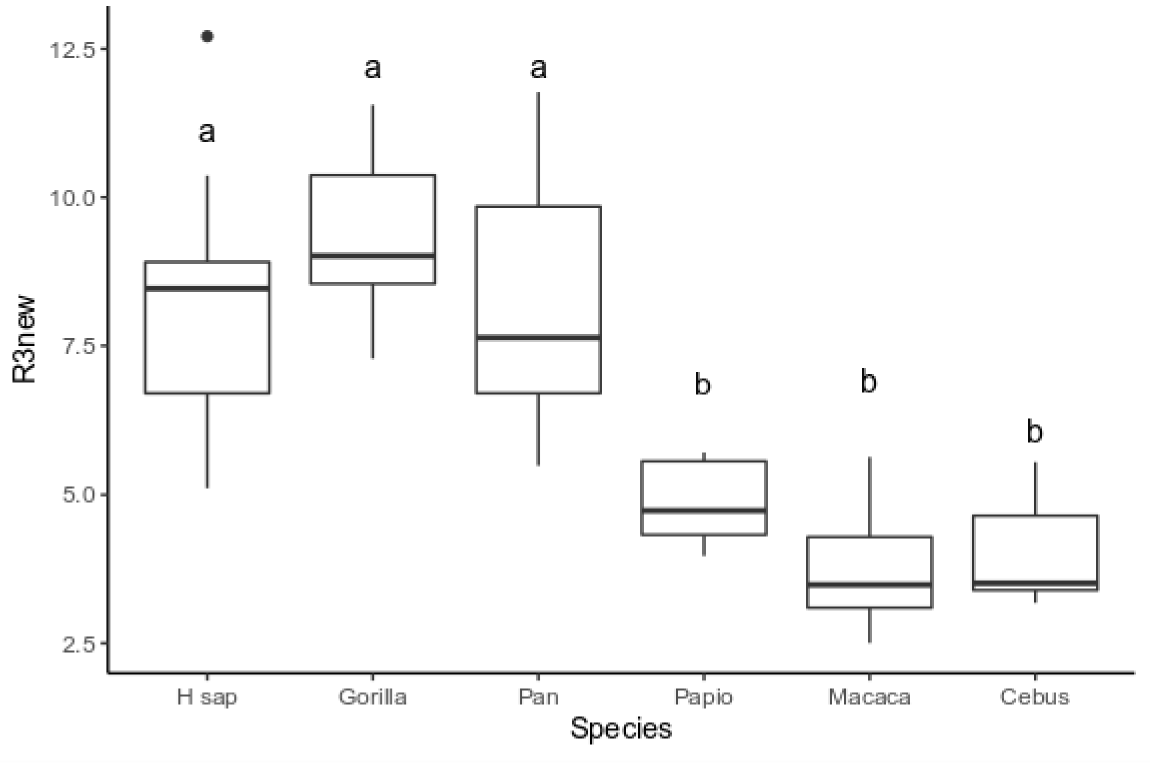

Figure 7: Radius (mm) of the third proximal digit. Mean radial curvature are represented by black lines, groups of statistical association marked by lower-case letters.

The results of the radius of phalanx curvature are consistent across phylogenetic relationships. Additionally, the radius of phalanx is consistent across locomotor patterns (i.e., knuckle-walking, and general hand use) as well. No statistical difference was present in the radial curvature of the second and third digits analyzed here. Visual and statistical groupings stayed consistent in all species and across both rays that were analyzed (Figs. 6, 7).

Included Angle

The second analysis of phalangeal curvature is included angle. Included angle creates an angle using the radial value extended from the terminal ends of a specimen's phalanx. Highly curved digital rays will have higher included angles using this technique and flat digital rays should have lower included angles. It is important to note included angle values are less influenced by the overall length of a phalanx.

The largest included angle measured was for Pan at 77 radians and the smallest was noted in *Homo sapiens* and *Cebus* at 55 and 56 radians, respectively. In contrast, the largest radial curvature was found in *Gorilla* and the smallest again in *Cebus*. *Pan* and *Gorilla* are closely associated to each other (Figs. 8, 9) in radial curvature. In addition to this grouping, *Macaca* and *Papio* have closely associated included angles, values also like that of the African apes. Surprisingly, *Homo sapiens* is not associated with the African apes and this observation may indicate that radial curvature was highly influenced by the length of the phalanx rather than by its actual curvature.

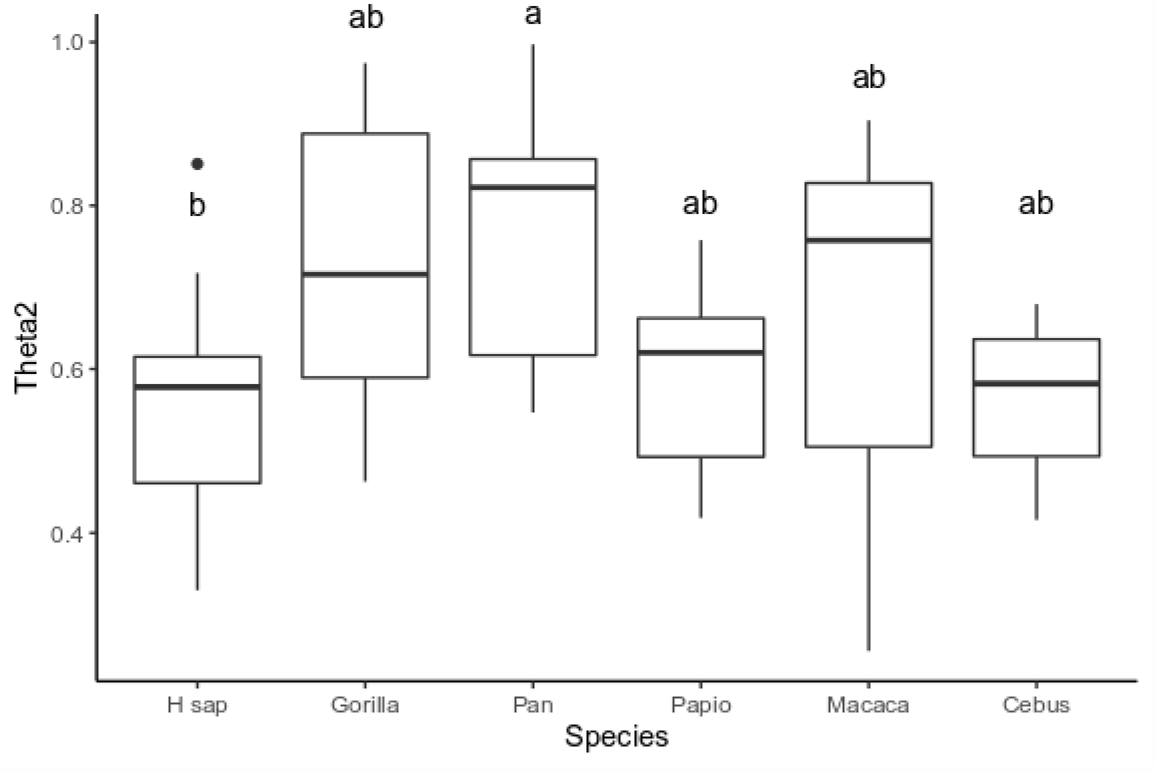

Figure 8: Included angle of the second proximal digit (theta2). Mean thetas are represented by black lines, groups of statistical association marked by lower-case letters described in Table 9.

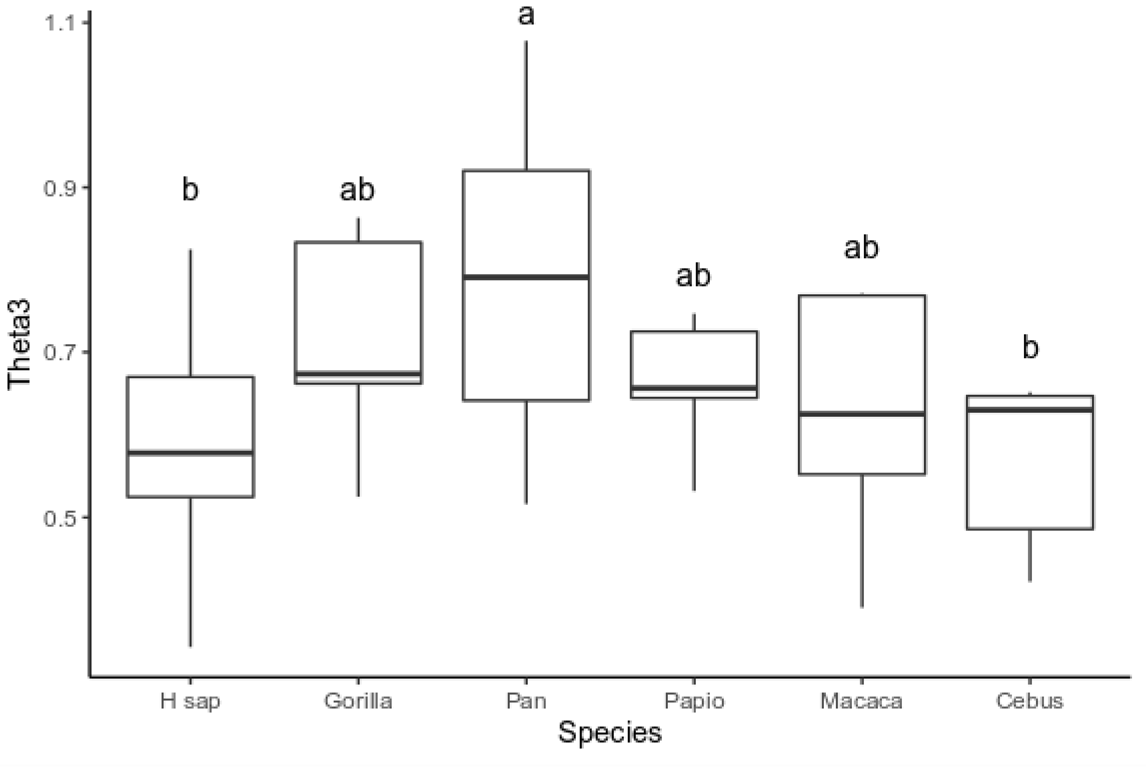

Figure 9: Included angle of the third proximal digit (Theta3). Mean thetas are represented by black lines, groups of statistical association marked by lower-case letters described in Table 10.

Results of the phalanx included angle analysis across species did vary relative to the radius of curvature analysis. Here, statistical groups were less contingent on phylogenetic relationship, as some groupings did correlate with phylogeny. No statistical difference was present in the results of the included angle measurements for the second and third proximal phalanges (Tables 9, 10). As expected, *Pan* and *Gorilla* were closely related. This close association could be the result of their similar locomotion pattern, terrestrial knuckle-walking, although phalangeal curvature is often associated with more suspensory movements rather than terrestrial gaits (Jungers et al., 1997; Richmond, 1998; Richmond, 2007; Matarazzo, 2007; Kivell, 2015; Richmond et al., 2016). Other statistical groupings (a from Table 4.1, 4.2) that could be associated with *Pan* and *Gorilla* were with *Macaca* and *Papio* which do not employ either a forelimb suspensory arboreal movement or terrestrial knuckle-walking (Patel, 2009a; Patel, 2009b; Patel et al., 2012).

The second statistical group (b from Table 9, 10) in this analysis consists of *Gorilla*, *Macaca*, *Papio, Cebus,* and *Homo sapiens.* While *Pan* is statistically similar with other included angle measurements, it is distinct enough here to be the only species that is not present in the second statistical grouping. This result could be indicative of a specialized hand morphology present only in *Pan*, since chimpanzees use both arboreal suspensory and knuckle-walking movements more often than *Gorillas* (Doran, 1993, 1997), creating a more extreme curvature than what is found in the larger and more terrestrial-oriented African ape relative.

Table 9: Tukey test analysis of phalanges included angle of the second ray, displaying means of groups

Species	n	Theta2
Cebus (b)	7	0.56 (± 0.994)
Macaca (ab)	8	0.64 (± 0.243)
Papio (ab)	9	0.60 (± 0.116)
Gorilla (ab)	8	0.72 (± 0.181)
Pan (a)	18	0.77 (± 0.148)
H. sapiens (b)	19	0.55 (± 0.133)

Table 10: Tukey test analysis of phalanges included angle of the third ray, displaying means of groups

Species	n	Theta3
Cebus (b)	6	.57 (± 0.108)
Macaca (ab)	5	.62 (± 0.159)
Papio (ab)	9	0.65 (± 0.078)
Gorilla (ab)	9	.71 (± 0.113)
Pan (a)	19	.78 (± 0.167)
H. sapiens (b)	20	.59 (± 0.117)

Carpal Architecture

Relative Joint Surface Area of the Trapezium

Relative joint surface area of the trapezium was measured to comment on the range of motion present in the hands of the species analyzed in this project. Relative joint surface area is a ratio between the total bone-to-joint surface present on the distal end of the bone. Hypothetically, higher relative joint surface areas would be indicative of a species ability for enhanced opposability. Opposability is an essential part of a primate's ability to create "true" and "modified" precision grips (Napier, 1956, 1962; Napier & Tuttle, 1993; Marzke & Marzke, 2000; Marzke, 2013).

Analysis of the relative joint surface area of the trapezium yielded surprising results (Fig. 10). The species with the largest relative joint surface area is *Papio*, in contrast to the species with the smallest, *Homo sapiens*. I hypothesized that species with already established abilities to employ "true" precision grips would have had the highest relative joint surface areas. This analysis shows the opposite result, with *Homo sapiens* expressing the lowest ratio value at 1.98. *Papio* has not been observed using either "true" or "modified" precision grips and it shows the highest value, being twice as large as that of *Homo sapiens* at 3.87.

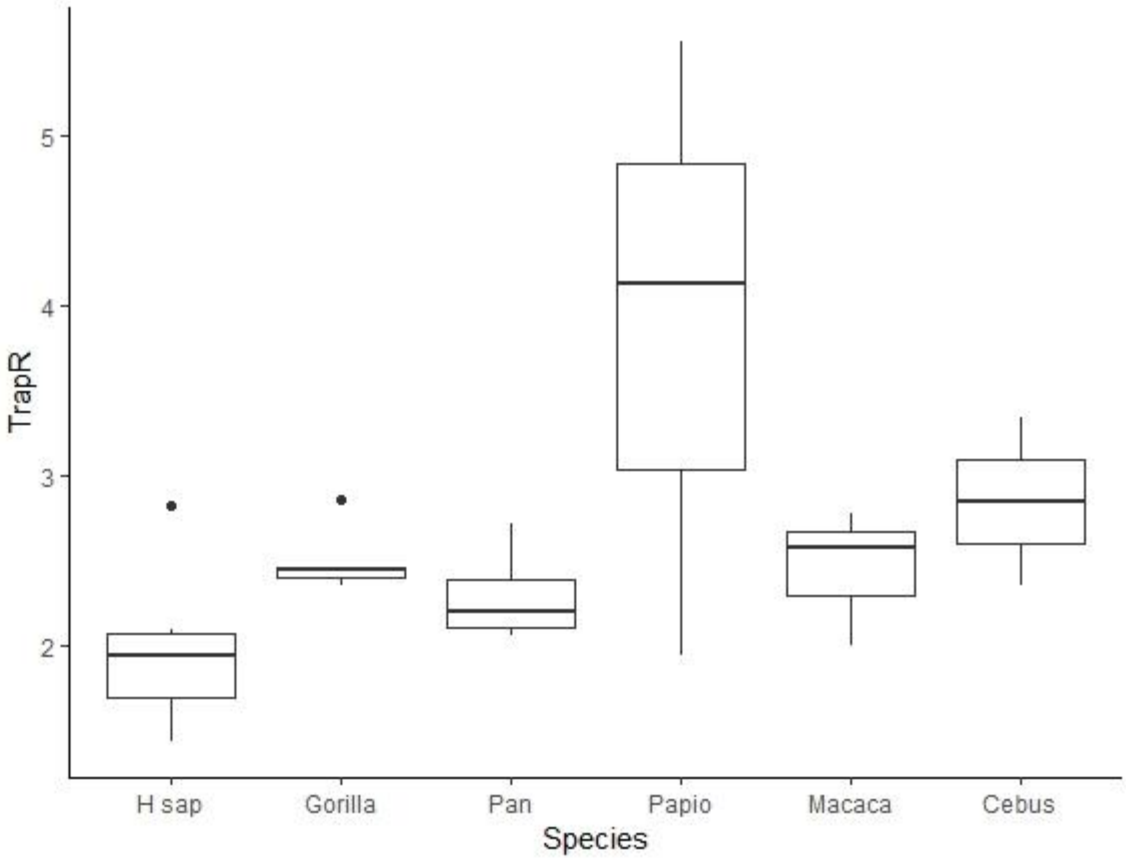

Figure 10: Relative joint surface area of the trapezium. Mean relative joint surface areas are represented by black lines, groups of statistical association marked by lower-case letters described in Table 11.

Statistical groupings in this analysis are not reliant on phylogenetic relationships or on locomotor patterns observed in these species. The first statistical group consists of *Papio, Cebus, Gorilla*, and *Macaca* (a from Table 11) and plenty of overlap is present between the two statistical groups that emerged through this analysis. The second statistical group consists of *Cebus*, *Gorilla, Macaca*, *Pan*, and *Homo sapiens* (b from Table 11).

Table 11: Tukey test analysis of trapezium relative joint surface across species, displaying means of groups

Species	n	Trapezium Relative Joint Surface
Cebus (ab)	2	2.84 (± 0.701)
Macaca (ab)	3	2.45 (± 0.399)
Papio (a)	3	3.87 (± 1.818)
Gorilla (ab)	5	2.50 (± 0.205)
Pan (b)	7	2.28 (± 0.241)
H. sapiens (b)	6	1.98 (± 0.481)

Shape of the Trapezoid

Trapezoid morphology measured through circularity (Fig. 11) and solidity (Fig. 12) did not show any statistical differences between species. While visually there are differences between the morphology of the trapezoid across species, no statistical differences were present in this analysis. In contrast to what Richmond et al. (2016) present, there do not seem to be important differences in the convexity of this bone.

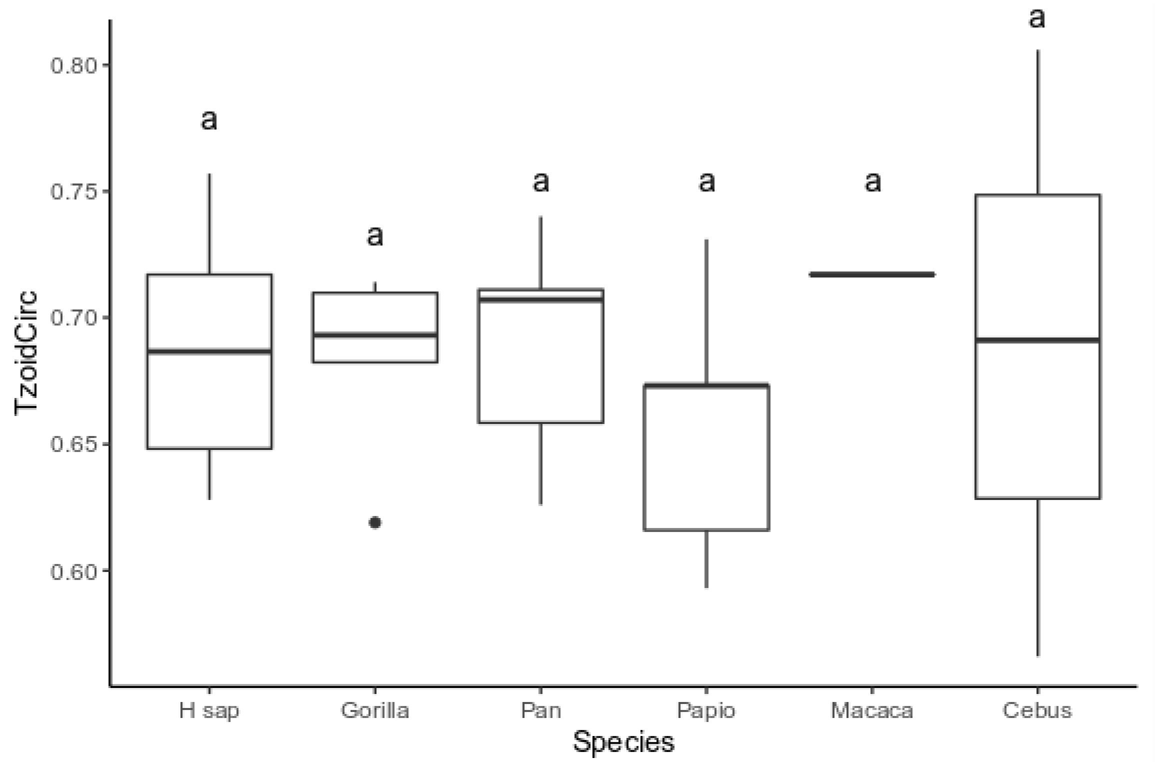

Figure 11: Morphology of trapezoid circularity in species analyzed. Mean circularity represented by black lines, lower-case letter associated with statistical grouping of species.

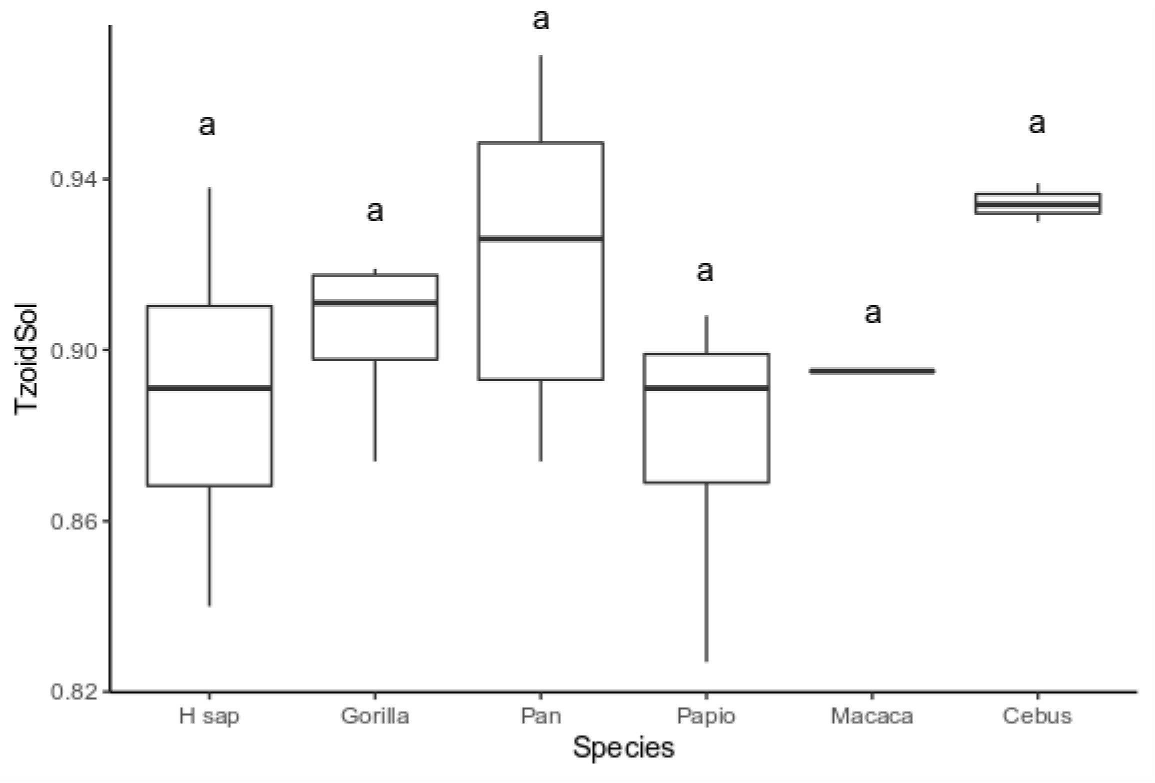

Figure 12: Morphology of trapezoid solidity in species analyzed. Mean solidity represented by black lines, lower-case letter associated with statistical grouping of species.

Principal Component Analysis

A principal component analysis (PCA) was conducted on the variables that were most complete across the species, that being the inner hand proportions and the radius and included angle of phalangeal curvature. Relative joint surface area of the trapezium and shape of the trapezoid were excluded due to incomplete data.

The PCA results show that the largest differences between primate species studied here can be accounted for by inner hand proportions (Fig. 13). *Pan* and *Gorilla* are grouped closely together since their inner hand proportions are similar, as is their phyletic similarity. In addition, to having similar inner hand proportion, *Pan* and *Gorilla* have similar phalangeal curvature (radius and included angle) and this means that the overlap of all variables in this analysis is expected and observable in the PCA plot. As predicted, *Homo sapiens* is not grouped with the other African apes. *Homo sapiens* is grouped closer to *Papio* and *Macaca* than to African apes, its phyletic relatives. *Cebus*, the only New World monkey analyzed, is grouped farthest away from the other primates, although this result could be a problem due to its small sample size.

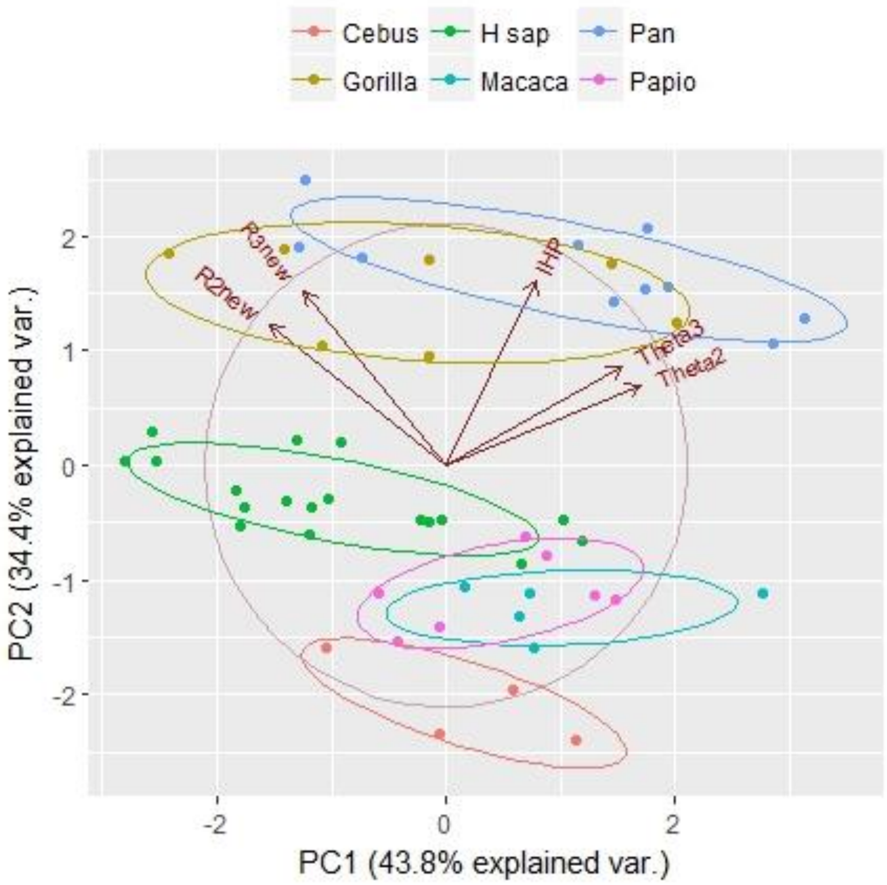

Figure 13: PCA analysis across species with inner hand proportions and phalangeal curvature (radius and included angle).

CHAPTER 5

DISCUSSION

Hand Proportions

Inner Hand Proportions

Hand proportions are an integral part of our ability to utilize a true precision grip. In contrast, non-human primates use their hands in a variety of ways including many types of specialized locomotor movements (e.g., knuckle-walking and brachiation) and these primates are unable to achieve a modified precision grip due to anatomical restrictions. Even African apes, our closest living relatives, do not exhibit hand proportions similar to the hands of modern and fossil humans.

Given that non-human primates with a more generalized pattern of hand use show inner hand proportions similar to modern humans and fossil hominins, I hypothesized that living primates should be capable of modified precision grips. Preuschoft et al. (1993), Fagergren et al. (2000), and Grinyagin et al. (2005) indicate that a true precision grip can be deemed biomechanically different from that of a modified precision grip. Hand biomechanics could account for these differences separating living primates from the genus *Homo* and our ability to make advanced stone tools.

Results of this study indicate that more research is needed regarding tool making and tool using abilities across living primates that do not show specialized types of locomotion. Rolian et al. (2011), for example, conclude that the thumb and hand anatomy of *Pan* or *Australopithecus* would present biomechanical challenges for habitual tool use. I suggest that the Rolian et al. (2011) conclusion may yield a different result if other living primates without specialized movements are analyzed in a similar manner.

Hand Proportions Including Geometric Means

This study did not show any different results from the inner hand proportion measurements and their proportions including using geometric means as a size standardizer after the Almecija et al. (2015) methodology. Using body mass to standardize the measurements of the inner hand proportions changed the units of measurement, but the ratio comparison of two rays were unchanged by this technique. The Almecija et al. (2015) visual representation of hand proportions, including geometric means, with a stacked bar graph is very similar to my representation of phalanx component ratios (Fig. 14). Overall the results of this technique were the same as inner hand proportions. Standardizing the length by body mass would not change the ratio because the ratios would need to equal a hundred to account for both rays in the equation. Splitting the graph between the two proportions only visually manipulates the data to seem as if the results differ, but when the relative lengths are summed up and turned into a ratio, they are exactly the same as inner hand proportions. In addition to this, when the hand proportions including geometric means are turned into percentages and compared to the phalange components that I analyzed, the percentages of the digit results were identical without standardizing for body mass. While Almecija et al. (2015) did use an Ornstien-Ulenbeck (OU) stabilization model in addition to their other method of analyzing hand proportions, the results for inner hand proportion in primates in this stabilization model would have been similar as the OU standardization model since this technique is a continuous-time analogue and would not require any standardization of these measurements (Doob, 1942; Gajda & Wylomanska, 2015).

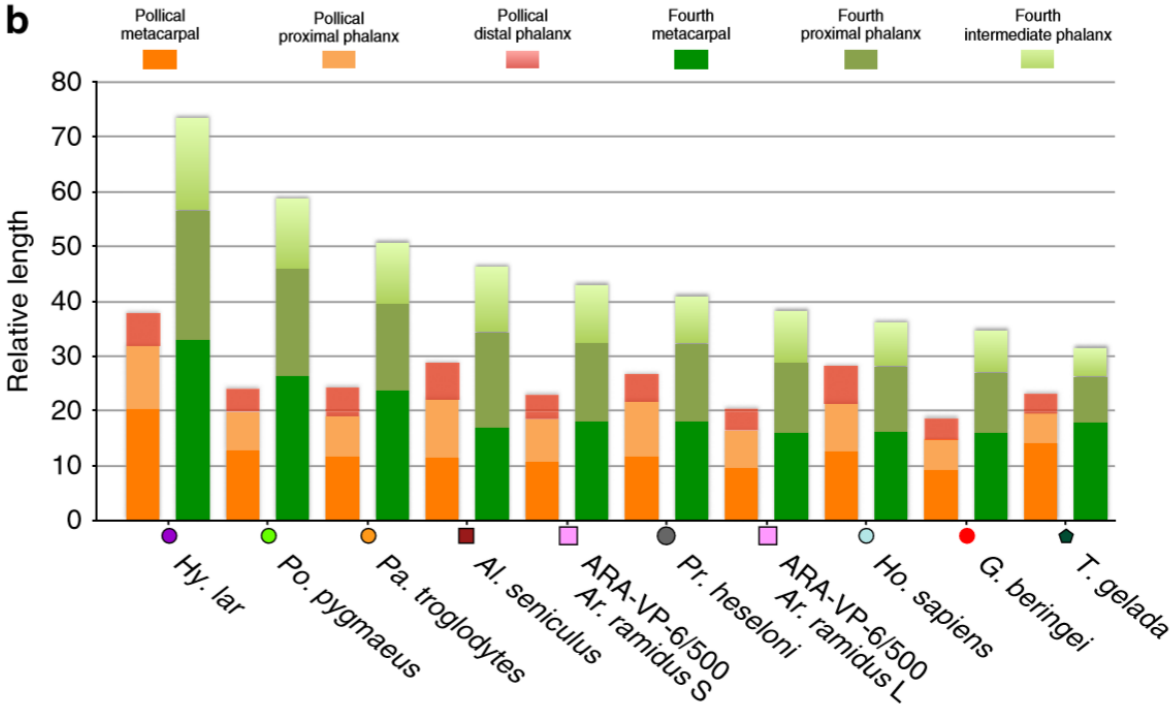

Figure 14: Extrinsic hand proportions of humans and other primates. Bar graph comparing relative length of species explored in Almecija et al. (2015) with the standardization of cubed root BM (body mass) in kg (Almecija et al., 2015)

Phalanx Ratios

Digit ratios for all three phalanges question current ideas concerning knuckle-walking as a symplesiomorphic feature in both *Gorilla* and *Pan*. Kivell and Schmitt (2009) suggest that

African apes independently evolved knuckle-walking through their analysis of the wrist and hand morphology of these African apes. They propose that bipedalism does not necessarily need to evolve from a knuckle-walking ancestral condition and is in fact more likely to evolve from an arboreal ancestor (Kivell & Schmitt, 2009). Finger bone ratios vary across the first and fourth rays in *Pan* and in *Gorilla*, which may be indicative of biomechanical differences in the way for genera knuckle-walk. While their results do show overlap in the relationships between *Pan* and *Gorilla,* there was enough variation across their bones to suggest a different developmental pattern across these genera. Two biomechanically different modes of knuckle-walking have been proposed by Kivell and Schmitt (2009): 1) an extended wrist posture in association with arboreality (*Pan*) and 2) a neutral, columnar hand posture for terrestrial living (*Gorilla*).

As expected, the ratio for phalanges in the genus *Homo* is consistently grouped together and suggestive of a specific hand morphology ideal for a true precision grip. The living primate most often grouped close to *Homo* is *Cebus*. While *Cebus* does not always group with modern human ratio proportions for the phalanges, *Homo naledi* was commonly grouped with *Cebus*. This suggests that the genus *Cebus* and its finger proportions are the most anatomically similar to our hands and this makes the hand of *Cebus* a model as we consider stone tool use in species of early *Homo*.

Of all the primates examined, *Theropithecus gelada* was the most divergent in its finger bone ratios. Gelada baboons have been observed using pad-to-pad finger grips similar to that observed in modern human hand use (Napier & Tuttle, 1993; Richmond et al., 2016). The results of this study suggest parallel evolution for this dexterity as *Theropithecus gelada* shows anatomical differences in the ratios of its hand components. Since extreme structural differences are present in gelada baboons and modern humans, we can safely assume that the behavioral characteristic of a true precision grip was independently evolved from different ecological pressures. Marzke and Shackely (1986), Napier and Tuttle (1993), Kivell et al. (2011) and Richmond et al. (2016) all note that the gelada true precision grip is facilitated by shortening of its fingers, but in this study, I show that first and fourth metacarpal for *Theropithecus gelada* were significantly long compared to its other digits. I suggest our genus, Homo, adapted both short thumbs and short fingers to evolve a true precision grip in contrast to *Theropithecus*.

Phalangeal Curvature

Jungers et al. (1997), Richmond (1998), Kivell (2015), and Richmond et al. (2016) link phalangeal curvature to suspensory behavior, but the results from this study show extreme phalangeal curvature might also be indicative of a knuckle-walking locomotor pattern. *Pan* and *Gorilla* show extreme phalangeal curvature through both their radius and included angle values. I hypothesized that if strong phalangeal curvature occurs in primates that are not considered arboreal in a full-time sense, then phalangeal curvature is likely a retained primitive characteristic from an ancestral condition.

Although phalangeal curvature may be thought as either a retained primitive characteristic or indicative of arboreal behavior during juvenile stages, the similarities and differences between *Pan* and *Gorilla* suggest that knuckle-walking influences this measure (Matarazzo, 2007). Richmond (1998) studied the angle of phalangeal curvature in *Gorilla* and he plotted angle measurements against the amount of arboreal support usage (Fig. 15; Jungers et al., 2002). While this study did support the idea that phalangeal curvature is affected by juvenile stages, the slight uptick in included angles of phalangeal curvature while suspensory support use was its lowest suggests that an increase in body size or knuckle-walking could be evident in the values of included angle measurements. While this increase in phalangeal curvature could be explained by sampling noise, it is also possible that with the increased body size of adult *Gorilla gorilla* more forces are generated through the hand while hanging below branches producing more curved phalanges. Although high radians of phalangeal curvature are evident in knuckle-walking in both *Gorilla* and *Pan*, this could also be accounted for as a compromise adaptation that allows arboreal apes to travel terrestrially while still maintaining features that aid in climbing (Tuttle, 1967; Richmond et al., 2001).

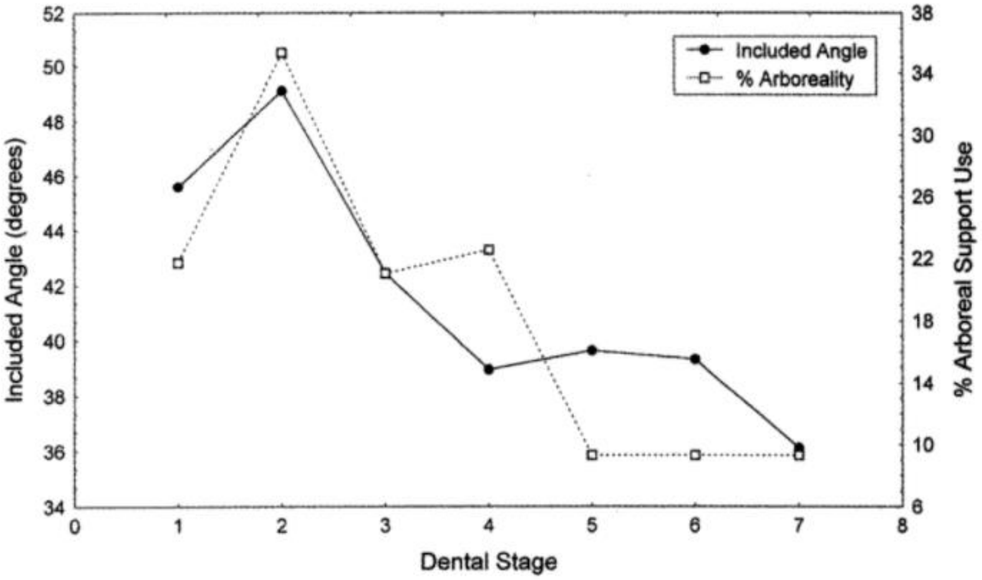

Figure 15: Ontogenetic relationships of included angle and suspensory arboreal support use in *Gorilla gorilla* (Jungers et al., 2002).

Extreme phalangeal curvature (radius and included angle) present in *Pan* and *Gorilla* could inhibit these two genera from employing a true precision grip. This statement is complicated, however, as *Homo sapiens* is similar to *Pan* and *Gorilla* with its radius phalangeal curvature measurement, although larger angle differences are present in the included angle values. Two curvature methods provide contrasting results making any inclusion or exclusion to employ a true precision grip in African apes problematic. These findings are partially due to the fact that radius curvature is size dependent, since the equation uses length of phalanx being analyzed. While I could omit these findings due to this, the equation of included angle does use radius curvature consequently making included angle slightly size dependent as well.

Carpal Architecture

Relative Joint Surface of the Trapezium

Theoretically, a relative measure for the relative joint surface of the trapezium should imply a value for the range of motion of the first digit (Harryman et al., 1990). Surprisingly, this measure shows *Homo sapiens* to possess the smallest relative joint surface of all taxa examined here while *Papio* had the largest relative joint surface. This contrast is indicative that a true precision grip is not necessarily contingent on the motion of the first digit's ray. It is possible that true precision grips require stability in the first metacarpal-trapezium joint and that stability allows higher forces to be better buttressed by this joint. During stone knapping, forceful opposition of the thumb has been divided into three grips by Marzke (1999) allowing the capacity of the thumb and the radial digits to generate forceful grips essential for early stone tool use (Rolian et al., 2011). These forceful opposition grips require a stability in the joint that limits the first digit range of motion, accounting for the small relative joint surface of *Homo*. This study supports this viewpoint.

Shape of the Trapezoid

Richmond et al. (2016) suggest that the shape of the trapezoid is essential to achieve a true precision grip. However, my measurements of the trapezoid's circularity or solidity did not yield any statistically significant results. All species analyzed were visually and statistically similar to one another. While my results did not provide evidence to support this hypothesis, I suggest that further investigation with 3-D morphometric comparisons may provide more insights into the validity of this idea.

Principal Component Analysis

The PCA results indicate that a large amount of variation is present across these phylogenetic groups. African apes, terrestrial knuckle-walkers, are separated from other species analyzed in the PCA results, with main differences accounted for in phalangeal curvature and hand proportions. *Gorilla* and *Pan* appear to have hand morphological adaptations that limit their abilities to employ pad-to-pad grips with their fingers. Not only does this make *Pan* and *Gorilla* unable to employ true precision grips, it inhibits their ability to use a modified precision grip as well. Modified precision grips were defined as pad-to-pad grips attempting to mimic the biomechanical forces of true precision grips as observed in modern-day humans.

Homo sapiens, *Macaca*, and *Papio* grouped closely together in the PCA analysis (Fig. 13), suggesting that *Macaca* and *Papio* could be able to employ a modified precision grip. *Macaca* do employ generalized hand postures during their use of quadrupedal locomotion (Patel, 2009a) and this supports the idea that specialized locomotor patterns may prevent enhanced dexterity of the hand. Surprisingly, *Papio* does employ a unique type of terrestrial quadrupedalism with a hand posture called digitigrady (Patel, 2009b). In this hand posture the phalanges are fully extended relative to the metacarpals. Digitigrady is thought to be employed over long distances to reduce biomechanical stresses of terrestrial locomotion, but studies have also shown that during high-speed movements *Papio* employs more generalized patterns of palmigrade hand use similar to that of *Macaca* (Patel, 2009b; Patel et al., 2012). This might explain why *Papio,* a species that employs a specialized locomotor type, may be able to use a modified precision grip.

Cebus does employ generalized hand postures (Patel, 2009b), but this genus is grouped away from *Homo sapiens*, *Macaca,* and *Papio* in this PCA analysis. While these results could indicate a difference in the overall hand characteristics across these primate species, small samples sizes may be the culprit. A larger sample size is needed to further comment on the relationships between *Cebus* and the other primate species. With larger sample sizes measurement variation could be better accounted for as I could only manage four specimens with all the variables present for *Cebus* in this PCA analysis.

CHAPTER 6

CONCLUSIONS

In this study I expected to find results that would point towards the evolution of true precision grip capabilities being earlier in human evolution than is currently accepted. Results of my study support my original hypothesis, although more research is needed to comment on when this evolution took place and if these morphological features were a by-product of locomotion or evolved specifically to enable more dexterous employment of hand postures. Availability and access to large sample sizes were limited due to restrictions on my time and funding; consequently, my results and conclusions suffer from these hinderances.

For most of the history associated with physical anthropology and human paleobiology, researchers have put an emphasis on “what makes us human” (Boesch, 2007; Lewis & Harmand, 2016; Proffitt et al., 2017) and tool use has especially been used as one of the anchor points for the separation of modern humans from the rest of the animal world (Boesch, 2007; Lewis & Harmand, 2016). To date more than 70 species of animals, including modern humans and non-human primates, have been classified as capable of tool manufacturing in a laboratory setting (Shumaker et al., 2011; Taylor & Gray, 2014). Researchers have more specifically defined the divide as the difference between making and using tools (Ambrose, 2001) and the ability to manufacture archaeologically identifiable stone tools (Mercada et al., 2002; Proffit et al., 2017)

As more observations of non-human primates in the wild continue to be conducted, the behavioral divide of stone tool use becomes less substantial (Boesch, 2007; Proffitt et al., 2017). While most studies have focused their research on West African chimpanzees (*Pan troglodytes*), no research to date has resulted in any diagnostic criteria similar to hominin flakes (de la Torre, 2004; Pelegrin, 2005; Proffitt et al., 2017). While nutcracking has been observed by West African chimpanzees with archaeologically identifiable stone flakes, less than 10% of the 479 pieces could be identifiable as hammer edges or noncortical flakes (Mercada et al., 2002). This means that the most likely explanation for these flaked pieces are not actual debitage or material produced during the process of lithic reduction purposely, but simply debris from using stones to crush nuts. I have suggested that chimpanzees and other living primates with limited hand motor function due to their specialized locomotive patterns would be unable to produce consistent stone tools due to their hand anatomy which is adapted for specific hand postures (i.e., knuckle-walking and brachiation).

According to Proffitt et al. (2017), wild capuchin monkeys have been observed making and re-using stone tools that resemble Oldowan technology. This observation challenged the current paradigm of human stone tool production being associated only with the *Homo* lineage, as the flakes and cores produced by these capuchins are archaeologically identifiable (Proffitt et al., 2017). Capuchin monkeys may be able to produce these stone tools due to their generalized hand postures and this generalized hand anatomy allows them to employ a modified or a true precision grip. Capuchin hands may be a good model for pre-australopithecine hand use and function.

This study supports the idea that non-human primates that are not limited by a specialized locomotor movement are anatomically capable of making and using stone tools. My results show that the hands of *Pan* and *Gorilla* are extremely different from *Homo*, even though these genera are closely related. I hypothesize that these hand differences are present since African apes practice a terrestrial mode of locomotion called knuckle-walking. This pattern of hand use requires the fingers to be folded back while the weight of the forelimb and body is borne through the phalangeal head of the proximal phalanx and at the metacarpophalangeal joint. Since knuckle-walking requires an extreme morphology of the hand, species that practice this mode of locomotion sacrifice their ability to employ a more dexterous grip posture including a modified or a true precision grip. Primate species with more generalized hand postures that use more generalized types of movements, taxa such as *Papio, Macaca*, and *Cebus*, are more capable of achieving a modified precision grip. This suggests that species of this type can anatomically achieve a pad-to-pad precision grip easier than the long-fingered apes.

While there can be some comment on functionality of hands that is the most comparable to modern humans from this project, this project does not hypothesize phylogenetic relationships of hands. According to these results, closest analogous hand functionality is *Papio*, *Macaca* and *Cebus.* In contrast, closest living relatives and potential *Ardipithecus* are not good models of similarities in hand functionality, meaning that modern human hands would need to change from the last common ancestor (LCA) with *Pan* and hands like *Papio, Macaca*, and *Cebus* are converging on stone tool making and using.

This study, in conjunction with the Proffitt et al. (2017) study, suggests that the locomotor freeing of primate hands is not an a priori necessity to begin the process of making and using stone tools as previously hypothesized (Darwin, 1871; Clarke, 1999; Kivell, 2015). Hand function with tool use does not have to be coupled with bipedalism, as other living primates seem capable of using stone tools. This hypothesis is further supported by the 800,000-year time gap between the first appearance of archaeologically identifiable stone tools (Semaw et al., 1997) and the earliest *Homo* species thought to be unique in its ability to achieve grips to aid in the manufacturing of stone tools (McPherron et al., 2010). The ability of non-human primates to employ modified precision grips before bipedalism appeared in the fossil record might well explain this timeline discrepancy.

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APPENDIX

LIST OF SPECIMENS USED IN STUDY INCLUDING SPECIES, SEX, AND LOCATION

Specimen	**Species**	**Sex**	**Location**
FMNH13263	Papio	Female	Field Museum (FM) – Chicago, IL
FMNH18868	Papio		FM – Chicago, IL
FMNH134614	Papio	Female	FM – Chicago, IL
FMNH60607	Papio	Female	FM – Chicago, IL
FMNH159984	Papio	Female	FM – Chicago, IL
FMNH46002	Papio	Male	FM – Chicago, IL
FMNH58944	Papio		FM – Chicago, IL
FMNH48945	Papio	Male	FM – Chicago, IL
FMNH46403	Papio	Male	FM – Chicago, IL
FMNH99426	Papio		FM – Chicago, IL
FMN123072	Papio	Male	FM – Chicago, IL
FMNH127279	Papio	Male	FM – Chicago, IL
FMNH135289	Papio	Male	FM – Chicago, IL
FMNH157994	Papio	Male	FM – Chicago, IL
FMNH159985	Papio		FM – Chicago, IL
FMNH47767	Theropitecus	Female	FM – Chicago, IL
FMNH62904	Macaca	Female	FM – Chicago, IL
FMNH56162	Macaca	Female	FM – Chicago, IL
FMNH61026	Macaca	Male	FM – Chicago, IL
FMNH62275	Macaca	Male	FM – Chicago, IL
FMNH56161	Macaca	Male	FM – Chicago, IL
FMNH68702	Macaca		FM – Chicago, IL
FMNH56160	Macaca	Female	FM – Chicago, IL
FMNH62276	Macaca		FM – Chicago, IL
FMNH68700	Macaca		FM – Chicago, IL
FMNH65451	Macaca		FM – Chicago, IL
FMNH105689	Macaca	Male	FM – Chicago, IL
FMNH99657	Macaca	Male	FM – Chicago, IL
FMNH62901	Macaca	Female	FM – Chicago, IL
FMNH60741	Macaca	Male	FM – Chicago, IL

FMNH62273	Macaca		FM – Chicago, IL
FMNH62902	Macaca		FM – Chicago, IL
FMNH135714	Macaca	Male	FM – Chicago, IL
FMNH93261	Cebus		FM – Chicago, IL
FMNH98046	Cebus		FM – Chicago, IL
FMNH95471	Cebus		FM – Chicago, IL
FMNH98044	Cebus		FM – Chicago, IL
FMNH95470	Cebus		FM – Chicago, IL
FMNH43907	Cebus	Female	FM – Chicago, IL
FMNH95336	Cebus		FM – Chicago, IL
FMNH95474	Cebus		FM – Chicago, IL
FMNH60751	Cebus	Male	FM – Chicago, IL
FMNH68843	Cebus	Male	FM – Chicago, IL
FMNH68842	Cebus	Female	FM – Chicago, IL
FMNH68841	Cebus	Male	FM – Chicago, IL
FMNH137076	Cebus	Male	FM – Chicago, IL
FMNH22396	Cebus		FM – Chicago, IL
FMNH68837	Cebus	Male	FM – Chicago, IL
FMNH159982	Cebus		FM – Chicago, IL
FMNH134482	Gorilla	Male	FM – Chicago, IL
FMNH126045	Gorilla	Male	FM – Chicago, IL
FMNH99092	Gorilla	Male	FM – Chicago, IL
FMNH135290	Gorilla		FM – Chicago, IL
FMNH57131	Gorilla	Female	FM – Chicago, IL
FMNH26065	Gorilla		FM – Chicago, IL
FMNH16344	Gorilla	Male	FM – Chicago, IL
FMNH27551	Gorilla		FM – Chicago, IL
FMNH27550	Gorilla	Female	FM – Chicago, IL
FMNH57201	Gorilla		FM – Chicago, IL
HTH093	H sap	Male	Natural History Museum (NHM) – Cleveland, OH
HTH092	H sap	Male	NHM – Cleveland, OH
HTH668	H sap	Female	NHM – Cleveland, OH
HTH706	H sap	Male	NHM – Cleveland, OH
HTH727	H sap	Female	NHM – Cleveland, OH
HTH115	H sap	Male	NMH – Cleveland, OH
HTH114	H sap	Male	NHM – Cleveland, OH
HTH726	H sap	Male	NHM – Cleveland, OH
HTH485	H sap	Female	NHM – Cleveland, OH
HTH461	H sap	Female	NHM – Cleveland, OH
HTH221	H sap	Female	NHM – Cleveland, OH
HTH226	H sap	Female	NHM – Cleveland, OH
HTH228	H sap	Female	NHM – Cleveland, OH

HTH584	H sap	Male	NHM – Cleveland, OH
HTH563	H sap	Male	NHM – Cleveland, OH
HTH243	H sap	Female	NHM – Cleveland, OH
HTH544	H sap	Male	NHM – Cleveland, OH
HTH630	H sap	Male	NHM – Cleveland, OH
HTH631	H sap	Female	NHM – Cleveland, OH
HTH442	H sap	Female	NHM – Cleveland, OH
HTB1722	Pan	Male	NHM – Cleveland, OH
HTB1723	Pan	Female	NHM – Cleveland, OH
HTB1748	Pan	Female	NHM – Cleveland, OH
HTB2730	Pan	Female	NHM – Cleveland, OH
HTB1761	Pan	Male	NHM – Cleveland, OH
HTB2747	Pan	Male	NHM – Cleveland, OH
HTB1758	Pan	Male	NHM – Cleveland, OH
HTB2746	Pan	Male	NHM – Cleveland, OH
HTB2771	Pan	Female	NHM – Cleveland, OH
HTB2026	Pan	Male	NHM – Cleveland, OH
HTB1741	Pan	Female	NHM – Cleveland, OH
HTB1843	Pan	Female	NHM – Cleveland, OH
HTB1708	Pan	Male	NHM – Cleveland, OH
HTB1745	Pan	Male	NHM – Cleveland, OH
HTB1744	Pan	Female	NHM – Cleveland, OH
HTB1880	Pan	Female	NHM – Cleveland, OH
HTB1882	Pan	Male	NHM – Cleveland, OH
HTB1726	Pan	Male	NHM – Cleveland, OH
HTB3551	Pan	Female	NHM – Cleveland, OH
HTB1056	Pan	Male	NHM – Cleveland, OH
MH2	A sed		Kivell, 2015
Hand 1	H nal		Kivell, 2015
Shanidar 4	H nean		Richmond et al., 2016

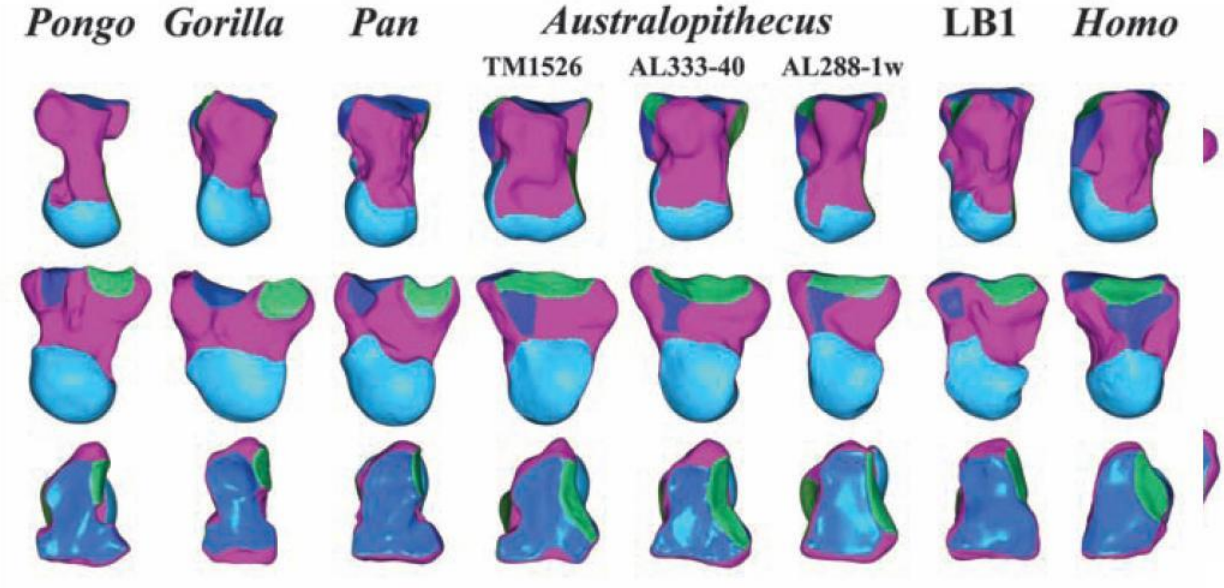

Figure 16: Demonstrated relative surface area measurements in Tocheri et al. (2007) with the capitate and trapezoid.