12-14-2016

Functional Morphology of the Distal Forelimb and the Evolution of Tool Use in Humans

Sarah Love

Recommended Citation

Love, Sarah, "Functional Morphology of the Distal Forelimb and the Evolution of Tool Use in Humans." Thesis, Georgia State University, 2016.
doi: https://doi.org/10.57709/9423951

FUNCTIONAL MORPHOLOGY OF THE DISTAL FORELIMB AND THE EVOLUTION OF TOOL USE IN HUMANS

by

SARAH LOVE

Under the Direction of Frank L'Engle Williams

ABSTRACT

Previous research on the biomechanics of tool use has focused heavily on traits correlated with locomotion, tool manufacturing, and habitual tool use. Features like the breadth of the metacarpals, relative length of the thumb, styloid process of the third metacarpal, and the breadth of the apical tufts are skeletal features associated with the use and development of stone tools. However, there are many traits of the distal forelimb that may also be correlated directly with the development and use of tools. The purpose of this research is to analyze morphological features of the hands and compare them to features of the arm in humans, fossil *Homo* and the great apes to understand how the hominin distal arm functions as a mosaic in response to the use of stone tools. The results indicate a separation between tool-users and non-tool users when all distal forelimb dimensions are examined. Omo 40-19 falls closer to non-tool users when univariate plots of ulna length and breadth are examined. Ratios of hand measurements to radius length are better at polarizing the tool-users from non-tool users than are hand dimensions to ulna length ratios. These results highlight the role of the radius in stabilizing the hand during stone tool production.

INDEX WORDS: paleoanthropology, functional morphology, hominin, human evolution

FUNCTIONAL MORPHOLOGY OF THE DISTAL FORELIMB AND THE EVOLUTION OF TOOL USE IN HUMANS

by

SARAH LOVE

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of
Master of Arts
in the College of Arts and Sciences
Georgia State University
2016

FUNCTIONAL MORPHOLOGY OF THE DISTAL FORELIMB AND THE EVOLUTION OF TOOL USE IN HUMANS

by

SARAH LOVE

Committee Chair: Frank L'Engle Williams

Committee: Frank L'Engle Williams

Bethany Turner-Livermore

Susan Kirkpatrick Smith

Electronic Version Approved:

Office of Graduate Studies

College of Arts and Sciences

Georgia State University

August 2016

DEDICATION

This thesis is dedicated, above all, to my dad. Plain and simple.

James B. Love 1947-2014

ACKNOWLEDGEMENTS

My biggest thank you is extended to my advisor and mentor, Dr. Frank L'Engle Williams, who throughout my graduate career marked by unexpected tragedies, setbacks, and detours, went above and beyond to ensure I remained optimistic, driven, and focused.

Thank you to my committee, Dr. Bethany Turner-Livermore and Dr. Susan Kirkpatrick Smith for providing insight and guidance on my project. My thanks to Dr. Turner would not be complete, however, if I did not say thank you for reminding me that sometimes, when you're balancing life, grief, and research, that it is perfectly acceptable to take a break from work and binge-watch Netflix.

Many thanks to Dr. Robert Franciscus at the University of Iowa for allowing me to access his fossil cast and human collections, providing extremely helpful advice, and for the shared excitement over Frank Lloyd Wright. Additional thanks to the Chicago Field Museum of Natural History for access to the primate collections in their care, and allowing me to use my research pass as free admission to such an awe-inspiring and stunning museum. Thank you to all of my friends in the Department of Anthropology, who supported me through life events from enduring a major loss to tackling a second, concurrent graduate degree (Masters of Historic Preservation). Thank you to my mom, Mary, for tolerating my mood swings, always making coffee, and reminding me that I would not have been in a position to write this if I were not capable. Thank you to my incredible dad who beamed with pride and bragged to his friends about my pursuits, and never missed an opportunity to tell me how proud he was of me. Additional thanks to my dad and my uncle, Jon, who instilled in me a curiosity about the world since I was a little "critter."

Thank you to past graduate students and scholars who have lent their knowledge and expertise to a field that has completely captivated me. To the graduate students of the future, there will be moments when you are stressed and want to give up, but your research will add to a body of knowledge that matters. Thank you for that.

Finally, I must extend a very special thank you to my wonderful friends, Joe and Emma, who in the final hours leading up to my defense, went above and beyond to ensure I stayed encouraged and maintained the focus necessary to complete this thesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1 INTRODUCTION

The earliest remnants of material culture produced by ancestors of anatomically modern humans belong to the category of manufactured stone tools. While the ability to manufacture and maneuver stone tools may be one of the major adaptations of the *H. sapiens* hand and forearm, evidence of morphological adaptations allowing for the creation and manipulation of stone tools have been discovered in much earlier *Australopithecus* fossil remains. Further evidence of this early tool use also lies in the presence of butchered skeletal remains recovered from sites attributed to *A. afarensis* (McPherron et al. 2010). It is possible that hand/arm morphology and stylistic changes in tool assemblages and have coevolved over time.

The precursors for some of the most useful skeletal adaptations for stone tool creation are related to locomotive behavior in fossil apes. Because the hand and arm play such an important role in both tool use and locomotion, these features cannot be regarded as an adaptation for solely one individual behavior over the other. Furthermore, morphologies in the hand related to stone tool creation cannot be isolated from the suite of traits in the arm that facilitate similar tool using behaviors. The forearms of modern and archaic humans facilitate the ability to create stone tool assemblages, but as a consequence of bipedality, aid in additional habitual behaviors not common among the great apes. Axial loading, signaling, lifting, throwing, tool manufacture, mass distribution, and energy conservation during bipedal locomotion are all advantages of biped forearm morphology (Cartmill and Smith 2009, Diogo et al. 2012) and serve as additional benefits to modern human distal forelimb morphology.

Purpose of the Study

Previous research published on the hominin hand and forearm has mostly been focused on isolated morphological elements associated with power gripping, precision gripping and locomotive behavior. While significant information has been gleaned by this approach, stone tool creation and use are inherently influenced by forces of both elements of the forearm as well as the positioning of the hands. Methodological approaches ranging from linear measurement ratios (Susman 1988) to experimental archaeology (Marzke and Marzke 2000) have been employed to analyze tool use potential in fossil hominins. The main goal of this study is to examine the relationship between the ulna, radius, and hand bones in tool users and non-tool users. Several Upper Pleistocene fossil hominins that preserve both forearm and hand elements are examined to provide a diachronic perspective. The majority of fossil individuals included in this study belong to archaic *H. sapiens* and *H. neanderthalensis.* Omo 40-19 is also included to investigate whether this isolated ulna can be assigned to a tool user or non-tool user category based on similar measurements of the forearms in apes and humans. Analyzing the sum of these variables of fossil hominins against ape and human comparative collections will lend insight to how the forearm and hand evolved as a mosaic of traits in response to tool manipulation, and how the bones of the forearm relate to the suite of traits in the hand that have been considered vital for habitual stone tool creation and other advanced manipulative behaviors.

Expected Results

Among the included individuals, it is very likely that Neanderthals will exceed anatomically modern humans in terms of relative hand robusticity when compared to the length of the forearm, but show similar results in terms of absolute forearm length due to the truncated forelimbs of the taxa. Archaic humans will most likely group closely with anatomically modern humans owing to the narrowing of the apical tuft and more gracile hand morphology than Neanderthals. Amongst the great apes, *G. gorilla* and P. *troglodytes* will likely be grouped more closely than either species is to *P. pygmaeus* which can be attributed to the arboreal locomotion of orangutans.

In tests of hand morphologies compared to forearm length, hand functions related to tool use will likely be more strongly associated with the radius due to the insertion points of the flexor pollicis longus, the extensor pollicis brevis, and the association of these muscles with stone tool creation.

2 LITERATURE REVIEW

Recovered Remains

Tool use has been inferred both skeletally and by observing fossil hominins in the same depositional context as stone tools. For example, raw lithic material and Mode 1 Oldowan tools have both been discovered at Swartkrans. Though the cave does not seem to be the tool manufacturing site due to its dark, unlit environment it is possible that both tools and associated debitage eroded into the cave with fossil remains or were carried into the cave by hominins. The lithic material recovered from Swartkrans has been found in Members 1-3 alongside fossils attributed to both *Australopithecus robustus* and *Homo erectus.* Member 1 contains fractured fragments of chert and quartz as well as one bifacially worked chopper and a retouched side-scraper (Clark 2004). Member 2 contained the greatest number of retouched flakes in conjunction with borers, possible hammers, and bifacially worked choppers. Member 3 contains the fewest artifacts, but the material culture does include side-scrapers and flakes (Clark 2004). Bone tools have been discovered in Members 1-3 and are characterized as tools by their tapered ends with smoothly worn points and surface polishing. Bone tools would have been beneficial to hominins during the procurement of roots and tubers present in the vicinity of Swartkrans. A particular bone tool from Member 3 was potentially used for piercing skins or other soft materials indicating that hominins at Swartkrans may have been using bags made from animal skins (Brain and Shipman 2004).

The materials from Swartkrans Members 1-3 have been interpreted as intentionally altered for tool use due to the unnatural pattern of flaking and thinning on stone assemblages and the polishing and tapering of wooden tools. The stratigraphic association of *Australopithecus* *robustus* and *Homo erectus* has led researchers to attribute stone tool manufacture and tool use to both species. Initially it was thought that *Australopithecus robustus* was not a likely candidate for tool use due to its small brain size and inferred vegetarian diet (Susman 1988). However, vegetarian diet and relatively small brain size would not have prevented *Australopithecus robustus* from utilizing the bone tools at Swartkrans. The cranial capacity of *Australopithecus robustus* overlaps with that of extant *Pan troglodytes* which has been observed using sticks as digging tools in the wild. Additionally, the use of bone instruments as digging tools for underground storage organs would correlate with the vegetarian diet of *Australopithecus robustus.* Therefore, stratigraphic association of stone and bone tools with the postcranial remains of *A. robustus* and *H. erectus* has supported the idea that both species were tool users.

Tool use has also been inferred by the potential presence of cut marks on faunal remains dating to 3.4 million years ago and the earliest stone tools from West Africa dated to 3.39 mya (Hammond et al., 2015).. Though highly contested, the presence of cut marks indicative of flesh removal and marrow extraction at the site of Dikika has suggested the possibility of *Australopithecus afarensis* potentially using stone tools to butcher mammals.

Experimental Archaeology

Reconstruction of tool use by examination of skeletal remains has been largely focused on singular traits. Multiple studies have demonstrated that certain traits in modern humans and fossil hominins play a large role in facilitating precision grips and protecting the hand and arm against external forces. The majority of studies have focused on the comparison of particular traits or have been limited to a specific region of the hand and arm. The lack of preservation of carpals and metacarpals is also an issue, but a more comprehensive study of the hand bones in relation to the arm bones may be possible, particularly when combined with an experimental approach.

Experimental archaeology has been employed to answer what grips are necessary for manufacture, what ranges and movements are associated with those grips, and what particular regions of the hands are stressed by those actions (Napier 1962, Marzke and Marzke 2000). For example, experimental approaches have also been used to identify (1) whether or not more ape-like hands are capable of creating crude, Oldowan style tools as well as (2) at what point in the archaeological record human hands would have been necessary for tool use (Marzke and Marzke 2000).

In regards to Oldowan style tools, experimental archaeology has shown that the tools can be created using an ape-like grip without strong opposition of the thumb (Napier 1964, Marzke and Marzke 2000, Savage-Rumbaugh and Lewin 1996). A study of observed external forces during the manufacture of stone tools (Marzke and Shackley 1986) identified distinct grips during the production process. During hard hammer percussion for removal of flakes from the core, the core is held in a cradle grip which requires the pads of the four fingers and is secured by the opposing pressure of the thumb. The 3-jaw chuck, or baseball style grip, of the hammerstone involves the fleshy pads and strong apical tufts of the thumb, index, and middle fingers. The cradle grip is considered a power grip, while the 3-jaw chuck is considered a forceful precision grip. The large stresses generated by the external force of the hammerstone are what acts against the hand during stone tool creation (Marzke and Marzke 2000). Marzke and Shackley (1986) also determined that during cutting and scraping, a firm pad-to-side precision grip between the index finger and thumb is employed. During the grasping of spherical and cylindrical objects, the modern human ability to rotate the 5th metacarpal toward the thumb was consistently employed during the retention of the core in the hand for one-handed clubbing and pounding (Marzke 1992). Experimental archaeology has played an important role in the understanding of stone tool creation, and helps to understand which areas of the skeleton are enduring the pressure of external forces. With that understanding, fossil remains can be properly researched when identifying morphological traits that relate to stone tool use and manufacture.

Skeletal Remains

One of the most frequently implemented methods of predicting past potential tool use has been to analyze skeletal morphology related to tool manufacture and trace those features back through well-dated hominin fossil remains**.** The majority of previous research has been on the evolution of hominin hand and wrist bones, and focused on the external forces that would be necessary to create stone tools.

One of the major issues concerning the way that hominin tool use has been reconstructed is that isolated fossils may be hard to associate with a specific fossil taxon. In the case of Swartkrans and other major sites, bones related to tool use like the metacarpals, carpals, ulnae, and radii may be intermingled with remains from other fossil taxa. Without being able to distinguish between two or more species, especially when remains are recovered in conjunction with stone tools and associated debitage, assessing the capacity to create tools may be difficult. Similar issues have been encountered at Members 1-3 at Sterkfontein, where even though there is a presence of Oldowan tools, it is difficult to know definitively which cranial and dental remains as well as postcranial remains belong to the stone tool producers (Cartmill and Smith 2009). A potential issue when examining small bones like carpals and metacarpals is that differential processes of sediment accumulation may have affected them differently than long bones, cranial bones and gnathic elements. Preservation of smaller bones is also problematic, as the representation of carpals and metacarpals in the fossil record is fractional when compared with cranial remains and long bones.

Hand Morphology

One of the necessary morphological features for effective tool production and tool use is the presence of relatively short fingers and a relatively long, robust thumb (Rolian et al. 2011). The length of the thumb in relation to the fingers is essential in producing a forceful precision grip between the thumb and radial digits II and III which is necessary for stabilizing the hand in the manufacture of tools. Concerning the skeletal anatomy of the hand, morphology of the distal phalanges, metacarpals, and carpals would have to support both precision and power grasping to facilitate stone tool use and manufacture. The wrist bones play a vital role in these functions as they connect the metacarpals to the ulna and radius. Modern human carpals have been distinguished from those of the great apes by proportionately larger joint surfaces on the trapezium for the first metacarpal and the scaphoid while the great apes have larger articular surfaces on the trapezoid for the scaphoid and medial second metacarpal. Anatomically modern humans also have proportionately more nonarticular area on the trapezoid whereas the great apes have more nonarticular area on the trapezium. The relatively larger joint surface area of the trapezium in tool users is likely due to forceful grasping and pinching that focuses large external forces on the joint between the first metacarpal and trapezium. External forces caused by the creation and use of stone tools may be accommodated by the relatively larger joint surfaces on the trapezium (Tocheri 2005). The saddle shaped nature of the trapezium in hominins combined with a relatively larger articular surface for the first metacarpal also increases flexion-extension (Rose 1992) which is vital in precision and power gripping. The first metacarpal surface also has a saddle configuration that allows for movement of the first metacarpal toward the fingers in opposition (Tocheri 2005, Marzke and Marzke 2000). The modern human trapezoid may have evolved in order to better distribute loads across the palmar aspect of the hand. The relatively larger joint surface areas on the trapezium for the trapezoid and on the trapezoid for the capitate support the idea that the accommodation for greater external forces was necessitated in tool users (Lewis 1989).

In modern humans, cupping of the hand is employed in the use of hammerstones during tool creation, and can be identified skeletally by a marked asymmetry of the 2nd and 5th metacarpal heads which allows the 2nd and 5th metacarpals to rotate toward each other during flexion and abduction. The 5th metacarpal in habitual tool users is also characterized by a saddle joint between the base of the 5th metacarpal and hamate which allows the 5th finger to rotate toward the index finger and thumb (Marzke and Marzke 2000). The robust head of the first metacarpal is associated with less-curved first carpometacarpal joint surfaces which facilitate the accommodation of large axial loads generated by strong precision grips (Ward et al. 2013). Susman’s (1988) study of the first metacarpal of *Australopithecus robustus* indicates that forceful precision grasping may be apparent in the first metacarpal of this hominin. The thumb of *Australopithecus robustus* possessed a marked insertion point for the flexor pollicis longus muscle (Susman 1988), a muscle well-defined in modern humans that is largely absent or vestigial in the great and lesser apes (Diogo et al. 2012). In addition to a well-defined insertion point for the flexor pollicis longus, the thumb of anatomically modern humans has well-developed oponens pollicis muscles. The oponens pollicis is the muscle that rotates the thumb in opposition to the fingers, a necessary trait for forceful precision grips, and forms a crest on the first metacarpal shaft (Susman 1998). Another distinct skeletal feature of tool users is a broad, expanded apical tuft on the distal end of the distal phalanx. Broad apical tufts are most developed in Neanderthals and humans and serve to provide bony support for well-innervated and vascularized fleshy fingertips (Marzke and Marzke 2000, Susan 1988). Conversely, nonhuman primates tend to have long, curved hands with narrow fingertips, which are ineffective in precision gripping. The pollical distal phalanx of apes also lacks the ventrobasal depression for the insertion of the flexor pollicis longus which is well-defined in hominin tool users (Susman 1994).

Due to the large amount of transarticular force that is placed upon the metacarpophalangeal joint of the first metacarpal, an expansion in breadth of the first metacarpal head can also be identified in known tool users, such as modern humans. In a comparison of *A. afarensis, P. robustus, H. erectus* and *H. sapiens neanderthalensis* against pygmy chimpanzees, common chimpanzees, and modern humans, Susman (1994) compared the breadth of the first metcarpal head in relation to its length. When metacarpal breadth was plotted against length, a relatively small first metacarpal head was consistent among great apes, while the head-breadth proportions of likely tool users were more consistent with modern human and known tool-user ratios (Susman 2014). Additional studies have shown that the head-breadth ratio of mountain gorillas falls within the range of variation for modern humans as well as the ratio for fossil taxa (McGrew et al. 1995). Though the two studies seem to be contradictory regarding the broad head of the first metacarpal as a necessary precursor for stone tool manufacture, the trait is consistent among fossil human tool users, such as *Australopithecus robustus* and Upper Pleistocene hominins, and likely belongs to a myriad of traits adapted for stone tool use.

Many of the traits associated with the distal forelimb evolved as a result of increased selection for complex hand manipulation and forceful precision and power grips which are seen in anatomically modern humans and Neanderthals. A trait that has been considered specific to *H. sapiens* is the styloid process of the third metacarpal. The third metacarpal styloid process is a projecting portion of bone that articulates with a reciprocally beveled surface on the capitate, second metacarpal, and sometimes a small portion of the trapezoid (Ward et al. 2013). The styloid process prevents hyperextension of the third metacarpal base when large forces are directed from the palm toward the head of the third metacarpal. This trait serves to protect the hand and wrist against large forces presumably associated with tool use. It also helps to stabilize the capitate from slipping dorsally during strong contractions of the thumb musculature. While this trait was originally thought to be unique to anatomically modern humans and Neanderthals, fossil evidence has demonstrated this trait is also found in KNM-WT-51260, a Pleistocene hominin that dates to 1.42 million years ago (Ward et al. 2013). While the styloid process is present in modern humans, Neanderthals, and KNM-WT-51260, the recovery of a third metacarpal has shown that the feature is absent in *A. afarensis* whose role in stone tool use is still under debate (Bush et al. 1982).

Non-tool users and potentially episodic tool users will have more phalangeal curvature than that of anatomically modern humans, Neanderthals, and other species in the genus *Homo.* Phalanges of habitual tool users will also be more likely to contain broader apical tufts to cushion the forces acting on the distal tips of the fingers. The distal phalanx of the first digit of habitual tool users has an insertion point for the flexor pollicis longus. A similar tendon is observed in certain individuals in great ape populations, but the insertion point does not provide the long lever arm that is observed in habitual tool users.

The trapezium of habitual tool users is more saddle shaped than in the great apes. This feature allows full opposition of the thumb to the fingers (Marzke and Marzke 2000) so episodic tool users will most likely have a saddle shaped joint somewhere in between anatomically modern humans and the great apes. Habitual tool users will also most likely exhibit a palmarly broadened trapezoid (Kibii et al. 2011) as this feature assists in more even distribution of radioulnarlydirected loads generated by a stronger thumb (Kibii et al. 2011).

The metacarpal bones of habitual tool users will exhibit similarities to anatomically modern humans such as relatively short fingers and relatively longer thumbs. The base of the second metacarpal will exhibit three articular surfaces for the trapezium, trapezoid, and capitate. Though Napier (1962) has shown that primitive or ape-like hand morphology is capable of producing stone tools, it is highly unlikely that habitual stone tool users retain symplesiomorphic morphology. Additionally, the second and fifth metacarpals will have marked asymmetry in comparison to more ape-like metacarpals in order to support rotation toward each other during flexion (Marzke and Marzke 2000). The styloid process on the proximal end of the third metacarpal is also a feature that has developed in response to habitual tool use. This feature is present dating back to *Homo erectus* and is absent in the hands of *Australopithecus afarensis* (Bush et al. 1982, Marzke and Marzke 2000). The styloid process of the third metacarpal may also be associated with episodic tool users as Stw 64, the 2.5 million year old fossil from Sterkfontein, also exhibits this feature. Both episodic and habitual tool users will have a relatively broader head of the first metacarpal relative to overall length. While humans have the broadest metacarpal head in relation to overall length, episodic tool users may have a ratio somewhere between anatomically modern humans and the great apes (Susman 1998).

Forearm Morphology

Previous publications on the hominin forearm and its relation to tool use describe the overall morphology of the proximal ulna and proximal and distal radius. The forearms of extant knuckle-walkers exhibit a more pronounced keel of the trochlear notch than is seen in anatomically modern humans and fossil bipeds (Drapeau 2008) in addition to a more medially displaced insertion point of the triceps brachii (Aiello 1999). Though these features are not strictly related to tool use, they can be used to distinguish fossil hominid forearms when isolated from other cranial or post-cranial remains as they are likely to serve as morphological precursors to tool use adaptation. In relation to the great apes, the proximal ulna of modern humans and Neanderthals have a more anterior facing trochlear notch (De Groote 2011, Drapeau 2008) in conjunction with a longer olecranon process in relation to overall length of the ulna (Aiello and Dean 1990). The radial shaft of anatomically modern humans is much straighter than is observed in modern chimpanzees. In chimpanzees, the curvature of the radius is likely an adaptation to locomotor behavior as a more laterally oriented insertion point for M. pronator teres muscle increases the lever action of the forearm (Aiello and Dean 1990). However, a slight curvature of the radial shaft is also exhibited in Neanderthals who are known to be habitual tool users. The radial curvature and more medially oriented radial tuberosity seen in Neanderthal remains is due to an increase in the lever strength of the M. biceps brachii muscle which increases the strength of supination (Aiello and Dean 1990, De Groote 2011). Though both Neanderthals and anatomically modern humans are considered to be habitual tool users, the differential morphology of the forearm and associated musculature is likely due to a difference in supination strength (De Groote 2011). In Neanderthal forearms, the lateral curvature may increase the strength of the forearm during flexion, while it serves a purpose directly related to locomotion in chimpanzees. Whereas these characteristics will be examined on the forearms of fossil hominin and extant comparative collections, they cannot be sole predictors of habitual tool use when examined as isolated morphological features. In order to adequately understand the evolution of the hominin forearm and hand in conjunction, it is necessary to examine relative and absolute lengths of the trochlear notch, olecranon process, radial head, scaphoid notch, and lengths and widths of the ulna and radius. Origin and insertion points for relevant muscle attachment, including the biceps brachii, triceps brachii, brachialis, pronator teres, and flexor pollicis longus will also be examined.

The shaft of the radius of tool users versus non-tool users will have to be taken into consideration alongside additional traits of the proximal and distal radius. Due to the curvature of the radial shaft facilitating two different behavioral functions in Neanderthals and chimpanzees, features like the shape of the radial head and scaphoid notch should also be analyzed. Regarding both the ulna and radius, the relative length of the forearm bones compared to the humerus should be shorter in habitual tool users and longer in non-tool users.

A significant portion of the force exerted in the production and use of tools is transmitted through the elbow joint. The elbow joint of anatomically modern humans restricts the range of extension in comparison with the great apes. The extension range of humans is largely due to the shape and size of the olecranon process which is the area of attachment for the triceps brachii and the depth of the trochlear notch where the ulna articulates with the humerus. In addition to a major difference in extension, the proximal elbow joint of modern humans plays a vital role in pronation and supination of the forearm. While in supinated position, the human forearm diverges laterally from the upper arm in what is called the carrying angle. The magnitude of the carrying angle is determined by the overall morphology of the trochlea which also may be related to tool use (Aiello 1990). While these traits are strongly associated with stone tool development, they are also adaptations to other uses of the forelimb.

The proximal ulna reflects unique adaptations in morphology that correlate with varying locomotor behaviors across modern humans, fossil hominins and the great apes. Hominoids have much straighter ulnas that allow for full extension of the elbow and increase stability throughout its enhanced arc of movement (Cartmill and Smith 2009). Hominoids also have a laterally facing radial notch, relatively short olecranon break, distally wide trochlear notch, marked median ridge with the trochlear notch, reduced olecranon process, strongly developed supinator ridge, and a more robust shaft. The trochlear notch is the part of the ulna that articulates with the distal humerus and which allows for extension of the upper limbs. Unlike the radius, the ulna is restricted in rotary motion. A distinctive feature of quadrupedal apes is the greater distance between the floor of the trochlea and the dorsal surface of the ulna. The distance strengthens and buttresses the proximal ulna and increases the area for muscle attachment for muscles used during locomotion (Aiello 1999).

Humans and gorillas similarly have flatter elbow joints in comparison with arboreal apes though they differ in the overall depth of the trochlea. Bipeds also have a more proximally oriented notch which is linked to greater range of flexion-extension and pronation-supination (Drapeau 2008). In comparison to humans, quadrupedal *G. gorilla* also exhibits a relatively long ulnar length compared to the overall size of the trochlear notch.

Features of the proximal elbow affect the strength of forearm flexion and extension, the degree of pronation and supination, and the carrying angle of modern humans. These functions can be inferred skeletally by the size and shape of the coronoid process, olecranon process and the trochlear notch. The distal forearm also facilitates pronation and supination in addition to wrist extension greater than that of ancient hominids and the great apes. The high degree of wrist extension in modern humans contributes to accuracy during stone tool manufacture in addition to a higher linear velocity of the hand and increased leverage while using a hammerstone.

The shortening of the forearms in anatomically modern humans may provide a means of greater efficiency while carrying loads during bipedal locomotion (Williams et al. 2015). The relatively shorter forearms of anatomically modern humans are in contrast with the longer forearms that aid nonhuman primates in arboreal locomotion. The swinging of the upper limbs in bipeds in a pendulum-like motion conserves energy by transferring angular momentum between the swinging arms and rotating pelvis. The shortening of the forearms requires slight muscular effort to keep the lower and upper limbs oscillating in unison due to the longer length of the lower limbs. Relatively shorter forearms in modern humans allows for heavy loads to be carried by the upper limbs and still conserve energy during bipedal locomotion despite the added weight (Cartmill and Smith 2009).

Particular traits that facilitate tool use may be primitive retentions from arboreal and suspensory locomotion. Features like full supination of the forearm and full extension of the elbow aid in the manufacture of stone tools, but evolved to allow for ape-like locomotion (Marzke 2009). While certain morphological traits evolved before the last common ancestor of *Homo sapiens* and the African apes, there are multiple skeletal features that differ based on manipulative and locomotive capabilities in humans and non-human primates. In regard to the forearm bones individually, both the ulna and radius exhibit distinct morphological features across taxa. The articular surface of the distal radii in knuckle-walking apes is more rectangular in shape than in bipedal hominins (Tallman 2012). Quadrupedal locomotion necessitates stabilization against vertical forces, and morphological adaptations of the distal forearm and wrists of knuckle-walkers serve to increase stability and limit extension (Aiello and Dean 1990, Kivell 2009). The distal radius of knuckle-walking apes is characterized by a distally projecting dorsal ridge to limit dorsiflexion, a deep scaphoid articular surface, and a smaller lunate articular surface than that of bipeds (Tallman 2001). In quadrupeds, the scaphoid dorsal concavity and scaphoid beak limit extension at the radiocarpal joint (Richmond et al. 2001), the capitate distal concavity limits the extension of the capitate-scaphoid joint, and the hamate doral ridge and hamate distal concavity limit extension at the triquetro-hamate joint (Kivell 2009). The scaphoid notch along the dorsal ridge of the distal radius is also relatively large in order to reduce stress by increasing the area of weight bearing in addition to being dorsally oriented in comparison to Asian apes (Richmond and Strait, 2000; Richmond et al. 2001). The presence of a highly circular radial head on the radii of bipeds represents greater radioulnar mobility which is indicative of a reduction in use of the forearm during locomotion. Similar to the distal radius, the proximal radius is designed to stabilize the arm against reactionary forces during quadrupedal locomotion. In African apes, the proximal articular surface is expanded medially and anteriorly providing a greater area of contact with the humerus – thus distributing the force on the greater surface of the humeroradial joint during locomotion (Patel 2005).

Significant differences between bipeds and quadrupeds can also be recognized by the presence of a relatively longer metacarpal I and relatively short metacarpals II-V in modern and Upper Pleistocene humans. Examination of carpals and metacarpals indicate that anatomically modern hands may have evolved as an adaption to external forces during stone tool manufacturing, therefore earlier bipeds may retain longer metacarpals II- V similar to modern African apes perhaps because climbing behaviors were heavily recruited. The hands of modern humans are distinguished from other primate taxa by the presence of the flexor pollicis longus, relatively longer thumbs, and relatively shorter fingers (Diogo et al. 2012). The metacarpal bases in African apes also have a keeled articular surface likely to resist twisting that could be caused by knuckle-walking (Marzke 1983, McHenry 1983).

Fossil Hominin Record of Distal Forelimb

Radii of multiple specimens of *Australopithecus africanus, A. afarensis, Paranthropus robustus,* and *Homo erectus* have been studied in conjunction with radius fossils of *A. anamensis, P. boisei,* and *H. habilis.* The radius of specimens KNM-ER 1812d, KNM-ER 3736, KNM-ER 3888, and Omo 75s are also present, but a definitive taxonomic designation for these specimens has not been assigned (Patel 2005). The radii of OH 62 and BOU-VP-12 are partial. They have been reconstructed to estimate length, however morphological qualities may not be properly assessed. OH 62 is attributed to *H. habilis* while BOU-VP-12 has not been assigned to a taxon, but can be dated to 2.5 million years ago (mya) (Reno et al. 2005). The proximal ulna of specimen DNH-109 from Drimolen has not been given any taxonomic designation, but is preserved well enough to identify morphological attributes of the Plio-Pleistocene subadult (Gallagher and Menter 2011).

Excavations of Liang Bua in Flores have produced right and left ulnae, right and left radii, metacarpal shafts, multiple phalanges, and a left scaphoid, capitate, hamate, trapezoid, and lunate of *Homo floresiensis (*Larson et al. 2009). The ulna and radius of *Oreopithecus bambolii* have been recovered, however the skeleton was mostly crushed and the overall morphology of the forearms have been distorted. The left hand of *O. bambolii* has been reconstructed and is represented by four middle phlanges, five distal phalanges, four metacarpals, the scaphoid, lunate, capitate, and hamate (Susman 2004). Hand bones of *H. habilis* are present (Marzke and Marzke 2000) including four middle phalange, three distal phalanges, a trapezium, and a scaphoid. Every metacarpal and phalanx is present of the Shanidar 4 Neanderthal (Churchill 2001, Trinkhaus 1996). Member 4 from Sterkfontein contained a right capitate (TM 1526) and Member 2 contained a right triquetrum. Recently, an additional well preserved scaphoid was excavated from Sterkfontein (Kibii et al. 2011).

Three ulnae belonging to OH 36, Omo L40-19, and KNM-BK 66 have been discovered from East Africa and morphological studies were carried out by Aiello (1999). These ulnae cannot be definitely attributed to a particular taxon, but the ulnae fit within the morphological characteristics of *H. erectus, P. boisei,* or *H. heidelbergensis* (Aiello 1999). Multiple forearm bones represent *H. neanderthalensis* including radii and ulnae from La Quina, La Ferassie, La Chapelle aux Saints, Kebara, Shanidar, and Le Moustier. Forelimbs of these Neanderthals have also been morphologically compared with the early *Homo sapien* remains from Combe Capelle, Abri Pataud, Dolni Vestonice, Qafzeh, Ohalo, and Skhul (De Groote 2011).

An archaic ulna from Chagyrskaya Cave was found in association with Mousterian tools and has been attributed to *Homo neanderthalensis* due to morphological similarity to the remains from Shanidar (Mednikova 2013). *Australopithecus afarensis* hand bones from Hadar have been studied by Marzke (1983) in addition to three hominind metacarpals from Swartkrans dated to 1.7-1.9 mya with no certain taxonomic designation (Marzke 1987). Functional analysis has also been done by Napier (1962) on hand bones excavated from Bed I of Olduvai. These hand bones have been attributed to *H. habilis* and consist of distal phalanges, the trapezium, metacarpals, and middle phalanges. The oldest distal phalange available in the hominin fossil record belongs to *Orrorin tugenensis* (Almecija et al.

2010). A recently discovered third metacarpal from Kaitio, Kenya has been dated to 1.42 mya and has been assigned to *H. erectus.* Near complete hands of *Ardipithecus ramidus* and *Australopithecus sediba* are also available (Ward et al. 2013). The first metacarpal of *Paranthropus robustus* is also preserved, which has been argued to indicate that the robust australopiths may have created and used stone tools (Susman 1988).

Hand and Forearm Musculature

Habitual tool use is partially facilitated by the presence of the flexor pollicis longus muscle which is located on the radial side of the forearm of modern humans. It arises from the grooved anterior surface on the radial shaft and runs to the distal phalanx of the thumb (Gray 1901, Diogo et al. 2012). Though chimpanzees and other apes have the capacity to use objects as tools, nonhuman primates lack the separation between the flexor pollicis longus and the flexor digitorum profundus meaning they cannot flex their first metacarpal independently of digits II-V (Susman 1994). Anatomically modern humans, the most habitual tool users, also have forearms that are characterized by more muscles than any extant ape. The extensor pollicis brevis runs from the dorsal surface of the radius to the proximal phalanx of digit I in modern humans and is lacking in other extant apes (Diogo et al. 2012). The flexor pollicis longus and extensor pollicis brevis allow for the range of extension and flexion of digit 1 in modern humans which aids in stone tool making and other manipulative behaviors.

The capabilities of apes to use power grips and precision grips will dictate not only their capability to create stone tools, but also how forces are distributed across the hand during manufacture. Napier (1956) noted that only anatomically modern human hands are capable of precision gripping and that the inability of extant apes to use precision gripping is due to their relatively short thumbs (Napier 1956, Rolian et al. 2011). The breadth of the head in relation to the length of metacarpal I aids in precision gripping (Susman 1988) meaning the gracile thumbs of African apes are capable only of power grips (Rolian et al. 2011). As tool manufacturing increased in complexity, skeletal structures began to develop in response to tool use beyond that of the breadth of the first metacarpal. The styloid process of the third metacarpal allows the third metacarpal to lock against the bones of the wrist which helps the palm withstand external forces during the creation of stone tools. Originally thought to be distinct to Neanderthals and humans, the styloid process of the third metacarpal has recently been identified in *H.erectus* (Ward et al. 2013). Other skeletal feature required to partake in precision gripping are broad apical tufts of the distal phalanges, which allow for greater amounts of pressure to be places on the distal phalanx during precision gripping. The ability to habitually use and create stone tools requires a suite of traits of the forearm and hand. Habitual tool use should be identifiable on the skeleton by the presence of a broad head of metacarpal 1, broad apical tufts, muscle markings for the flexor pollicis longus, a styloid process on the third metacarpal, and a broad head on metacarpal V to also aid in precision gripping. Episodic tool use may be identifiable early in the fossil record by the earliest of these traits, which was likely the relatively broad head of metacarpal I. Extant great apes could also be considered episodic tool users, but definitely not stone tool creators. Episodic tool users exhibit pronation-supination of the forearm, but do not have the entire suite of traits specific to the hand.

3 METHODS

Fossil cast collections containing the forearm and hand bones of Neanderthals, archaic humans, and anatomically modern humans were examined in order to create a comprehensive database of relevant measurements for tool users. Fossil hominin ulnae, radii, metacarpals, carpals, and phalanges were analyzed with comparative collections of anatomically modern humans, chimpanzees, gorillas and orangutans. In the absence of quantitative data, a qualitative description and comparative analysis of hominin individuals will be included to provide contextual information for potential morphological relationships.

A comparative collection of great ape individuals was collected at the Field Museum of Natural History in Chicago. Data collection included individuals belonging to *G. gorilla berengei, G. gorilla gorilla*, *Pongo pygmaeus*, *Pan troglodytes,* and *Pan paniscus.* The available individuals from the great ape species are mostly male merely due to availability. Measurements on the long bones of the forearm were performed according to the methods described by Buikstra and Ubelaker (1994). Measurements of the ulna include maximum length, anterior-posterior breadth, and medial lateral breadth. Radial measurements were measured using identical standards with the addition of the breadth of the radial head. Because the radial head has been associated with an increase in radioulnar mobility (Patel 2005), the anterior-posterior breadth has been collected to determine its relationship among all collected measurements. Physiological length of the ulna as defined by the Buikstra and Ubelaker (1994), defined by the most inferior point of the coronoid process to the inferior surface of the distal head, was not included in this study.

Because metacarpal and phalanx measurements are not defined in the Chicago Standards (Buikstra and Ubelaker 1994), measurements from previous studies of tool use were chosen and included the length and breadth of the first and third metacarpals and the length and breadth of the third distal phalanx (Marzke and Marzke 2000, Niewohner 2001, Rolian et al. 2011, Susman 1988). Carpal measurements were not available at the time of data collection, although the breadth of the third metacarpal was collected at the metacarpal head. The third distal phalanx was chosen and breadth was measured at the widest point of the apical tuft. In addition to the maximum length and breadth and breadth of the radial head, anterior-posterior lengths were collected from the scaphoid and lunate notches. Collection of this measurement was included because previous research linked the scaphoid notch to changes in locomotor behavior. Specifically, morphology of the scaphoid notch has been linked to knuckle-walking, and a larger articular surface of the scaphoid notch assists knuckle-walkers with added surface area for resisting external forces during locomotion (Richmond and Strait, 2000). The inclusion of these traits of the distal radius may provide additional insight as to whether they are equally associated with tool use as they are with locomotion.

Fossil hominin and human comparative data was collected from the Department of Anthropology University of Iowa fossil cast and human skeletal collections. Fossil hominins included materials attributed to Kebara 2, Tabun 1, La Ferrassie 1, La Quina 5, Omo L40-19, and Qafzeh 9, 10, and 11. All the elements present for each individual were measured, but due to the preservation difficulties associated with smaller fossil remains, certain measurements were lacking. All measurements recorded from the great ape comparative collection were subsequently collected from the modern human sample. While the styloid process was accessible for measurement in this collection, it was excluded to remain consistent with measurements collected from the great ape sample. The human collection of ten individuals was divided evenly among males and females. In order to provide a wider range of modern human variation, individuals displaying varying robusticity and stature were chosen. All measurements were taken from the right hand and arm unless otherwise noted in Tables 3.1 and 3.2.

Table 3-1 Measured Great Ape individuals with location, sex, and age

Individual	**Location**	**Origin**	**Sex**	**Age**
Pan paniscus 60770	Field Museum of Natural History	Fort Wayne Zoo	Male	Adult
Pan troglodytes 47321	Field Museum of Natural History	Zoo	Male	Adult
Pan troglodytes 137079	Field Museum of Natural History	Zoo	Female	Adult
Pan troglodytes 137078	Field Museum of Natural History	Zoo	Female	Adult
Pan troglodytes 127419	Field Museum of Natural History	Zoo	Unknown	Adult
Pan troglodytes 51319	Field Museum of Natural History	Zoo	Male	Adult
Pan troglodytes 180116	Field Museum of Natural History	Zoo	Male	Adult
Gorilla gorilla 180665	Field Museum of Natural History	Zoo	Female	Adult
Gorilla gorilla 81532	Field Museum of Natural History	Ethiopia	Unknown	Adult
Gorilla gorilla 186434	Field Museum of Natural History	Zoo	Female	Adult
Gorilla gorilla	Field Museum of	Zoo	Male	Adult

135290	Natural History			
Gorilla gorilla 18402	Field Museum of Natural History	Cameroon	Male	Adult
Gorilla gorilla 27551	Field Museum of Natural History	Zaire	Male	Adult
Gorilla gorilla 16344	Field Museum of Natural History	Cameroon	Male	Adult
Gorilla gorilla 26065	Field Museum of Natural History	Uganda	Male	Adult
Gorilla gorilla 18401	Field Museum of Natural History	Gabon	Male	Adult
Pongo pygmaeus 57231	Field Museum of Natural History	Zoo	Male	Adult
Pongo pygmaeus 53203	Field Museum of Natural History	Zoo	Female	Adult
Pongo pygmaeus 153745	Field Museum of Natural History	Zoo	Male	Adult
Pongo pygmaeus 153744	Field Museum of Natural History	Zoo	Male	Adult
Pongo pygmaeus 91723	Field Museum of Natural History	Zoo	Male	Adult
Pongo pygmaeus 35533	Field Museum of Natural History	Zoo in India	Male	Adult

Pongo pygmaeus 33536	Field Museum of Natural History	Zoo in Malaysia	Female	Adult
Pongo pygmaeus 47411	Field Museum of Natural History	Zoo	Male	Adult

Table 3-2 Measured modern human, archaic human, and Neanderthal individuals with origin, sex, and age

Individual	**Location**	**Origin**	**Sex**	**Age**
Human 1	University of Iowa	Unknown	Female	Adult
Human 2	University of Iowa	Unknown	Female	Adult
Human 3	University of Iowa	Unknown	Female	Adult
Human 4	University of Iowa	Unknown	Female	Adult
Human 5	University of Iowa	Unknown	Female	Elderly Adult
Human 6	University of Iowa	Unknown	Male	Adult
Human 7	University of Iowa	Unknown	Male	Adult
Human 8	University of Iowa	Unknown	Male	Adult
Human 9	University of Iowa	Unknown	Male	Adult
Human 10	University of Iowa	Unknown	Male	Adult

Tabun 1 Neanderthal	University of Iowa	Mount Carmel, Israel	Female	Adult, Approx. 100kya, Middle Paleolithic
Qafzeh 9 Archaic Human	University of Iowa	Qafzeh, Israel	Female	Late Adolescent, Approx 100kya, Middle Paleolithic
La Ferrassie 1 Neanderthal	University of Iowa	La Ferrassie, France	Male	Adult, 70-50 kya Middle Paleolithic
Kebara 2	University of Iowa	Kebara, Israel	Unknown	Adult, 60 kya, Middle Paleolithic
Omo L40-19 Species Indeterminate	University of Iowa	Omo Basin, Ethiopia	Unknown	Adult
Qafzeh 10	University of Iowa	Qafzeh, Israel	Unknown	Juvenile, Approx 100kya, Middle Paleolithic
Qafzeh 11	University of Iowa	Qafzeh, Israel		Juvenile, Approx 100kya, Middle Paleolithic
La Quina 5	University of Iowa	La Quina, France		Adult, Approx 65kya, Middle Paleolithic

A variety of statistical analyses have been employed to identify relationships among hominins and associated functional morphology. After physical measurements from the forearm, first and third metacarpals, and third distal phalanx were recorded in Systat 10, an Analysis of Variance, Discriminant Function Analyses and univariate plots were performed. The analysis of these variables allows for the identification of morphological similarities between individuals and measures the amount of between-group variation between different species.

Univariate plots were utilized to examine Omo 50-19 in relation to the other taxa since only an isolated ulna is available for comparison. Ulna anteroposterior breadth and ulna length were plotted by each extant taxon, with males and females separated, as well as each of the fossil individuals in the sample. An Analysis of Variance (ANOVA) was used because the number of groups cannot be accommodated by a standard t-test. By calculating the means and standard deviation of radius, ulna, metacarpal and phalanx measurements across the sampled species, the ANOVA grouped based on the similarity of means which provides insight into whether the variation between groups is larger than the variation within groups for each measurement.

Discriminant Function Analyses were performed to assess which particular variables from the aforementioned measurements are the most influential in discriminating between groups, and whether multiple variables together can separate tool users from non-tool users. Discriminant Function Analyses included tests considering all variables, and two additional analyses that included hand measurements divided by the absolute length of the ulna and radius to determine which set of long bone ratios best separates tool users from non-tool users.

The utilization of these statistical analyses of measurement data from the forearm and hand bones of fossil hominin, extant apes, and anatomically modern humans will ideally provide a better understanding of how the hand and forearm measurements, both alone and together, reflect tool use and manufacture, or lack thereof, in these taxa.

4 RESULTS

An Analysis of Variance (ANOVA) performed for each measured variable, including ulnar, radial, metacarpal, and phalanx measurements, resulted in P-Values less than 0.05 indicating significant difference between groups (Table 4.1). The F-ratios, measuring the between-group to within group differences in the means of each variable, range from 4.031-14.923 with the length of Metacarpal 1 representing the lowest F-ratio (Figure 4.1) and the breadth of the radial head the highest (Figure 4.2). The range of F-ratios indicates that the greatest between-group variation is related to the absolute lengths of the ulna and the radius, the breadth of the radial head, and the length of the third metacarpal.

Table 4-1 ANOVA results of all collected measurements from great apes, modern and archaic humans, and Neanderthal individuals.

Variable	**F-ratio**	**P-value**
Radial Length	14.281	0.000
Radial Breadth (M-L)	4.723	0.001
Radial Breadth (A-P)	9.575	0.000
Radial Head Breadth	14.923	0.000
Ulna Length	12.888	0.000
Ulna Breadth (M-L)	4.762	0.001
Ulna Breadth (A-P)	5.161	0.000
Metacarpal 1 Length	4.031	0.003
Metacarpal 1 Breadth	7.494	0.000
Metacarpal 3 Length	10.317	0.000
Metacarpal 3 Breadth	9.845	0.000
Distal Phalanx 3 Length	6.557	0.000
Distal Phalanx 3 Breadth	7.740	0.000

Omo L40-19 Univariate Plots

Due to the limited number of measurements representing Omo L40-19, only variables from the available ulna were plotted. Employing two univariate plots, the absolute length of the ulna and the anteroposterior breadth of the ulna were plotted against the same measurements from each of the other species (Figures 4.1 and 4.2).

Omo Absolute Length

In the univariate plot analyzing the absolute length of the ulna (Figure 4.1), *G. gorilla* and *P. pygmaeus* are entirely separated from the range of variation between known tool users and *Pan*, and display the absolute longest ulnae of all species. The Omo L40-19 ulna is located central to the univariate plot, but is mostly excluded from the range of variation for *G. gorilla* and *P. pygmaeus.* Though *Pan*, a non-tool user, is similar in absolute length to humans and other known tool users, the Omo ulna falls outside of this range of variation as well.

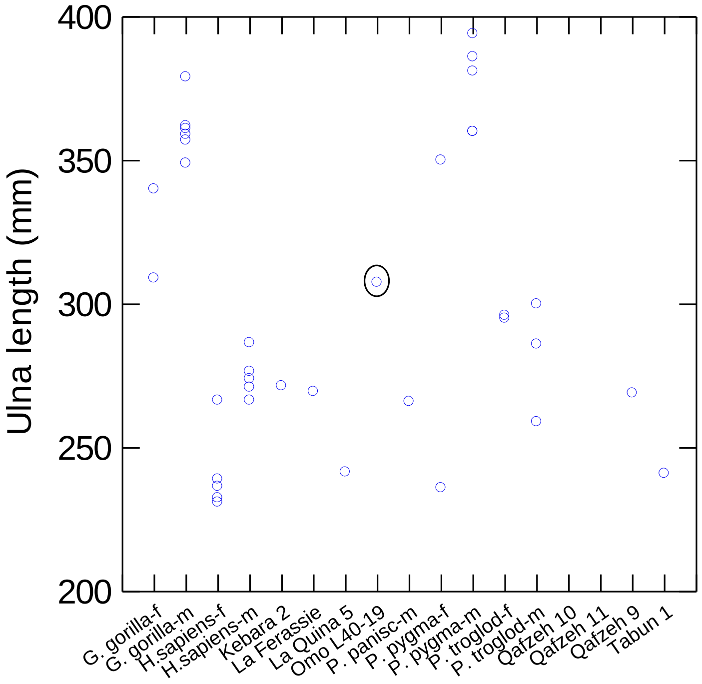


Figure 4-1 Univariate plot of Absolute Ulna Length for each individual/group with a circle surrounding Omo 40-19

Omo Anteroposterior Breadth

The second univariate plot (Figure 4.2) displays greater overlap among species in regard to the absolute anteroposterior breadth of the ulna. *G. gorilla* and *P. pygmaeus* have the absolute thickest ulnae measurements, but unlike the measurement of absolute length, both species exhibit a greater degree of overlap with the absolute breadth of *Pan*, humans, and the fossil hominins. A single *G. gorilla* individual overlaps with the grouping of human males, while the individuals belonging to *P. pygmaeus* overlap with each individual belong to both human males and gorillas with the exclusion of one member of *G. gorilla*. *Pan paniscus* and *Pan troglodytes* fit within the range of human males, and there is minimal overlap in absolute breadth between human males and human females. Each individual belonging to Neanderthals and archaic *H. sapiens* fits within the range of modern human males and females, with La Quina 5 occupying the low end of the range and Kebara 2 the high end. Similar to the first univariate plot, the Omo ulna is excluded from the range of anatomically modern humans, archaic *H. sapiens* and Neanderthals. Regarding absolute breadth, the Omo L40-19 ulna fits within the range of *P. pygmaeus* and *G. gorilla* rather than known tool users or manufacturers.

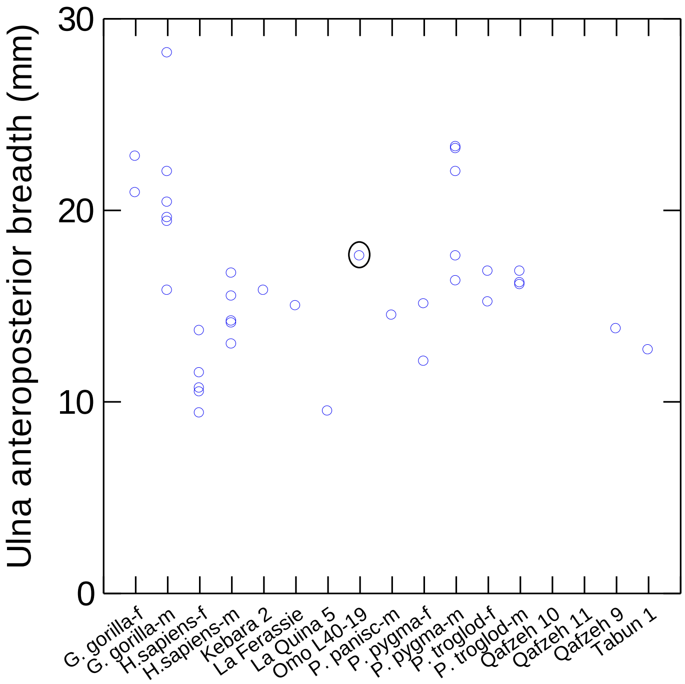


Figure 4-2 Anterior-Posterior Breadth of the Ulna (Axis 1) according to individual/group (Axis 2) with a circle surrounding Omo 40-19

Discriminant Function Analyses

All Variables

Discrimant Function Analysis was performed to assess the relationships between variables and identify species groupings. These Discrimant Function Analyses (Figures 4.3 and 4.4) included all measurements from the forearms, metacarpals, and phalanges with the exclusion of the scaphoid and lunate notches. Because the scaphoid and lunate notches were not able to be measured on each individual during the data collection phase, including those measurements would have excluded too many individuals from this analysis since complete dataset are needed to conduct multivariate statistics. Each individual in *G. gorilla* is male due to each female gorilla lacking measurements from the first metacarpal which consequently excluded them from the Discriminant Function Analyses. La Quina 5, Omo L40-19, and Qafzeh 10 and 11 were excluded from the Discriminant Function Analyses that assessed all variables due to the lack of measurements from these fossils.

The three highest weighted canonical scores are shown in Table 4.2. Canonical Score Axis 1 accounts for 58.4% of the variation with the anteroposterior breadth of the radius and the length of the third metacarpal as the most heavily weighted differences. Canonical Score Axis 2 accounts for 22.8% of variation between groups with the absolute length of the ulna and the anteroposterior breadth of the radial head representing the most heavily weighted differences. Canonical Score Axis 3 accounts for 9.2% of the variation with absolute length of the ulna and absolute length of the radius representing the most extreme differences from zero.

In Figure 4.3, Canonical Score Axis 1 separates tool users from non tool users with areas of overlap between *G. gorilla* and *P. troglodytes. Pan paniscus* falls outside of the *P. troglodytes* grouping (68% sample ellipse) but is closely associated with this group on axes 1 and 2. Tabun 1 and Kebara 2 group with human males, and La Ferrassie falls outside the group for both sexes of anatomically modern humans.

Canonical Score Axis 2 also separates tool manufacturers and habitual tool users from non tool users based mostly on absolute length of the ulna and the breadth of the radial head. *Pongo pygmaeus* is scaled completely opposite of *G. gorilla* from a relatively elongated ulna length in *P. pygmaeus* and a relatively large radial head in *G. gorilla* (Table 4.2) most likely due to differences in features related to locomotion. On axis 2, La Ferrassie 1 appears to be closer to *Pan* in absolute measurements than to human males or females.

Lastly, Canonical Score Axis 3 (Figure 4.4) separates Qafzeh 9, Kebara 2, and Tabun 1 from both humans and the great apes. There are areas of overlap between human males and females and between *P. troglodytes* and *G. gorilla.* Individuals belonging to *P. pygmaeus* group together, but are completely excluded from overlap with the other great ape species. *Pan paniscus* is also excluded from great ape groupings, but is located extremely close to *P. troglodytes*.

Table 4-2 Canonical Axis Scores 1-3

	1	2	3
RADIAL_LENG	1.335	0.363	4.354
RADIAL_BML	0.765	-1.587	-0.324
RADIAL_BAP	-2.529	-1.411	3.403
RADIAL_HAP	0.611	3.044	-1.878
ULNA_LENG	1.110	-2.314	-4.592
ULNA_B_ML	0.211	0.254	-1.128
ULNA_B_AP	0.443	1.288	0.299
MC1_LENG	-2.431	-0.926	-0.075
MC1_BREADTH	-0.050	-0.289	-2.356
MC3_LENTH	2.669	0.757	-1.563
MC3_BRETH	-1.285	0.776	2.831
DIS_PH3_LTH	-0.713	0.732	0.401
DIS_PH3_BR	-0.428	0.125	0.716

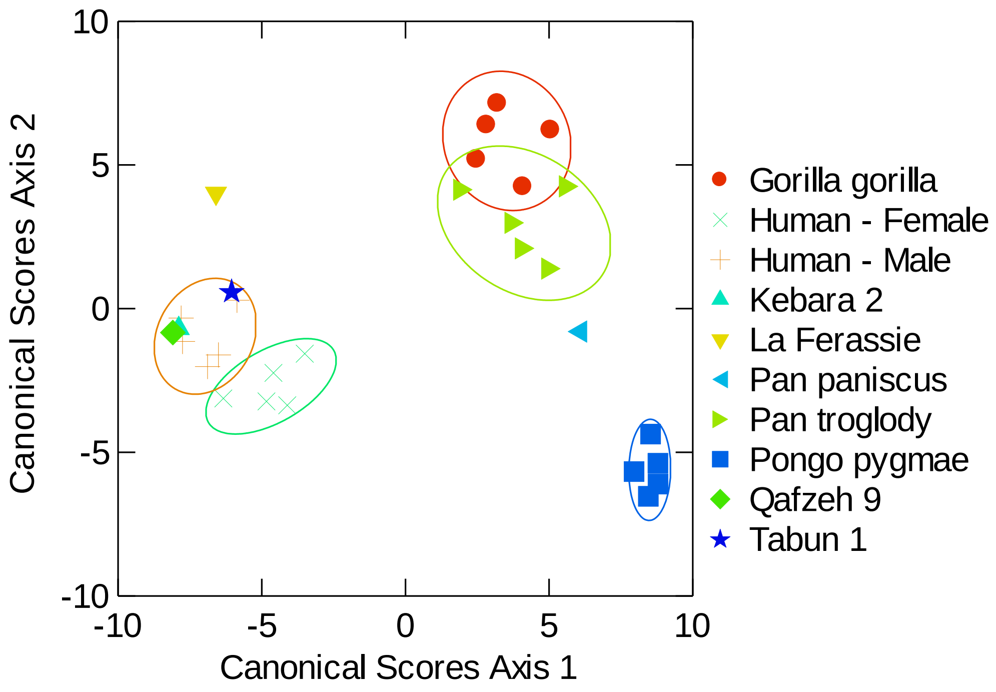


Figure 4-3: Canonical Scores Axis 1 and 2 for all measurements. Taxa are grouped using 68% confidence ellipses.

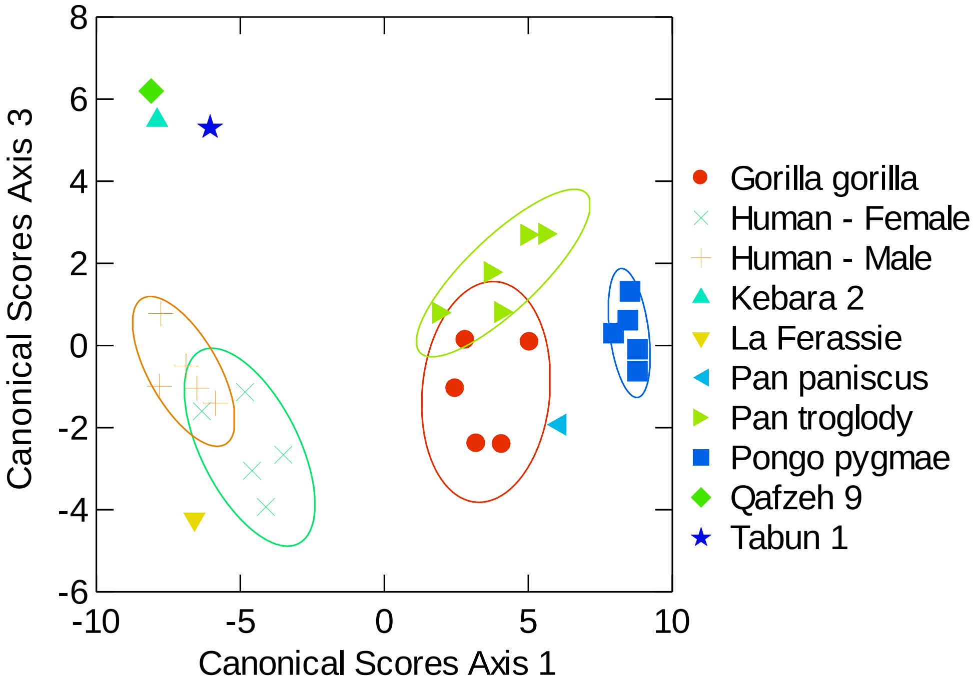


Figure 4-4: Canonical Scores Axis 1 and 3 for all measurements. Taxa are grouped using 68% confidence ellipses.

Hand Ratios to Absolute Forearm Lengths

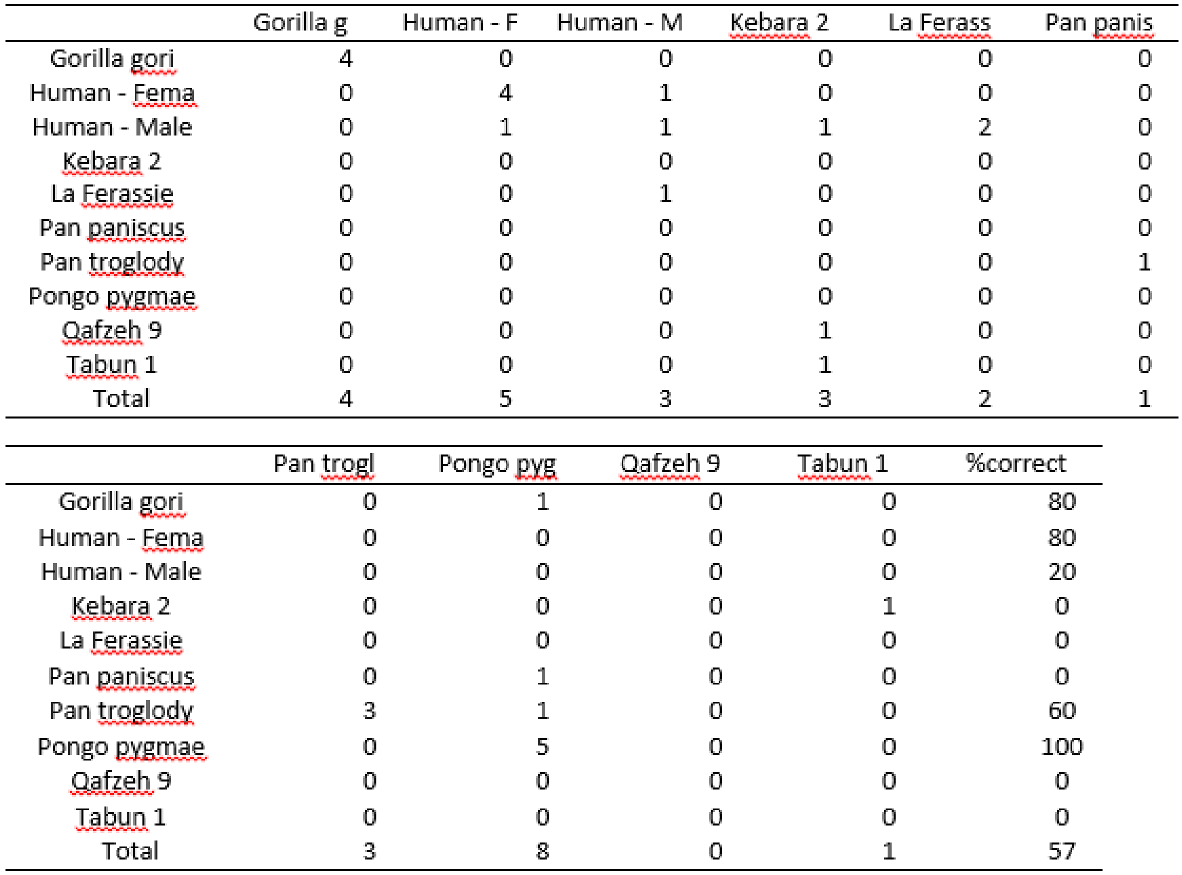
Additional Discriminant Function Analyses were performed comparing a ratio of metacarpal and phalangeal measurements to the absolute length of the radius and ulna. Similar to the prior Discriminant Function Analyses, each individual belonging to *G. gorilla* is male due to the female individuals missing measurements of the first metacarpal. Canonical Scores axes of these hand ratios divided by the absolute length of the radius are shown in Figure 4.5 and those divided by the ulna are presented in Figure 4.6.

Hand Ratios to Absolute Radius Length

In Figure 4.5, which displays the Discriminant Function Analysis comparing hand ratios to radius length, the variables influencing groupings the most along Canonical Scores Axis 1 are the ratio of the third and first metacarpal lengths divided by the length of the radius. Along Canonical Scores Axis, 2, the variables displaying the most influence in separating groups are the breadth of the third and the first metacarpals divided by radial length. The Discriminant Function Analysis separates habitual tool users from non-tool users along Canonical Scores Axis 1. A slight area of overlap between human males and human females includes one male individual and two female individuals. Though none of the fossil hominins are including within the human groupings, Tabun 1, Kebara 2, and La Ferrassie are close in proximity on both axes to human males. There are areas of overlap between the great apes as well, with *P. paniscus* excluded from any specific group but strongly associated with *P. pygmaeus.*

A Jackknifed classification of metacarpal and phalangeal ratios against absolute radius length (Table 4.3) categorizes Kebara 2 as Qafzeh 9, La Ferrassie as human male, and Tabun 1 as Kebara 2.

Table 4-3: Classification matrix



	Gorilla g	Human - F	Human - M	Kebara 2	La Ferass	Pan panis	Pan trogl	Pongo pyg	Qafzeh 9	Tabun 1	%correct
Gorilla gori	4	0	0	0	0	0	0	1	0	0	80
Human - Fema	0	4	1	0	0	0	0	0	0	0	80
Human - Male	0	1	1	1	2	0	0	0	0	0	20
Kebara 2	0	0	0	0	0	0	0	0	0	1	0
La Ferassie	0	0	1	0	0	0	0	0	0	0	0
Pan paniscus	0	0	0	0	0	0	0	1	0	0	0
Pan troglody	0	0	0	0	0	1	3	1	0	0	60
Pongo pygmae	0	0	0	0	0	0	0	5	0	0	100
Qafzeh 9	0	0	0	1	0	0	0	0	0	0	0
Tabun 1	0	0	0	1	0	0	0	0	0	0	0
Total	4	5	3	3	2	1	3	8	0	1	57

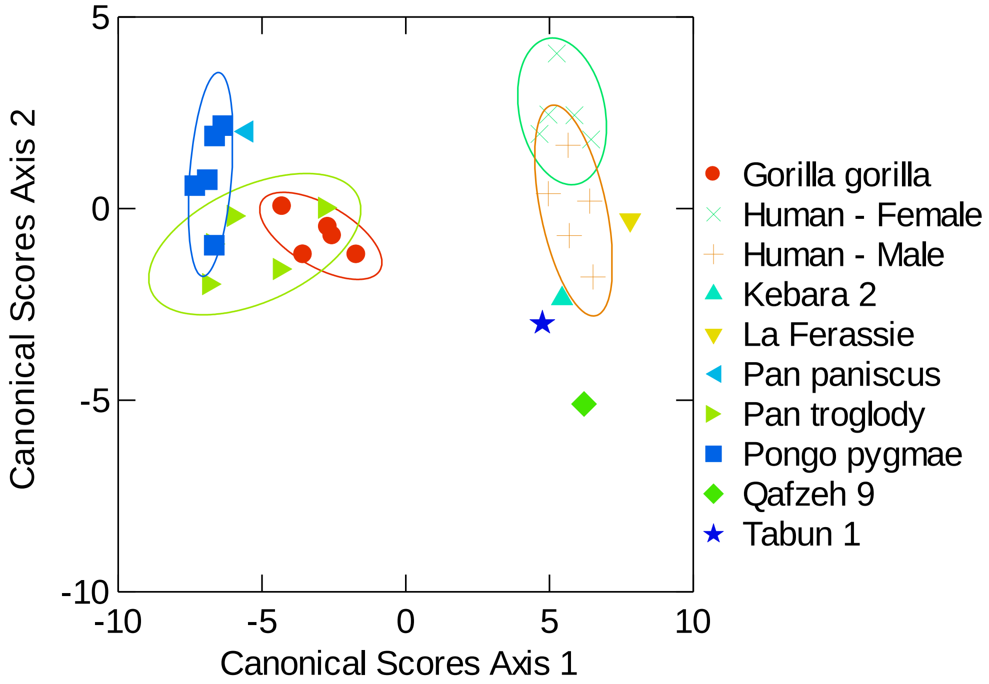


Figure 4-5: Canonical Scores Axis 1 and 2 of hand ratios divided into radial length. Taxa are grouped using 68% confidence ellipses.

Hand Ratios to Absolute Ulna Length

The Discriminant Function Analysis of metacarpal and phalangeal ratios compared to absolute ulna length exhibits similar groupings, but no areas of overlap except for human males and females. Along Canonical Axis 1, differences between groups are mostly driven by the ratio of the third and first metacarpal lengths divided by the length of the ulna. Axis 1 separates habitual tool users and non-tool users. Canonical Scores Axis 2 groupings are most strongly influenced by the ratio of the third metacarpal breadth when compared to ulnar length and breadth, and the ratio of the third distal phalanx. Fossil hominins are mostly excluded from specific groupings with the exception of Kebara 2 which groups with human males. Qafzeh 9, La Ferrassie 1 and Tabun 1 are also grouped closely, but not within, the human male grouping. Canonical Scores Axis 2 does not clearly separate habitual tool users from non-tool users, and appears to group according to the robusticity of metacarpal and phalangeal elements when compared to absolute ulna length.

A Jackknifed Classification categorizes one human female as human male, Kebara 2 as human male, La Ferrassie 1 as human male, one *P. paniscus* as *P. pygmaeus* and Tabun 1 as Kebara 2.

Table 4-4: Classification matrix

	Gorilla g	Human - F	Human - M	Kebara 2	La Ferass	Pan panis	Pan trogl	Pongo pyg	Qafzeh 9	Tabun 1	%correct
Gorilla gori	4	0	0	0	0	0	0	1	0	0	80
Human - Fema	0	4	1	0	0	0	0	0	0	0	80
Human - Male	0	1	1	2	1	0	0	0	0	0	20
Kebara 2	0	0	0	0	0	0	0	0	0	1	0
La Ferassie	0	0	1	0	0	0	0	0	0	0	0
Pan paniscus	0	0	0	0	0	0	0	1	0	0	0
Pan troglody	1	0	0	0	0	0	3	1	0	0	60
Pongo pygmae	0	0	0	0	0	2	0	3	0	0	60
Qafzeh 9	0	0	0	1	0	0	0	0	0	0	0
Tabun 1	0	0	0	1	0	0	0	0	0	0	0
Total	5	5	3	4	1	2	3	6	0	1	50

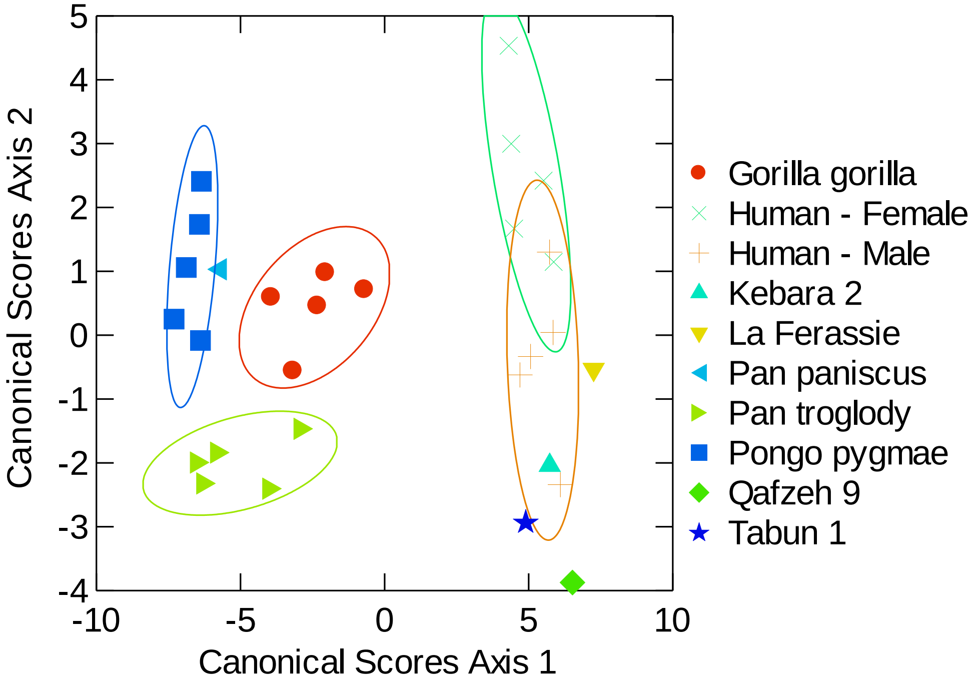


Figure 4-6: Canonical Scores Axis 1 and 2 of hand ratios divided into ulna length. Taxa are grouped using 68% confidence ellipses.

5 DISCUSSION

The ANOVA for all variables conveys the highest between-group variation for the anteroposterior breadth of the radial head and the least between-group variation for the absolute length of the first metacarpal. The largest between-group difference is radial head breadth between male *G. gorilla* and female *P. pygmaeus.* Across tool users, there appears to be less significant differences between human males, human females, Neanderthals, and archaic *H. sapiens.* The significant difference in radial head size between *Gorilla* and *Pongo* is likely due to locomotive behavior and represents a morphological separation between knuckle-walking and arboreal locomotion. The fact that the absolute breadth of the radial head is one of the driving factors of group separation is not surprising. Previous research has suggested that anterior and medial expansion of the articular surface of the radial head protects against external forces during knuckle-walking (Patel 2005) explaining why *G. gorilla* has the largest measurements. Because the radial head is an articular surface, reduction in size is linked to decreased mobility of the radioulnar joint (Patel 2005). This reduction is present in anatomically modern humans, and the ANOVA indicates a degree of similarity in the size of the radial head across the fossil hominins and modern humans. The individual with the absolute smallest radial head is a *P. pygmaeus* female, and the small size is likely linked to sexual dimorphism and arboreal locomotion. Qafzeh 9 and Tabun 1, both Middle Paleolithic tool users, are also smaller than the average human female, but it is unclear whether their small size is a consequence of sexual dimorphism, or a decrease in forearm mobility.

High F-ratios (Table 4.1) are assigned to absolute radial length, absolute ulna length, length of the third metacarpal, and breadth of the third metacarpal. Radial length and ulnar length exhibit the highest between-group variation after the breadth of the radial head. These groupings are not surprising given the extensive research on absolute and relative lengths of the forearms and how the ulna and radius relate to locomotor behavior and axial loading.

The F-ratio of first metacarpal length is 4.031 while the breadth is 7.494. Therefore, the between-group variation of first metacarpal breadth exceeds that of the first metacarpal length. This difference in F-ratios may suggest that the relative breadth of the first metacarpal is a more important factor when determining tool use than relative length of the thumb. Research suggests that more gracile thumbs are only capable of power gripping within the great apes (Rolian et al. 2011) and a broader first metacarpal aids in precision gripping (Susman 1988). Susman's work also suggests that the breadth of the head, as compared to the length, is a strong indicator of tool use and that metacarpal breadth plays a larger role than simply a relatively longer thumb.

The univariate plots of the Omo L40-19 ulna only included absolute length of the ulna and the breadth of the ulna taken in anterior-posterior position. When anteroposterior breadth and length of the ulna were plotted against species and fossil individuals, the Omo ulna was excluded from the range of variation for both habitual and non-tool users and fell slightly within the range of *G. gorilla* and *P. pygmaeus*. Based on ulna measurements alone, the individual represented by the Omo 40-19 ulna mostly likely did not use stone tools.

In the first Discriminant Function Analysis (Figure 4.1) assessing the relationship between all variables, habitual tool users and non-tool users are separated on Canonical Scores Axis 1. This separation is mostly driven by anteroposterior breadth of the radius and the length of the third metacarpal. In the Analysis of Variance, the F-ratio for the length of the third metacarpal also indicated more between-group variation than many other features. Canonical Score Axis 2 separates knuckle-walkers from highly arboreal apes and is likely driven by breadth of the radial head, which also produced the greatest between-group variation in the Analysis of Variance. This trait is larger in *G. gorilla* and *Pan.* Axis 2 places La Ferrassie 1 closer to *Pan* in absolute size than to modern male or female humans, likely due to the larger size of this particular individual. *Pongo pygmaeus* is separated from the other great apes on axis 2. This separation is most likely due to the relatively long ulna length which characterizes this highly arboreal ape, and perhaps the diminutive size of the radial head which does not bear excessive axial loading compared to the knuckle-walking apes. In Figure 4.7, habitual tool users and non tool users remain separated on axis 3, but Qafzeh 9, Kebara 2, and Tabun 1 are projected opposite of anatomically modern humans and La Ferrassie 1. There is a slight area of overlap between human males and females which can easily be attributed to within-group variation of modern humans. La Ferrassie 1 is closer to human males than to any of the other Neanderthals or archaic *H. Sapiens*. This placement on Canonical Scores Axis 3 is likely due to the hyper-robusticity of La Ferrassie 1.

The relationship between the breadths of the apical tufts and metacarpals relative to their absolute length has been established in previous literature. Ratios for the first and third metacarpals and the third distal phalanx first against the length of the radius, and second against the length of the ulna were plotted in two Discriminant Function Analyses -. Figure 4.9 displays the analysis performed for the hand ratios against the length of the radius. There is minimal, yet present, overlap between human males and females, and slight areas of overlap between the great apes. Axis 1 separates habitual tool users from non-tool users, and axis 2 appears to separate individuals based on overall robusticity. *Pan paniscus* is not included within any specific group, but is most closely associated with *P. pygmaeus* due to more gracile measurements. La Ferrassie 1, Kebara 2, and Tabun 1 are all closely associated with human males when hand ratios are compared to absolute radial length. The close association with human males is indicative of more robust metacarpal measurements when compared to forearm lengths, as none of the fossil hominins are located closer to human females or the region of overlap between modern human sexes. Qafzeh 9 is separated from the other fossil hominins and anatomically modern humans on Canonical Scores Axis 2, and is also separated from non-tool users. While Qafzeh 9 is thought to be a female individual (Cartmill and Smith 2009), it is highly unlikely that this separation is attributable to sexual dimorphism as the individual is located furthest away from human females and is not categorized as any other individual in a jackknifed classification.

Figure 4.11 compares the same hand ratios to overall length of the ulna. Similar to the comparison to the radius, habitual tool users are separated from non tool users on Axis 1. Interestingly, Axis 2 separates individuals in a very similar manner to the analysis of hand ratios to radial length, but the between-group variation when hand ratios are compared to ulnar length appear to be greater. Whereas the previous analysis exhibited areas of overlap among the great apes, when absolute length of the ulna is used as a size surrogate, the apes are completely separated. The range of anatomically modern human males and females are more spread out, but still exhibit a slight degree of overlap. The fossil hominins are consistently grouped closely with human males, with Qafzeh 9 separated from both human groups and the rest of the fossil hominins. These tests indicate greater between-group variation of the absolute length of the ulna over the radius when both measurements are compared to ratios from the phalanges and metacarpals, indicating a potentially stronger relationship between hand robusticity and the length of the ulna.

6 CONCLUSION

The univaritate plot employed in the analysis of the Omo L40-19 ulna presented similar conclusions to Aiello's (1999) comparative analysis of Omo L40-19 and OH 36. The Omo ulna, which was recently assigned to *Paranthropus boisei,* does not appear to group strongly enough with any other species to make a definitive determination on whether Omo L40-19 was a habitual or non-tool user. Conflicting dates assigned to the ulna further confuse species assignment (Aiello 1999). When absolute length of the ulna and anteroposterior breadth were plotted, Omo L40-19 was excluded from the range of variation for both *P. troglodytes* and modern humans, and was located more closely to *G. gorilla* and *P. pygmaeus.* Based on these measurements alone, Omo L40-19 most likely was not a habitual tool user.

When absolute lengths of the ulnae and radii were compared to ratios of the metacarpals and third distal phalanx, each graph produced similar results. While overall relationships appear to be similar among the two tests, the graphs indicate a greater degree of between-group and within-group variation when hand ratios are plotted against overall length of the ulna. Previous research on the hands of archaic humans and Neanderthals suggest that Neanderthals were more well suited to transverse power grips than anatomically modern human due to differences in hand measurements (Niewohner 2006), and that the individuals from Qafzeh are more similar in hand proportions to anatomically modern humans than to Neanderthals. The comparison of hand ratios to arm lengths suggests there may be a less pronounced degree of separation between Neanderthals and archaic humans than when hand measurements are analyzed in isolation. Whereas the degree of between-group separation is greater when the ulna is compared with hand ratios, the smaller degree of within-group separation between hand to radius length ratios implies a stronger relationship between the radius and the behaviors determining metacarpal and phalanx proportions.

Prior research highlights the similarities in proportion between anatomically modern humans and the individuals recovered at Qafzeh. Less robust musculature attachments and narrower fingertips differentiate Qafzeh individuals from Neanderthals and suggest that Qafzeh humans may have been more capable of oblique grips and finer manipulation. These conclusions make the separation of Qafzeh 9 from extant humans and Neanderthals slightly curious considering the absolute measurements do not appear drastically different. Other archaic humans, like Kebara 2 and Tabun 1, group closely with human males which is likely tied to robusticity of the hands in relation to the forearm. La Ferrassie 1, which exhibits the most relative robusticity, also groups more closely with human males. It is possible that the separation of Qafzeh 9 is a consequence of age, as this individual has been identified as a late adolescent (Cartmill and Smith 2009), and that the robusticity exhibited in habitual tool users is associated with adult skeletal development.

REFERENCES

Aiello, L. 1999. Morphological and Taxonimin Affinities of the Olduvai Ulna (OH 36) *American Journal of Physical Anthropology* 109: 89-110

Aiello, L and Dean, C. 1990. *An Introduction to Human Evolutionary Anatomy*. Academic Press

Andrews, P. and Banham, P. 1991. *Late Cenozoic environments and hominid evolution: A tribute to the late Bill Bishop*. Geological Society of London

Cartmill, M. and Smith, F.H. 2009. The Human Lineage. Wiley-Blackwell: Hoboken, NJ.

Churchill, S.E. 2001. Hand Morphology, Manipulation, and Tool Use in Neanderthals and Early Modern Humans of the Near East. *Proceedings of the National Academy of Sciences* 98, 2953-2955

De Groote, I. 2011. The Neanderthal Lower Arm. *Journal of Human Evolution* 61, 396 – 410.

Diogo, R., Richmond, B.G. and Wood, B. 2012. Evolution and homologies of primate and modern human hand and forearm muscles with notes on thumb movement and tool use. *Journal of Human Evolution* 63, 64-78

Drapeau, M.S.M., C.V. Ward., W.H. Kimbel, D.C. Johanson, and Y. Rak. 2005. Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *Journal of Human Evolution* 48, 593-642

Green, D.J. and Gordon, A.D. 2006. Limb-size proportions in *Australopithecus afarensis* and *Australopithecus africanus. Journal of Human Evolution* 52, 187-200.

Marzke, M.W. and Marzke, R.F. 2000. Evolution of the human hand: Approaches to acquiring, analyzing, and interpreting the anatomical evidence. *Journal of Anatomy* 197, 121-140

Mediknova, M.B. 2013. An archaic human ulna from Chagyrskaya Cave, Altai: Morphology and taxonomy. *Archaeology Ethnology & Anthropology of Eurasia* 41/1: 66-77

Napier, J.R. 1956. The prehensile movements of the human hand. *Journal of Bone Joint Surgery* 38, 902-913.

Patel, Biren A. 2005. The hominoid proximal radius: re-interpreting locomotor behaviors in early hominins. *Journal of Human Evolution* 48, 415-432

Richmond, B.G., Fleagle, J.G., Kappelman, J., Swisher, CC., 1998. First hominoid from the Miocene of Ethiopia and the evolution of the catarrhine elbow. *American Journal of Physical Anthropology* 105, 257-277.

Rolian, C., Lieberman, D.E. and Zermeno, J.P. 2011. Hand biomechanics during simulated stone tool use. *Journal of Human Evolution* 61, 26-41

Susman, R.L. 1988. Hand of *Paranthropus robustus* from Member 1, Swartkrans: Fossil Evidence for tool behavior. *Science* 240, 781-784.

Susman, R.L. 1994. Fossil evidence for early hominid tool use. *Science* 265, 1570-1573.

Tallman, Melissa. 2012. Morphology of the distal radius in extant hominoids and fossil hominins: Implications for the evolution of bipedalism. *The Anatomical Record* 295, 454-464.

Ward et al. 2013. Early Pleistocene third metacarpal from Kenya and the evolution of modern human-like hand morphology. *Proceedings of the National Academy of Sciences of the United States of America* 111 No. 1, 121-124

Williams, F.L., Cunningham, D.L., Amaral, L.Q. 2015. Forelimb proportions in *Homo sapiens*, *Australopithecus afarensis* and the great apes. *Homo—Journal of Comparative Human Biology* 66, 477-491.