

Patterns of Integration and Modularity in the Hominoid Wrist

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B.S. in Anthropology, May 2015, Arizona State University

A Thesis submitted to

The Faculty of  
The Columbian College of Arts and Sciences  
of The George Washington University  
in partial fulfillment of the requirements  
for the degree of Master of Science

August 31, 2018

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## Chapter 1: Introduction

Evolutionary changes in the bones of the carpus, or wrist, have long been integral to the discussion of the locomotor capabilities of fossil and extant hominoids (e.g., Lewis, 1969; Tocheri et al., 2008; Almécija et al., 2009; Williams, 2010; Nakatsukasa et al., 2016). Specifically, researchers have often turned to the wrist for evidence pointing towards the ancestral locomotor repertoire of hominoids, including the predecessors of bipedalism (e.g., Jenkins and Fleagle, 1975; Richmond and Strait, 2000; Begun, 2004; Kivell and Schmitt, 2009). Much debate has focused on whether *Pan* and *Homo* evolved from a knuckle-walking or more generalized arboreal ancestor (e.g., Tuttle, 1967; Richmond and Strait, 2000; Kivell and Schmitt, 2009; Lovejoy et al., 2009a; Williams, 2010). However, identifying the functional significance of wrist morphology, as well as other postcranial regions, in fossil skeletons is often complicated by the biological phenomenon of “mosaic evolution” observed in the hominoid fossils record (e.g., Köhler and Moyà-Solà, 1997; Moyà-Solà et al., 2004; Almécija et al., 2009; Young et al., 2010; Hamrick, 2012; Kivell et al., 2013; Tallman et al., 2013). Mosaic evolution is the concept that evolutionary change in morphology occurs at different rates among anatomical regions (Wagner and Altenberg, 1996). The hominoid fossil record shows that skeletal morphology has evolved in a mosaic fashion, where fossil skeletons often appear to exhibit a “patchwork” of conflicting adaptations. The morphological combinations observed in the appendicular skeletons of fossil apes are not found in living analogues, making it unclear whether the individual morphologies we observe in the fossil record are functionally relevant or merely retentions from an ancestral species.

In addition to the issue of mosaic evolution in the wrist, the complexity within these

structures is often ignored. The wrist contains several bones that work in concert during a variety of behaviors, including locomotion, foraging, and tool-making and use (Whitehead, 1993; Fleagle, 2013). Despite the strong anatomical and functional relationship among carpal bones, current studies investigating the evolution of carpal morphology often focus on single bones rather than the carpus as a cohesive unit (e.g., Tocheri et al., 2005; Kivell, 2009; Nakatsukasa et al., 2016; Ogihara et al., 2016). When bones of this region are considered in conjunction, they are often separated into two modules: a proximal and distal row (Richmond and Strait, 2000). However, modern humans have been hypothesized to have an “oval-ring” modular configuration based on the ligamentous connections between the scaphoid, lunate, capitate, and triquetrum. Furthermore, primates—particularly modern humans—differ in their patterns of wrist movement (e.g., Craigen and Stanley, 1995; Williams, 2010; Kivell et al., 2013). This variation may indicate that there may not be a single set of functional modules across primates, which may have implications for form and function of the wrist in fossil apes. It is therefore possible that these widely used functional groupings ignore the morphological and functional complexity of the wrist, as well as the phylogenetic and locomotor signals that may be driving the relationships among the bones of the wrist. To better understand the evolutionary trajectory and ancestral condition of functional adaptations of the forelimb and more accurately infer locomotion from functional morphology in fossil apes, an improved understanding of the evolutionary relationships between and within the primate carpus is needed.

To interpret the functional complexity of the wrist, we can investigate trends of integration and modularity between structures in the wrists of extant and fossil primates (Young et al., 2010; Klingenberg et al., 2012; Kivell et al., 2013; Klingenberg and

Marugán-Lobón, 2013; Klingenberg, 2014). Integration refers to the covariation of traits that results from developmental and evolutionary processes that produce morphology, whereas modularity pertains to units in a complex system that have high levels of trait integration within the unit, but do not covary strongly with other units (Klingenberg, 2008). Thus, trait covariation is a means by which we can evaluate integration between structures and define functional modules in the wrist. Analyses further evaluating the covariational structure of the carpal bones will supplement our hypotheses reconstructing the locomotor behavior of Miocene apes such as *Ekembo* and *Pierolapithecus*, and early hominins such as *Australopithecus* (Dart, 1925; Napier and David, 1959; Stern and Susman, 1983; Latimer and Lovejoy, 1989; Ward, 1993; Moyà-Solà et al., 2004; Berger et al., 2010), which will help us understand the ancestral conditions and predecessors to bipedalism. However, until now, no one has studied the complexity and modular nature of these structures using contemporary morphometric methods. Therefore, this project aims to develop our understanding of morphology in the wrists of fossil apes by establishing patterns of integration and modularity among hominoid primates with different habitual locomotor repertoires.

**Major Objectives.** This project aims to address the primary research question: **Are prevalent functional module theories reflected in the covariation structure of the anthropoid carpus?** by accomplishing the following objectives:

Aim 1. Examine whether competing modularity hypotheses are reflected in the bony morphology of the human wrist and if these configurations have changed over time

Aim 2. Test if knucklewalking apes (chimpanzees and gorillas) exhibit different

patterns of wrist integration based on the functional module theories set forward by Kivell and Schmitt (2009) to imply independent evolution of knucklewalking

Aim 3. Determine if both orangutans and hylobatids exhibit "ball-and-socket-like" suspensory wrist complex adapted for suspensory behaviors

**Intellectual Merit.** This study is one of the first to use modern morphometric techniques, such as 3-dimensional geometric morphometrics (3D GM) and shape covariation analyses, for considering integration and modularity of the wrist. This undertaking will result in the digitization and quantification of shape variation in approximately 1470 wrist elements across 212 individuals and 19 taxa, further developing our understanding of hominoid functional morphology. The data obtained throughout the duration of this project will contribute to an expansive 3D database of primate skeletal morphology created by the PI and colleagues. Furthermore, studying the covariation of functional traits in the wrist can help inform our interpretations of locomotion in fossil primates, especially given their mosaic body plans and often fragmented or incomplete remains.

## Chapter 2: Background

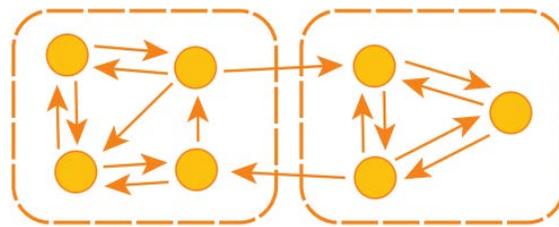
**Origins of Hominoids & Locomotion in Fossil Apes.** Hominoidea is a superfamily within Catarrhini that branched off from other catarrhines approximately 27 – 31 million years ago (MYA) (Steiper et al., 2004; Raaum et al., 2005; Steiper and Young, 2006; Stevens et al., 2013). Hominoidea includes the two families Hylobatidae (gibbons and siamangs) and Hominidae (great apes and humans). While hominoids inhabit an array of ecological niches, members of Hylobatidae inhabit southeast Asia, and are primarily known for their brachiating abilities (Lewis, 1971). The Asian apes, including the hylobatids and *Pongo*, are the most arboreal and suspensory of the apes (Thorpe and Crompton, 2006). The African apes, *Pan* and *Gorilla*, are traditionally classified as knuckle-walkers, meaning they typically place the dorsal aspect of their intermediate phalanges in contact with the ground during quadrupedal walking (e.g., Tuttle, 1967), though *Pan* is known to participate in more palmigrade and arboreal behaviors throughout life than *Gorilla* (Doran, 1992, 1993, 1997). Members of the genus *Homo* are obligate bipeds, which shared a last common ancestor with *Pan* approximately 4 – 7 MYA (Sarich and Wilson, 1967; Ruvolo, 1997), though recent genetic evidence suggests a 12.1 MYA divergence (Moorjani et al., 2016).

Despite a preservation bias towards recovering larger fossils (Ricklan, 1986), many carpal bones have been preserved from Miocene ape and early/putative hominin fossil assemblages, informing our hypotheses of the ancestral condition of hominoid locomotor repertoires (e.g., Beard et al., 1986; Lewis, 1989; Beard et al., 1993; Ishida et al., 2004; Moyà-Solà et al., 2004; Kivell and Begun, 2009; Lovejoy et al., 2009; Ruff et al., 2011; Ogiwara et al., 2016). While the locomotor behavior of these fossil taxa can be difficult to interpret due to mosaic evolution (e.g., Bastir and Rosas, 2009; Kivell et al., 2011, 2013;

Rein et al., 2011; Hamrick, 2012; Tallman et al., 2013), several studies have presented hypotheses considering the locomotion and postures used by these organisms (e.g., Begun, 2004; Moyà-Solà et al., 2004; Kivell and Begun, 2009; Lovejoy et al., 2009). For example, debate has surrounded the locomotor repertoire hypotheses of the early, and arguably most well-known, basal hominoid, *Ekembo (Proconsul)* (Napier and David, 1959; McNulty et al., 2015). In the scaphoid of *Ekembo*, the expansive radial facet is most like hominoids, whereas the hamulus of the hamate is more gracile like a monkey (Beard et al., 1986). All carpal bones except for the pisiform have also been found for *Pierolapithecus* (Moyà-Solà et al., 2004), which has been debated to be less suspensory than great apes (Begun and Ward, 2005; Moyà-Solà and Kohn, 2005; Deane and Begun, 2008, 2010; Alba et al., 2010). The locomotor repertoire of early hominin *Australopithecus* has also been debated, exhibiting conflicting adaptations for bipedality and arboreality (e.g., Stern and Susman, 1983; Latimer and Lovejoy, 1989; Ward, 2002; Chevalier, 2006; Kivell et al., 2011). More recently, the hand of *Homo naledi* (Berger et al., 2015) has displayed a mosaic of adaptations; where the longer and more curved finger bones suggest arboreality and climbing while the wrist is relatively modern human-like (Kivell et al., 2015). This variation in locomotor adaptations exhibited among fossil apes has led to competing hypotheses surrounding predecessors to bipedal locomotion. Various studies have looked to the wrist in an attempt to answer this question (Tuttle, 1967; Jenkins and Fleagle, 1975; Pilbeam, 1996; Richmond and Strait, 2000; Begun, 2004; Kivell and Schmitt, 2009; Lovejoy et al., 2009b). Despite the extensive literature on this topic, the debate still stands. However, studying integration and modularity of the wrists across species will supplement hypotheses concerning the locomotor behavior of these taxa as well as hypotheses about

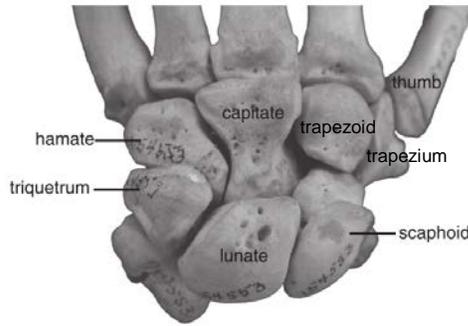
the precursors to bipedal locomotion in *Australopithecus* and *Homo*.

**Integration and modularity in the wrist.** Integration and modularity are closely related concepts but are commonly confused. Simply, “*integration* is the cohesion among traits that results from interactions of the biological processes producing the phenotypic structures under study” (Klingenberg, p. 116, 2008), or the propensity for a system to produce covariation (Hallgrímsson et al., 2009). *Modularity* pertains to units in a complex system that have high levels of integration between traits **within** the unit but are less integrated to other units (**Figure 1**). With this definition, the principles of morphological integration and modularity can be applied to any complex group of structures within the skeletal system, such as the wrist.



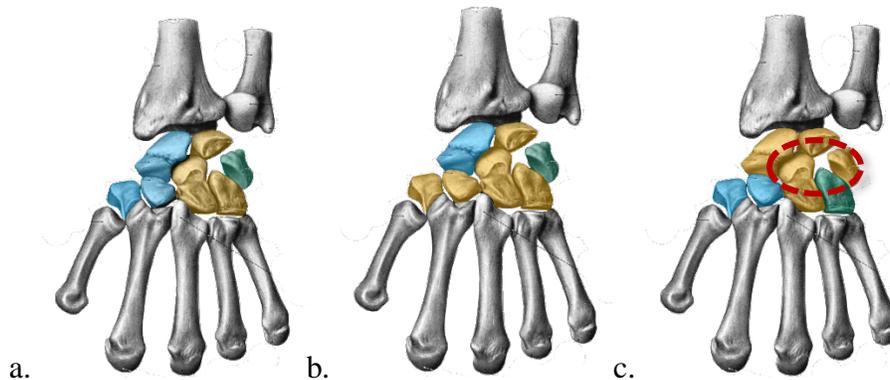
**Figure 1.** Schematic representation of integration and modularity; dotted lines represent boundaries between modules; arrows represent integration (Klingenberg, 2008).

The carpus is itself a complex system. The primate wrist contains 8 to 9 bones that are traditionally separated into two rows: a proximal and distal row. Generally, in primates, the proximal row includes the scaphoid, *os centrale*, lunate, triquetrum, and pisiform, while the distal row includes the trapezium, trapezoid, capitate, and hamate (**Figure 2**). The *os centrale* of African apes, humans, and some strepsirrhines is fused to the scaphoid (e.g.,



**Figure 2.** Left gorilla carpus in dorsal view (Kivell et al., 2013).

Lewis, 1974; Sarmiento, 1988; Kivell and Begun, 2007). In addition to the cluster of bones that make up the carpus, there are also several extrinsic and intrinsic ligaments, and muscles that work together during a variety of behaviors. This makes the carpus an ideal region of the skeleton to study in terms of integration and modularity.



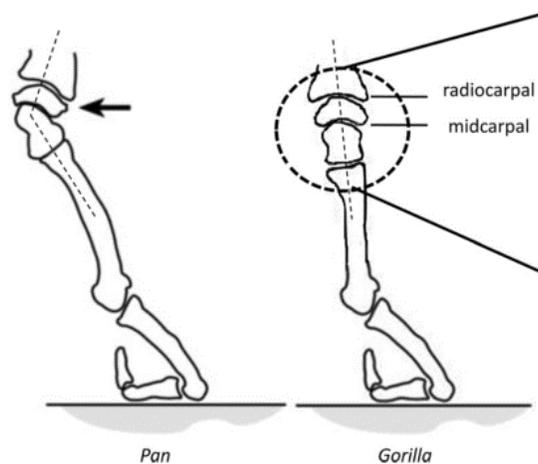
**Figure 3.** **a.** Navarro's columnar concept of the human wrist **b.** Taleisnik's central column/distal row concept **c.** Lichtman's "oval-ring" concept. Adapted from Lichtman et al. (1981).

**Wrist module theories.** Many hypotheses have been proposed considering the organization and modularity of the wrist in modern humans. Navarro (1921) had first posited that the wrist was organized into three columns; a medial, lateral, and central column. In this hypothesis, the medial column contains the triquetrum and pisiform; the central column includes the lunate, capitate, and hamate; and the scaphoid, trapezium, and trapezoid make up the lateral column (**Figure 3.a**). This model assumes that flexion and

extension is mainly occurring at the midcarpal joint of the central column, between the lunate and capitate-hamate heads. Navarro's early concept was later modified by Taleisnik (1976) to account for the idea that the distal row works as a single unit during flexion and extension on the lunate (**Figure 3.b**). The "oval-ring concept" was later introduced as a modification of a more traditional proximal-distal theory suggesting that the capitate, scaphoid, lunate, and triquetrum form a ring to ensure carpal stability during axial loading (**Figure 3.c**; Lichtman et al., 1981). This is the most widely accepted model in humans, given it has been found that the scaphoid participates in flexion when the wrist is axially loaded (Garcia-Elias, 2013). The capability of extreme extension may have led to specialized behaviors in humans such as tool-making (Williams et al., 2010) and throwing (Wolfe et al., 2006; Moritomo et al., 2007; Rodin et al., 2010; Roach et al., 2013; Roach and Lieberman, 2014). This spurs the question of whether this 'oval-ring' modular pattern is reflected in the shape and covariational structure of the wrist bones of humans, and whether certain factors distinguish this pattern from the carpal morphology of other taxa.

The anthropoid primates exhibit a wide array of adaptations for locomotion in their wrists. For many non-human anthropoid primates, kinematic data show that the wrist appears to deviate from an "oval-ring" concept. Recent kinematic studies on the wrists of anthropoid primates indicate that knuckle-walking and digitigrade monkeys are characterized by low ranges of motion (ROMs) at the midcarpal joints, while palmigrade monkeys are capable of greater flexion and extension at the midcarpal joint (Orr, 2017). This also supports the idea that the wrists of knuckle-walking apes, including *Pan* and *Gorilla*, are more specialized to maintain stability in the wrist during locomotion (Tuttle, 1967; Moritomo et al., 2006; Orr et al., 2010; Orr, 2017). However, based on behavioral

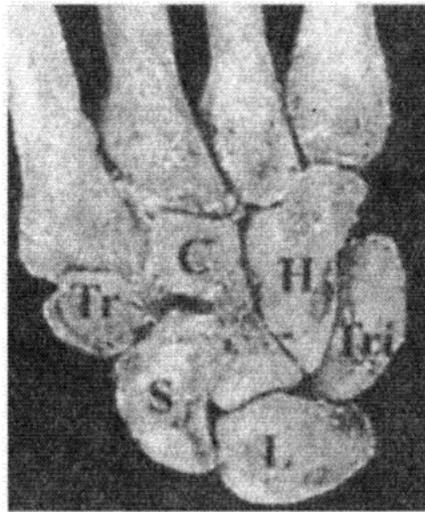
data, gorillas are hypothesized to have a more columnar wrist posture for support during knuckle-walking, chimpanzees may use a more extended wrist posture (Kivell and Schmitt, 2009) (**Figure 4**). This may be related to the fact that *Pan* has been shown to participate in some palmigrade walking and greater amounts of arboreal behavior than gorillas, requiring more extension in the wrist (Doran, 1992, 1997). These hypotheses concerning the wrist posture in chimps and gorillas have been used to support the hypothesis that knuckle-walking evolved independently in gorillas and chimpanzees (Dainton and Macho, 1999; Kivell and Schmitt, 2009). However, as in the modern human wrist, little is known about whether these functional modules correspond to morphological modules, making it difficult to make functional inferences based on the wrists of fossil specimens.



**Figure 4.** The extended midcarpal joint of *Pan* vs. the more columnar wrist posture in *Gorilla* (Kivell and Schmitt, 2009).

In contrast to the African apes and modern humans, the Asian apes (*Pongo* and Hylobatidae) have been characterized as both having midcarpal joints that strongly resemble a “ball-and-socket” (**Figure 5**); the hamate and capitate comprise the “ball” and triquetrum, lunate, and scaphoid comprise the “socket” (Jenkins, 1981). This pattern has been hypothesized to be an adaptation for greater mobility and less for stability (Jenkins,

1981). However, *Pongo* and hylobatids perform disparate suspensory behaviors; *Pongo* participates in more torso-orthograde multi-limb suspension (e.g., Manduell et al., 2011), while Hylobatidae exhibits a manual style of locomotion with free-flight phases from branch to branch (i.e., 'brachiation'; e.g., Fleagle, 1974, 1976). Furthermore, the carpal morphology has been shown to vary considerably between the hylobatids and *Pongo* (Kivell et al., 2013; Almécija et al., 2015). The variation in carpal bones among suspensory hominoids conflicts with the hypothesis that there may be a 'suspensory wrist complex.' Therefore, to help inform the functional inferences based on the wrists of fossil specimens, this project seeks to understand if these hypothesized functional modules are reflected in the bony morphology of extant anthropoid primates.



**Figure 5.** *Pongo* wrist exhibiting a “ball-and-socket” midcarpal joint (Begun, 2004). Socket in orange, ball in blue.

### Chapter 3: Aims & Hypotheses

The following aims are intended to help us better understand the evolutionary trajectory of functional adaptations and configurations in the hominoid fore-limb and more accurately infer locomotion from functional morphology in fossil apes and early hominins.

**Aim 1. Examine whether competing module hypotheses are reflected in the bony morphology of the modern human wrist and if these configurations have changed over time.** Several module theories have been set forward for the wrist; from rows, to columnar, to an “oval-ring” (Navarro, 1921; Taleisnik, 1976; Lichtman et al., 1981) (**Figure 3**). However, limited research has been done to determine if this is reflected in the bony morphology of humans and therefore, in fossil humans. Module theories will be evaluated by quantifying which clusters of bones are most integrated. Therefore, the hypothesis for aim 1 is:

Hypothesis 1.1: If the “oval-ring” modular pattern described for the modern human wrist is reflected in the bony morphology, then we expect that:

1. *Homo sapiens* will exhibit more integration between the scaphoid, lunate, capitate, and triquetrum than between other carpal bones.

Hypothesis 1.2: The wrist of *Australopithecus sediba* displays a mosaic of modern human-like and arboreal adaptations

1. *Australopithecus sediba* will exhibit a similar modular structure to modern humans. Assuming Hypothesis 1.1 is correct, *Australopithecus sediba* will display greater integration between the scaphoid, lunate, capitate, and triquetrum than between other carpal bones.

Hypothesis 1.3: The wrist of *Homo naledi* was modern human-like

1. *Homo naledi* will exhibit a similar modular structure to modern humans. Assuming Hypothesis 1.1 is correct, *Homo naledi* will display greater integration between the scaphoid, lunate, capitate, and triquetrum than between other carpal bones.

**Aim 2. Test if chimpanzees and gorillas exhibit different patterns of wrist modularity.**

This aim is intended to quantify patterns of covariation among knuckle-walking primates using a comparative sample of digitigrade and palmigrade primates (including, *Pan*, *Gorilla*, and digitigrade and arboreal cercopithecoid monkeys). Kivell and Schmitt (2009) posited that *Gorilla* and digitigrade monkeys exhibit a more columnar wrist posture to maintain stability during locomotion, whereas *Pan* and arboreal monkeys exhibit a more extended wrist during locomotion (**Figure 4**); these hypotheses have been used to infer independent evolution of knuckle-walking in chimpanzees and gorillas. Therefore, the hypothesis for aim 1 is:

Hypothesis 2.1: *Pan* exhibits a “row-like” modular pattern, whereas *Gorilla* exhibits a more columnar modular pattern in the wrist. If this is correct then we expect that:

1. *Pan* and arboreal monkeys will exhibit greater integration between the proximal carpal elements (lunate, scaphoid, triquetrum) and distal carpal elements (hamate, capitate, trapezoid, and trapezium), respectively, than *Gorilla* and digitigrade monkeys.
2. *Gorilla* and digitigrade monkeys will exhibit greater integration between hamate, capitate, and lunate and scaphoid, trapezium, and trapezoid, respectively, than *Pan* and arboreal monkeys.

**Aim 3. Test the ball-and-socket-like module hypothesis in the wrists of *Pongo* and hylobatids.** *Pongo* and hylobatids participate in distinct types of arboreal locomotor

behaviors; *Pongo* exhibits quadrumanous suspensory behaviors, while hylobatids typically perform bimanual brachiation (Fleagle, 1974, 1976; Thorpe and Crompton, 2006; Manduelli et al., 2011). However, it has been hypothesized that the high mobility of the wrists of both *Pongo* and hylobatids is permitted by a “ball-and-socket”-like junction between the hamate, lunate, triquetrum, and capitate (Jenkins, 1981) (**Figure 5**). Therefore, the hypothesis and predictions for aim 3 are:

Hypothesis 3.1: Both *Pongo* and Hylobatidae evolved a ball-and-socket-like joint as an adaptation towards specialized suspensory and brachiating behaviors (Jenkins, 1981). If this is true, then we expect:

1. Both *Pongo* and hylobatids will exhibit strong morphological integration between their hamate, lunate, triquetrum, and capitate than compared to other wrist bones.
2. Both *Pongo* and hylobatids will exhibit strong integration between the capitate and hamate (which create the “ball”) and their lunate and triquetrum (which create the “socket”), respectively, than compared to other wrist bones.

## Chapter 4: Methods

**3D geometric morphometrics (3DGM).** The field of geometric morphometrics represents a suite of methods that are used to capture shape information of biologically important morphological traits (e.g., Rohlf and Marcus, 1993; Adams et al., 2004; Lockwood et al., 2004; Zelditch et al., 2004; Slice, 2005). In traditional morphometrics, linear measurements are taken on the structures of interest and subsequently analyzed to assess differences in shape among individuals (Adams et al., 2004). However, in both 2D and 3DGM, landmarks of homologous structures are digitized, respectively, into 2D or 3D coordinate points, capturing the complex surface topography and not just the overall proportions of the bone (Bookstein, 1991; Rohlf and Marcus, 1993), which is valuable for condensed, morphologically complex structures like the carpal bones. The use of geometric morphometrics has expanded in recent years now that many researchers have opted for collecting measurements from 3D models. Digital models of skeletal elements can be produced using a variety of methods (computed tomography, laser and light scanners, photogrammetry) and used in together in analyses without significantly effecting results of morphometric studies (Tocheri et al., 2011; Shearer et al., 2017).

The raw coordinate data produced from 3DGM methods must be adjusted in order to perform subsequent analyses. To control for variables that may have an impact on the shape of a structure, such as size and orientation of the landmark configuration, Generalized Procrustes Analysis (GPA) can be applied to the raw coordinate data (Gower, 1975; Dryden and Mardia, 1998). GPA takes the landmark coordinate data for each specimen and transforms the coordinates so each landmark configuration for each individual is superimposed on a central point (the centroid) (Gower, 1975; Zelditch et al.,

2004; Mitterøcker et al., 2013). GPA then rotates each centralized configuration, so they are all in the same orientation, and lastly, GPA will scale the landmark configurations, so they are all the same size. What is left after GPA is just the shape of each specimen. Subsequent analyses can then be performed on the new Procrustes coordinate configurations (Mitterøcker et al., 2013). The configurations are then visualized in thin plate spline (TPS) warps (Bookstein, 1991). This method involves mapping the individual landmark configurations to the average “atlas” and measuring the Euclidean distances between the individuals and atlas in order to assess the shape variation in the sample (Bookstein, 1991).

**Quantification and analysis.** To better understand the patterns of shape covariation in the skeleton, an improved understanding of the evolutionary relationships between multiple structures is needed – particularly within complex modules with many elements, such as the wrist. However, most studies of carpal bones evaluate single elements, rather than multiple bones in conjunction, and little is known about the varied degrees of integration between each carpal bone (Kivell et al., 2013). Many statistical methods have been proposed to study covariation, integration, and modularity (Adams and Felice, 2014; Denton and Adams, 2015; Adams, 2016; Goswami and Finarelli, 2016).

The application of two-block partial least squares analysis (2B-PLS) on GM data (Rohlf and Corti, 2000) is common practice when assessing **the degree of integration** or coevolution between two structures (e.g., Gómez-Robles et al., 2011; Singh et al., 2012; Klingenberg and Marugán-Lobón, 2013; Martín-Serra et al., 2015; Noback and Harvati, 2015; Bailey et al., 2016). Much like a principal components analysis calculates the major axes of variation in a sample, 2B-PLS calculates the major axes of *covariation* shared

between two blocks of variables, for instance, the capitate and hamate; each succeeding pair of axes contributes gradually less of the shared covariance (Rohlf and Corti, 2000). However, as the name suggests, 2B-PLS is limited to evaluating two blocks of variables, or in the case of this study, two carpal bones at a time. Additionally, 2B-PLS results are typically calculated using the RV coefficient, a ratio of within-block covariation to between-block covariation (Robert and Escoufier, 1976) which has been shown to be sensitive sample size (Adams, 2016). To solve this issue, Adams (2016) proposed a method called the Covariance Ratio (CR), which implements the pairwise covariances between variables to quantify modular organization. Unlike 2B-PLS, the CR can be applied to more than two blocks by averaging the pairwise CRs, and since it is not sensitive to sample size, it is more accurate in establishing degrees of modularity in phenotypic datasets (Adams, 2016).

**Aim 1. Examine whether competing module hypotheses are reflected in the bony morphology of the modern human wrist.**

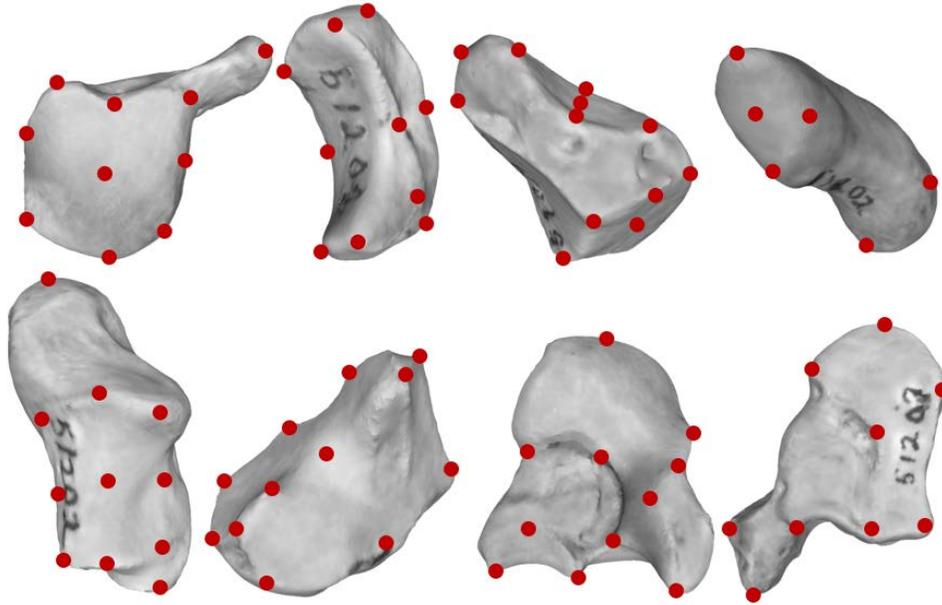
*Sample 1.* The target sample will include 50 adult modern humans, as well as the fossil specimens *Australopithecus sediba* and *Homo naledi* (**Table 1**). Though this aim primarily focuses on modern human wrist organization, *Pan troglodytes troglodytes* will be included in the analysis as an outgroup. Each individual in the sample should possess all 8 carpal bones of interest: the capitate, hamate, lunate, triquetrum, trapezoid, trapezium, and pisiform. The *os centrale* will be excluded from analysis since it is fused to the scaphoid in African apes and humans (Kivell and Begun, 2007). The fossil sample will be obtained from MorphoSource. This extant sample has already been digitized 3-dimensionally by the PI and colleagues using medical and micro CT, a Geomagic Lightscanner, and a

NextEngine laser scanner at the American Museum of Natural History (AMNH), The George Washington University (GWU), and Stony Brook University (SBU) collections. While using the same digitization method is preferable, the above methods produce comparable models and do not significantly impact results (Tocheri et al., 2011; Shearer et al., 2017).

**Table 1.** Target extant sample sizes for **Aim 1**. All extant individuals have all 8 carpal bones of interest present. Locomotor categories derived from Hunt et al. (1996) and Orr (2017).

<b>Species</b>	<b>Common Name</b>	<b>Locomotor use of hand</b>	<b><i>n</i> ♀</b>	<b><i>n</i> ♂</b>
<i>Homo sapiens</i>	human	None, but palmigrade-capable (extended-wrist)	25	25
<i>Homo naledi</i>				
<i>Pan troglodytes troglodytes</i>	chimpanzee	Knuckle-walking, climbing/suspension	5	5
<i>Australopithecus sediba</i> (MH-2)		scaphoid; lunate; triquetrum; capitate; hamate	1	--

*Measures 1.* As interobserver error can be high in landmark-based morphometric studies (Shearer et al., 2017), the co-PI, ANGELA, will be the sole researcher collecting the 3D coordinate landmarks on each carpal bone for every individual in the sample stated above. The landmark protocol for the hamate is cited in Alméjija et al., (2015). The landmark protocols for the pisiform, scaphoid, lunate, triquetrum, trapezium, trapezoid, and capitate were developed by the PI and co-PI and are primarily focused on the articular surfaces of each bone to optimize functionally related shape differences. We have included figures of the landmarks digitized as opposed to full descriptions due to space limitations (**Figure 6**). Intraobserver error will be also be calculated to ensure repeatability of the landmarking protocols following the procedure set out in Shearer et al. (2017).



**Figure 6.** Landmark protocols for the carpals included in this study. Selected images below are taken in a single view (due to lack of space), but landmarks protocols were designed to capture the overall 3D morphology. Top, left to right: capitate, hamate, lunate, triquetrum. Bottom, left to right: trapezoid, trapezium, and scaphoid. Hamate landmark protocol from Almécija et al. (2015). Specimen is *Pan troglodytes*.

*Analysis 1.* The strength of modularity will be computed using the average CR (Adams, 2016) of pairwise blocks of bones using the function ‘modularity.test’ in the ‘R’ v.3.5.1 (R Development Core Team, 2018) package, ‘geomorph’ (Adams et al., 2017). To assess the significance of the modularity, we will use a maximum likelihood approach comparing the CRs all possible module combinations. The combinations of possible modules will be based on the module hypotheses stated in the background, as well randomly assigned using the ‘define.modules’ function in geomorph (Adams et al., 2017). To account for allometric effects, or changes associated with the size of the individual, a regression of the independent contrasts of the log-transformed centroid size will be applied to the Procrustes adjusted coordinates of the sample (Klingenberg et al., 2012; Rodríguez-González et al., 2016).

**Aim 2. Test if chimpanzees and gorillas exhibit different patterns of wrist modularity.**

*Sample 2.* The target sample will include about 10 adult individuals from each species of *Pan*, *Gorilla* and the monkeys in **Table 2**. Like the sample in Aim 1, the specimens have already been digitized by the PI and colleagues. Only individuals with all 8 carpals of interest will be included in the analysis.

**Table 2.** Target extant sample sizes for **Aim 2**. All individuals have all 8 carpal bones of interest present. Locomotor categories derived from Hunt et al. (1996) and Orr (2017).

\*same specimens from **Aim 1**.

Species	Common Name	Locomotor use of hand	<i>n</i> ♀	<i>n</i> ♂
<i>Gorilla gorilla</i>	Western gorilla	Knuckle-walking, climbing	5	5
<i>Gorilla beringei beringei</i>	mountain gorilla	Knuckle-walking, climbing	5	5
<i>Gorilla beringei graueri</i>	Grauer’s gorilla	Knuckle-walking, climbing	5	5
<i>Pan pansicus</i>	bonobo	Knuckle-walking, climbing/ suspension, frequent “palmigrade” postures reported on smaller boughs, but exact wrist/hand positioning on arboreal supports is unclear.	5	5
<i>Pan troglodytes troglodytes*</i>	chimpanzee	Knuckle-walking, climbing/ suspension	5	5
<i>Cercopithecus</i> spp.	guenon	arboreal palmigrade	5	5
<i>Colobus</i> spp.	colobus monkey	Palmigrade (extended-wrist)	5	5
<i>Erythrocebus patas</i>	patas monkey	Palmigrade (extended-wrist)	5	5
<i>Macaca mulatta</i>	rhesus macaque	Digitigrade, but palmigrade capable (extended-wrist)	5	5
<i>Macaca fascicularis</i>	crab-eating macaque	arboreal palmigrade	5	5
<i>Nasalis larvatus</i>	proboscis monkey	Palmigrade (extended-wrist)	5	5
<i>Papio</i> spp.	Baboon	Digitigrade, “palmigrade” hand positions noted at high speeds, but wrist does not appear to be fully extended, and wrist mobility appears to prohibit true extended- wrist palmigrady	5	5

*Measures 2.* Elements from these specimens will follow the same procedure listed in Aim

1.

*Analysis 2.* In addition to the analyses employed in Aim 1, phylogenetic effects will be accounted for using phylogenetic independent contrasts (Felsenstein, 1985) with a phylogeny from 10ktrees (Arnold et al., 2010).

**Aim 3. Test the ball-and-socket-like module hypothesis in the wrists of *Pongo* and hylobatids.**

*Sample 3.* To evaluate if both *Pongo* and hylobatids exhibit a profound “ball-and-socket” mid-carpus in comparison to other primates, the target sample for Aim 3 will also include about 10 adult individuals from each species of *Pongo* and hylobatid detailed in **Table 3**, in addition to the samples listed above. These elements have also been digitized by the PI and colleagues. Only individuals with all 8 carpals of interest will be included in the analysis.

*Measures 3.* Elements from these specimens will follow the same procedure listed in Aim 1. Locomotor style of the hand will be assigned in accordance with Hunt et al. (1996) and Orr (2017) (**Table 3**).

**Table 3.** Target extant sample sizes for **Aim 3**. All individuals have all 8 carpal bones of interest present. Aim 3 sample will also include individuals from **Tables 1** and **2**. Locomotor categories derived from Hunt et al. (1996) and Orr (2017).

<b>Species</b>	<b>Common Name</b>	<b>Locomotor use of hand</b>	<b><i>n</i> ♀</b>	<b><i>n</i> ♂</b>
<i>Pongo abelii</i>	Sumatran orangutan	Climbing/suspension, palmigrade-capable (partially to fully extended wrist)	5	5
<i>Pongo pygmaeus</i>	Bornean orangutan	Climbing/suspension, palmigrade-capable (partially to fully extended wrist)	5	5
<i>Hylobates lar</i>	gibbon	Climbing/suspension, palmigrade-capable (extended-wrist)	5	5
<i>Symphalangus syndactylus</i>	siamang	Climbing/suspension, palmigrade-capable (extended-wrist)	5	5

*Analysis 3.* In addition to the analyses employed in Aims 1 & 2, an ANOVA will also be used to assess how much of the variance in CR can be attributed to locomotion and thus if the “ball-and-socket” is an adaptation for suspensory behavior.

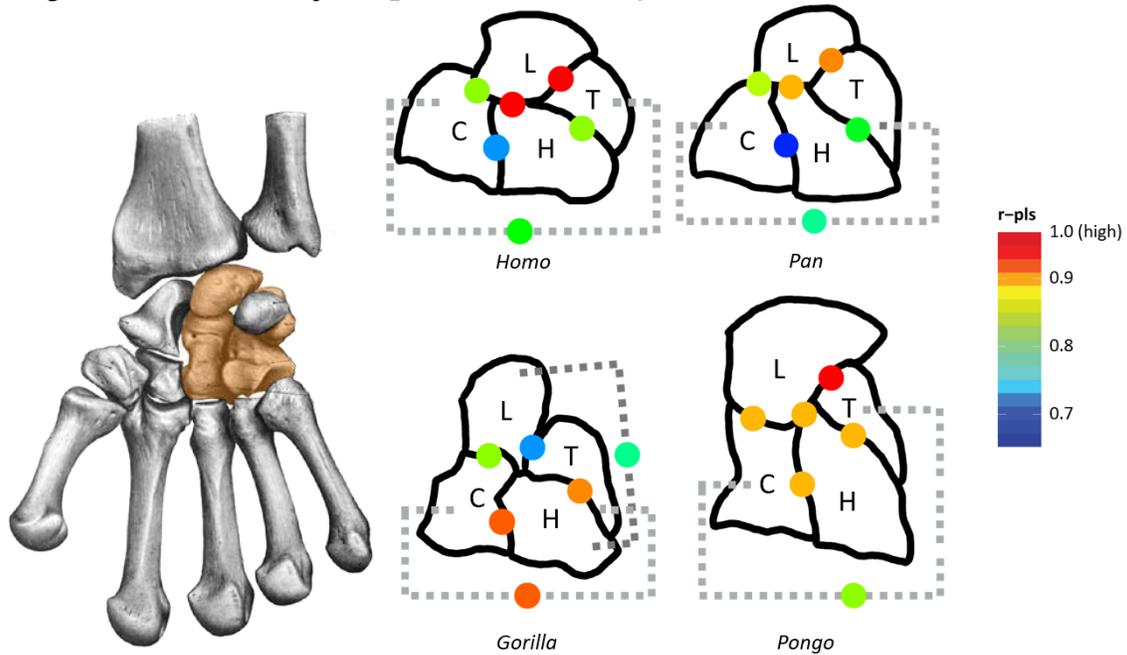
Chapter 5: Preliminary Results & Discussion

The co-PI has performed a series of preliminary analyses evaluating the pairwise shape covariation of the ulnar carpal bones (triquetrum, capitate, hamate, and lunate) in *Homo*, *Pan*, *Gorilla*, and *Pongo* ( $n = 10$  each). Fixed landmarks were digitized on the four carpals bones from each individual to capture their shape complexity. 2B-PLS was then used on the Procrustes-superimposed landmark coordinates of each pairwise combination of the bones to quantify the level of integration between structures. A permutation test was conducted on each analysis 1000 times to test for significance. Overall, 30 pairwise 2B-PLS analyses were executed to compare the strength and pattern of integration among all bone pairs; 6 including all taxa and 24 separate analyses for each genus (**Table 4**).

**Table 4.** Pilot data results from pairwise 2B-PLS analyses. Significant results are indicated in **bold** font.

Comparison	Genus	r-pls	p	Comparison	Genus	r-pls	p
Capitate ↔ Hamate	<b>All</b>	<b>.894</b>	<b>.001</b>	Hamate ↔ Triquetrum	<b>All</b>	<b>.816</b>	<b>.001</b>
	<i>Homo</i>	.71	.98		<i>Homo</i>	.841	.915
	<i>Pan</i>	.654	.956		<i>Pan</i>	.811	.564
	<i>Gorilla</i>	.938	.391		<b><i>Gorilla</i></b>	<b>.909</b>	<b>.025</b>
	<i>Pongo</i>	.886	.559		<i>Pongo</i>	.893	.35
Capitate ↔ Triquetrum	<b>All</b>	<b>.786</b>	<b>.001</b>	Hamate ↔ Lunate	<b>All</b>	<b>.853</b>	<b>.001</b>
	<i>Homo</i>	.817	.78		<i>Homo</i>	.949	.102
	<i>Pan</i>	.767	.512		<i>Pan</i>	.893	.25
	<i>Gorilla</i>	<b>.925</b>	<b>.026</b>		<i>Gorilla</i>	.797	.363
	<i>Pongo</i>	.846	.771		<i>Pongo</i>	.897	.643
Capitate ↔ Lunate	<b>All</b>	<b>.834</b>	<b>.002</b>	Triquetrum ↔ Lunate	<b>All</b>	<b>.852</b>	<b>.001</b>
	<i>Homo</i>	.849	.699		<b><i>Homo</i></b>	<b>.974</b>	<b>.049</b>
	<i>Pan</i>	.849	.324		<i>Pan</i>	.906	.373
	<i>Gorilla</i>	.833	.139		<i>Gorilla</i>	.715	.656
	<i>Pongo</i>	.887	.752		<b><i>Pongo</i></b>	<b>.966</b>	<b>.016</b>

**Figure 7.** 2B-PLS heat map for preliminary results on ulnar wrist elements including the capitate, lunate, triquetrum, and hamate (in orange). Colored dots represent strength of integration between two joining bones based on r-pls.



As expected, the results demonstrate strong integration between all bone pairs. The pattern of integration, however, differs between most taxa (**Figure 7**) suggesting that the pattern of integration between ulnar wrist bones is not conserved among all taxa. *Pongo* displays the most integration between the four wrist elements than any other taxon, suggesting that all four ulnar bones make up a tightly integrated module (**Figure 7**). This pattern seen only in *Pongo* may lend support to the ball and socket hypothesis, but of course, to relate this back to the other module hypotheses stated in the background, we will need to include the other carpal elements; the scaphoid, trapezium, trapezoid, and pisiform. This is also the case considering the integration configurations displayed in the other 3 taxa (**Figure 7**). While it is interesting that the four taxa studied each display different patterns of integration in the ulnar side of the wrist, we cannot infer total wrist modularity based solely on 2B-PLS analyses of the ulnar side of the wrist. Therefore, future studies will

perform CR on the entire wrist complex, as well as contain a greater representation of taxa, to evaluate carpal bone modularity across primates.

**Broader Impacts.** Though this project is focused on the primate carpus, it will lend insight into a whole-body perspective on integration and modularity. This project may also inform future studies concerning integration and modularity of the tarsus. Additionally, scans and data produced from this project will be made publicly available on an online digital repository. Digital models of structures allow data to be easily transferred from researcher to researcher and prevent inevitable damage of the actual bones and fossils during the data collection process. This database will make specimens more readily available to researchers contribute to future studies involving integration and modularity and 3DGM.

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