KNUCKLE-WALKING SIGNATURES IN HOMINOID SCAPULAE

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by

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CHAPTER I

INTRODUCTION

The scapula serves as an important point of muscle attachment for the back, neck and upper limbs, and is a link between the axial and appendicular skeleton. Variation in primate scapular form is often viewed as a reflection of different behavioral, locomotor, or musculoskeletal function in different species (e.g., Ashton and Oxford, 1964; Larson, 1995; Young, 2008). In many primates, scapular morphology is claimed to largely reflect the need for scapular rotation during suspensory locomotion (Larson, 1993). The increased need for shoulder mobility may impact many scapular characteristics, including glenohumeral joint morphology and points of muscle attachment and location (Larson, 1993). In dedicated terrestrial quadrupeds, movement of the scapula is largely restricted to the parasagittal plane, and function resides primarily in walking as in dogs (Young, 2006). Few studies have concentrated on how scapular morphology might be indicative of knuckle-walking in primates, because primates that utilize this form of locomotion often participate in a variety of other locomotor behaviors, and knuckle-walking may be a secondary locomotor pattern.

Previous observations and studies have reported that hominoid primates, including *P. troglodytes* and *G. gorilla* use different forms of knuckle-walking during terrestrial locomotion (Thorpe and Crompton, 2006; Matarazzo, 2008). These apes also perform orthograde suspensory locomotion when moving through the canopy (Thorpe and Crompton, 2006). Species of apes differentially utilize knuckle-walking and
suspensory locomotion during different life phases. Members of *G. gorilla* are highly dependent on knuckle-walking as adults, but brachiate frequently as subadults (Inouya, 1994). *P. troglodytes* individuals utilize brachiation and knuckle-walking interchangeably as adults; and *P. pygmaeus* and *Hylobates* are primarily brachiators throughout life and do not knuckle-walk (Inouya, 1994; Thorpe and Crompton, 2006).

Unfortunately, as whole, previous studies of knuckle-walking have not been as detailed as have some other studies of other forms of primate locomotion. For example, many studies that have examined suspensory locomotion in primates have included behavioral observations, muscle contracting patterns, and osteological features, and have often relied heavily on forearm anatomy (e.g. Jenkins et al., 1978; Stern and Larson, 2001; Larson, 1993). Studies of knuckle-walking have concentrated primarily on forearm posture and musculature, and skeletal morphology of the wrists, metacarpals, and phalanges (e.g. Jenkins and Fleagle, 1975; Richmond et al., 2001; Matarazzo, 2008). There have been few references of the impact of knuckle-walking on scapula form.

The main goal of this study was to document any impact knuckle-walking has on hominoid primate scapular form. I have attempted to record interspecies and intraspecies variation in scapular morphology in adult and subadult specimens of *G. gorilla*, *P. troglodytes*, and *H. sapiens*, and adult specimens of *Hylobates*. I chose these species because they use a variety of locomotor behaviors including knuckle-walking, brachiation, and bipedalism. *G. gorilla* serves as the dedicated knuckle-walker, *Hylobates* as a dedicated brachiator, and *P. troglodytes* as a species that uses both locomotor strategies throughout its life. *H. sapiens* performs none of these behaviors. I included
subadult and adult specimens to document any changes or consistency in scapular form that may occur during maturation. Also I hoped to document any areas of scapular morphology that may reflect a mixture of knuckle-walking and suspensory behaviors in the subadult state, since both subadult *G. gorilla* and subadult *P. troglodytes* utilize these behaviors on a regular basis. Also I intended to document any trend in scapular form that appeared associated with a certain type of locomotor pattern. For example, if the glenoid cavity has differing relationships to other scapular landmarks among species, this may suggest that its position is tied to a locomotor pattern.

![Figure 1](image1.png)  
(A) Adult *G. gorilla* scapula  
(B) Subadult *G. gorilla* scapula

![Figure 2](image2.png)  
(A) Adult *H. sapiens* scapula  
(B) Subadult *H. sapiens* scapula

![Figure 3](image3.png)  
(A) Adult *P. troglodytes* scapula  
(B) Subadult *P. troglodytes* scapula

![Figure 4](image4.png)  
Adult *Hylobates* scapula
For this study, direct scapular measurements were taken using digital calipers. Also I used photographs to measure angles between scapular landmarks. I used independent sample t-tests for interspecies and intraspecies mean-comparisons.

Scatterplots supplied a visual representation of the variables, and displayed both trends and areas of overlap in the species. I used principal component analysis to partition the variance of different species groupings, in order to clarify differences among species.

The results of the statistical analyses were expected to provide significantly different findings for the majority of the variables, because of the size differences between the species in the study. For example, *G. gorilla* specimens are substantially larger than those of *Hylobates*. Therefore, I attempted to correct for body size.

Ultimately, I intended to explore the effects knuckle-walking had on hominoid scapular form. Also, I hoped to document any trends observed in subadults and adults of the same species. The results of this study could also lay the groundwork for future examinations of knuckle-walking and its relationship to other hominoid anatomical feature.
CHAPTER 2.

LITERATURE REVIEW

This portion of the study has three subsections: 1) scapular morphology and scapular landmarks, 2) measurements used in this study, and 3) evaluate the previous work on knuckle-walking. I will discuss the impact of knuckle-walking on upper-limb morphology, although, I found little on its effect on scapular form.

2.1 Scapular Form and Shoulder Mobility

Several authors (e.g. Roberts, 1974; Larson, 1993, 1995; Larson and Stern, 1986) have discussed the role of forelimb function in dictating scapular shape. In quadrupedal primates, the scapula functions in retractile–propulsive motions that limit movement of the forearms above the head (Larson, 1993; Young, 2006). In suspensory primates, it is widely accepted that the scapula’s shape and location along the back allows for greater mobility and extended use of the forelimb above the head (Fleagle, 1988; Young, 2006). This seems likely to be the case in knuckle-walkers as well since these primates use suspension extensively.

A number of authors (e.g. Erikson, 1963; Fleagle, 1988; Swartz, 1989) have argued that the form and location of the glenohumeral joint evolved to increase shoulder mobility for suspensory locomotion. Fleagle (1988) notes that the hominoid glenohumeral joint consists of a small glenoid fossa and a large humeral head, and
according to Ashton and Oxnard (1964), orientation of the glenoid correlates with the degree of shoulder mobility. Primates with cranially oriented glenoid fossae have the highest degree of shoulder mobility (Ashton and Oxnard 1964), which is the case in hominoids and lorines (Chan, 2008). Additionally, Roberts (1974) states that in hominoids and suspensory New World Monkeys, the craniocaudal curvature of the glenoid fossa allows for concentric rotation of the humerus, which in turn enables an increase in arm movement over the head. According to Lewis (1985) and Cant (1986), location of the scapula contributes to the range of upper limb motion. Hominoid primates have a more dorsally positioned scapula, which Lewis and Cant claim increases shoulder mobility for brachiation.

In addition to range-of-motion in the shoulder, muscle function reportedly influences scapular form (Oxnard, 1967, 1969; Roberts, 1974). Oxnard’s (1967, 1969) studies explored scapular form in relation to normal stress. Oxnard (1967, 1969) found that the scapula of quadrupedal primates withstood compression forces along the vertebral border, whereas the hominoid scapula withstood torsional stress across the blade. Roberts (1974) replicated Oxnard’s work with an updated technique, and agreed that the scapular structure reflects muscle force. However, much of the research preceded our current understanding of the genomic influence on bone form (Lovejoy, et al., 2003).

As a result of Oxnard’s and Roberts’ early work, some suggested that differential growth occurs in the area of bone nearest the points of highest strain (Carter et al. 1998; Herring et al. 2002). Young (2006) suggests that scapular shape variation may be a product of strain on the bone. Young’s (2006) study concludes that quadrupedal primates
are significantly more canalized, or have reduced phenotypic variation, in scapular shape than non-quadrupeds (Gibson & Wagner, 2000). Accordingly, quadruped scapulae were more alike within a species, whereas suspensory scapulae possessed more intraspecies variation. Thus, variation in hominoids (and in suspensory monkeys) should be larger than in quadrupeds, which move through an environment with relatively consistent movements.

Unfortunately, Young (2006) did not address the impact of different forms of locomotion utilized by “suspenory” hominoids and other primates as a means of explaining increased variation in scapular morphology. Stern and Larson (2001) remarked that suspensory hominoids show different morphology than suspensory monkeys, especially in the structures and range of forearm rotation. Hominoid species also differentially use suspensory and knuckle-walking behaviors not only in daily life, but throughout their life stages (Inouya, 1994; Thorpe & Crompton, 2006; Matarazzo, 2008).

However, suspensory behaviors were not the only form on locomotion thought to impact hominoid shoulder form. Some researchers proposed vertical clinging as another effect on hominoid scapular morphology. In studies conducted by Stern et al. (1977, 1980a,b), and Jungers and Stern (1980), the electrical activity patterns of shoulder muscles for both vertical clinging and arm-swinging were found to be very similar. Also, Fleagle et al. (1981) found bone strain on the ulna to be similar during brachiation and vertical clinging. These findings support similarity for both muscle use and forelimb strain among brachiation and climbing behaviors, however the authors did not directly address whether
these locomotor behaviors acted exclusively on the free portion of the upper limb, or also had an impact on scapular form. Both suspensory and vertical clinging behaviors may impact scapular form.

Others researches have proposed that since hominoids and lorines share such similar scapular morphology (Chan, 2008; Cartmill & Milton, 1977; Lewis 1985), something other than suspensory behaviors must determine the form of the scapula. The slow climbing hypothesis is an attempt to unify scapular form between the two groups, and to explain why they differed from the rest of living primates (Chan, 2008). This hypothesis arose from Cartmill and Milton’s (1977) and Lewis’s (1985) observations that some features of the hominoid wrists are found in lorises and sloths, which are habitual climbers and not brachiators. These features, however, are not found in New World primates that are habitual brachiators (Chan, 2008). Cartmill and Milton (1977) further state that hominoid and lorines share many aspects of scapular form, leading them to the proposition that the hominoid shoulder is not adapted for brachiation, but is more mobile because it is suited for slow climbing as seen in lorines. Chan (2007) adds that hominoids could have used a type of locomotion called orthograde scrambling rather than slow climbing. Orthograde scrambling is very similar to slow climbing except the upper limbs are primarily used for suspension and not stabilization (Chan, 2007).

Some have argued that the hominoid shoulder has no more mobility than those of other primates, especially other brachiators. In a live animal study conducted by Chan (2008), the shoulders of 17 primate species with varying locomotor patterns were assessed for degree of mobility. All of the primates appeared to have similar
cranioventral and caudoventral movements, which Chan argues was expected due to restrictions induced by similar anatomy (Chan, 2008). The effect of caudodorsal mobility on the scapula was unknown, since that type of motion is not often observed except for perineal care (Chan, 2008). Circumduction in the craniodorsal direction may affect the ability to brachiate (Chan, 2008), based on the findings by Jenkins et al. (1978) and Jungers and Stern (1984) that during brachiation the trailing arm is directed in the craniodorsal direction. *Hylobates* is the only hominoid that showed significant craniodorsal mobility among the studied primates (Chan, 2008). The other hominoids show similar or less craniodorsal mobility than arboreal quadruped monkeys.

Chan (2008) also found that non-hylobatid hominoids and lorines had similar shoulder mobility caused by different morphology. He suggests that although non-hylobatid hominoid scapulae are dorsally positioned, low glenohumeral mobility and a long clavicle negated the advantage of the dorsal location of the scapula as reported by Lewis (1985), Cant (1986) and Chan (2008). Lorines, however, are limited by a small clavicle and a less dorsally located scapula, but a more mobile glenohumeral joint (Chan, 2008). These findings did not appear to support the slow climbing hypothesis for hominoid shoulder form due to the differences between non-hylobatid hominoids and lorines. Chan’s results did show support that scapulae possess features that are adaptations for brachiation, however, the results also show how limited shoulder mobility is in non-hylobatid hominoids. This claim differs greatly from previous claims of hominoid shoulder mobility.
As this pertains to knuckle-walking, Hunt (1991) states that quadrupedal locomotion is compromised and comparatively inefficient in hominoid primates especially in chimpanzees. If this is indeed true then species that have both knuckle-walking and suspensory behaviors in their locomotor repertoire might have a scapular form with increased efficiencies imposed knuckle-walking morphology (Pontzer & Wrangham, 2004). This would mean that knuckle-walking primates should have scapulae designed for the more energy efficient suspensory behaviors. If knuckle-walking proved less-efficient as Hunt suggests, scapula form for dedicated knuckler-walkers should still heavily reflect suspensory behaviors into adulthood. One purpose of the study was to include both subadult and adult specimens for *P. troglodytes* and *G. gorilla* in order to examine this statement. If Pontzer and Wrangham (2004) and Hunt (1991) are correct, then *G. gorilla* should have a scapula showing characteristics of the more “efficient” brachiation, even though the adult *G. gorilla* relies more on knuckle-walking than subadults.

2.2 Orientation and Position of the Scapular Spine

Several studies note the importance of the scapular spine because of its involvement in structure of the scapula. Ashton and Oxnard (1964) initially proposed that the spine’s orientation from its base to its crest could estimate the mechanical advantage of the cranial trapezius muscle in arm elevation in different primate locomotor patterns. Further studies by Larson et al. (1991) show that in large bodied hominoids, the cranial trapezius is involved in head-turning and not arm-raising. Larson and Stern (1986) suggest that scapular spine orientation could be related to suspensory behaviors since the
spine’s orientation would also influence the infraspinatus muscle. Importantly, the infraspinatus is the only muscle found to work at stabilizing the glenohumeral joint during suspensory locomotion and postures in chimpanzees (Larson & Stern, 1986).

Haile-Selassie et al. (2010) reported on scapular spine orientation, in their examination of an *Australopithecus afarensis* specimen. Based on scapular x-rays, Haile-Selassie et al. (2010) reported that the orientation of the scapular spine to the axillary scapular border is more acute in *P. troglodytes* and *G. gorilla* than in *H. sapiens*. This measurement reflects the functional muscle orientation of rotator cuff muscles, such as the infraspinatus and supraspinatus (Haile-Selassie et al., 2010).

There also appears to be a shift in the scapular spine away from the axial border in living hominoid primates (Senut, 1981; Larson, 1995). Senut (1981) noted the movement of the position of the spine, but did not give an explanation for the phenomenon or how it influences muscle attachment or movement. Larson (1995) stated that the shift of the base of the spine may be a modification to accommodate the infraspinatus during suspensory postures and locomotion, and may indicate an abductory component to the infraspinatus.

For this study, I took two measurements to record scapular spine orientation: the angle between the scapular spine and the glenoid cavity, and the angle of the scapular spine to the medial scapular border.

**2.3 Subscapular Fossa: Lateral Expansion**

The origin of the subscapularis muscle is the entire anterior expanse of the subscapular fossa (Jenkins, 2002; Larson, 1995). The subscapularis muscle, in humans, is involved in arm rotation (Jenkins, 2002), but in a number of other primates it has a
critical role in the “pull-up” phase of vertical climbing (Larson, 1995). The size of the subscapular fossa shows the relative importance of climbing in a primate species’ locomotor range (Larson and Stern, 1986; Larson, 1995). According to these studies, for suspensory hominids, the lateral expanse portion of the subscapular fossa should be larger in relative size than in their knuckle-walking counterparts. In this study, I divided the lateral expansion of the subscapular fossa into two measurements: width of the lateral expansion at the scapular neck and length of the lateral expansion at the scapular neck (metrics 10 and 11 in Figure 7).

2.4 Glenoid Fossa Size

Glenoid fossa size can be estimated by two measurements: the fossa’s breadth and length (Alemseged et al., 2006; Larson, 1995). These can be used as a means for approximating body size in specimens of unknown weight and stature, and was used for this purpose in the present study (Alemseged et al., 2006; Larson, 1995). I also noted the orientation of the glenoid cavity by examining the angle between the glenoid cavity and scapular spine, the angle between the glenoid cavity and the lateral border, and the angle between the glenoid cavity and medial border. The glenoid cavity served as a stationary point of scapular anatomy, which enabled me to make observations in other scapular changes in relation to the glenoid.

2.5 The Glenoid Fossa Angle Relative to Medial and Lateral Scapular Borders

Alemseged et al., (2006) reported that the angle of the glenoid fossa and spine relative to the medial (vertebral) scapular border describes the line of attachment of the
serratus and rhomboid muscles. However, according to Lovejoy (personal communication, March 4, 2013) the angle between the glenoid fossa and spine only denotes the angle between the two scapular landmarks, and has no bearing on the serratus and rhomboid muscles. The origin of the muscles cannot be determined by the scapula alone, and both muscle groups attach to the medial border (between superior and inferior angles of the scapula for the serratus muscles, and between the scapular spine and the inferior angle of the scapula for the rhomboids muscles), where the line of action for these muscles is anterior to the position of the scapular spine. The serratus muscle is responsible for protraction of the scapula and upward rotation of the glenoid cavity in humans (Jenkins, 2002). The rhomboid muscle is responsible for elevation and retraction of scapula, and downward rotation of glenoid cavity in humans (Jenkins, 2002). I included this measurement in the study to observe any changes during growth that may impact the angle between the glenoid cavity and medial scapular border.

Based on scapular x-rays, Haile-Selassie et al. (2010) reported on the angle of the glenoid fossa to a portion of the lateral (axillary) scapular border. Called the “bar-glenoid”, this measurement takes the angle between the glenoid cavity and a straight line drawn from the middle of the glenoid down the thick bone of the lateral border. They used this as a means to estimate the orientation of the glenoid plane. Their findings show that *H. sapiens* has the largest mean angle, and but there is overlap with *P. troglodytes* (smallest mean angle) and *G. gorilla* (intermediate mean angle). For this study, I used a similar measurement to examine the orientation of the glenoid cavity and the lateral scapular border, the results of which do not replicate Haile-Selassie et al. (2010) findings,
although they exhibit the same trend. I also included this measurement to observe any changes during growth that may impact the angle between the glenoid cavity and lateral scapular border.

2.6 Supraspinous Fossa Breadth and Infraspinous Fossa Breadth

The supraspinatus and infraspinatus muscles are a part of the rotator cuff, along with teres minor and subscapularis muscles. The supraspinatus and infraspinatus muscles are responsible for shoulder stabilization and forelimb movement (Roberts, 1974; Jenkins, 2002). In suspensory primates (like chimpanzees) the infraspinatus muscle also stabilizes the glenohumeral joint (Larson and Stern, 1986). The size of the supraspinous and infraspinous fossae can be estimated by two different methods: along the medial scapular border and perpendicular to the scapular spine (Alemseged et al., 2006). Each measurement reflects separate aspects of scapular shape and growth (Alemseged et al., 2006). In this study, I used both measurements for the supraspinous and infraspinous fossae to explore the growth of the scapulae from subadult to adult.

The breadths of the supraspinous fossa and infraspinous fossa along the medial border may be used to represent the relative expanse of these muscles in each primate species (Roberts, 1974; Alemseged et al., 2006). The development of these fossae, according to Roberts (1974), is pertinent in understanding the relationship between scapular form and function. Roberts found that both fossae, as a reflection of their muscle counterparts, vary considerably between primate groups and among locomotor repertoires (Roberts, 1974). There is a relative trend, where the area of infraspinous fossa tends to increase as the area of the supraspinous fossa increases, however the area of the
supraspinous fossa did not depend on the size of the infraspinous fossa (Roberts, 1974). The reason for this remained unclear, and the trait was observed among primates with different locomotor patterns.

Roberts (1974) examined these fossae in different primate taxa and grouped species by scapular shape and locomotion. He divided the hominoids into three groups: Group VIII: *Hylobates lar* and *Pongo pygmaeus*, Group IX: *Gorilla gorilla, Pan paniscus* and *Pan troglodytes*, Group X: *Homo sapiens* and *Australopithecus*

Group VIII contained the arboreal hominoids. According to Roberts (1974), the broad infraspinous fossa is a result of quadrumanous climbing, where the supraspinous fossa corresponds positively to the range of circumduction. Both fossae show evidence for the need to increase shoulder stability due to habitual suspension (Roberts, 1974). *Hylobates* have a narrower infraspinous fossa than that of *Pongo*, which probably is a consequence of body weight or a response to *Hylobates* specialized locomotion (Roberts, 1974).

Group IX contained the knuckle-walking hominoids. Roberts (1974) noted that a large amount of overlap is apparent between groups VIII and IX, as a result of these primates utilizing a variety of locomotor modes. The overall scapula is broad, with large fossa (Roberts, 1974). He observed that gorillas, as the most dedicated knuckle-walker, have the relatively largest supraspinous fossa (Roberts, 1974). Roberts (1974) suggested that the size of the fossa is a consequence of the gorillas’ unique forelimb posture, aiding them in moving their center of mass underneath the hind-limbs.
Group X contained the specialized bipedal hominoids. Roberts (1974) stated that the infraspinous fossa is broad, with a thick border. The supraspinous fossa is less developed, which he claimed was a reflection of the arm habitually held below shoulder level (Roberts, 1974).

Roberts’ division of primate taxa based on supraspinous and infraspinous fossae size and shape showed a proposed relationship between scapulae form and function. If Roberts’ findings hold true, *P. troglodytes* and *G. gorilla* should have similar shaped supraspinous fossae and infraspinous fossae, in the current study. For *H. sapiens*, however, the shape of the supraspinous fossa and infraspinous fossa should be different from the other hominids because of the lack of arm extension over the head.

Few researchers have conducted studies of the relationship of knuckle-walking locomotion to its possible impact on the glenohumeral joint stability or scapular morphology, even though however, its impact on other forelimb structures in the hand and wrist has been discussed.

Therefore this study includes direct measurement of the supraspinous fossa and infraspinous fossa, and the perpendicular measurements of each fossae to the scapular spine (metrics 5-8 in Figure 6).
CHAPTER 3.

MATERIALS AND METHOD

3.1 Material

For this study I collected data from a total of 165 scapulae. I measured both right and left scapulae when available for each specimen. The sample consisted of adult and subadult *Homo sapiens* (adult n=43, subadult n=28), *Gorilla gorilla* (adult n=20, subadult n=18), and *Pan troglodytes* (adult n=18, subadult n=20) scapula, and 18 adult *Hylobates* scapulae. Adult scapulae samples for all taxa, subadult *G. gorilla* and *P. troglodytes* were collected from the Hamman-Todd Osteological Collection and the Primate Collection at the Cleveland Museum of Natural History. Also a sample of adult *H. sapiens* specimens and all the subadult *H. sapiens* specimens were from the Libben Collection at Kent State University.

A number of non-human primate samples from the Primate Collection were obtained by museum expeditions in the 1920’s and 1930’s to South America and Africa (Cleveland Museum of Natural History, 2009). Since then, primate specimens had been donated from local zoos to increase the collection size and diversity (Cleveland Museum of Natural History, 2009).

The adult *H. sapiens* samples from the Hamman-Todd Collection consisted of both European and American born individuals classified as “Caucasian” or “Black” born between 1825 and 1910 (Grafton, 1996). Collected between 1910 and 1940 by Case
Western University in Cleveland, Ohio (Mensforth and Latimer, 1989; Grafton, 1996) the sample represents an urban population, prior to antimicrobial drugs, hormone replacements, or nutrition supplements. The adult and subadult *H. sapiens* samples from the Libben Collection consisted of a homogeneous population from a Late Woodland ossuary (Lovejoy et al., 1977). Radiocarbon dates indicate the Libben site was habituated between 800-1100 (Lovejoy et al., 1977). The population’s diet consisted of mostly of animal proteins, with sparse vegetable food-stuff, and possible corn agriculture during the occupation (Lovejoy et al., 1977). The two sets of adult *H. sapiens* specimens were used to explore population variation for these measurements, and to have a consistent example of adult and subadult *H. sapiens* from the same population. Specimens from the Libben collection were classified male or female based on pelvic examination, if sex was unable to be determined, the specimens were excluded from sex-based statistical analyses.

I measured each scapula once for thirteen different traits. The measurements guidelines were taken from Larson (1995) and Alemseged et. al (2006). I photographed each scapula in the same position to ensure consistency. I used digital calipers to obtain nine metric measurements and used digital photographs and the program Imagej for three of the angle measurements. Due to the nature of the angle of the glenoid fossa to the medial border, I used a protractor to determine the angle.

I used SPSS statistical package for all statistical analysis. The level of significance was set at $\alpha = .05$ for all statistical testing. Several different statistical tests were used in this analysis including independent sample t-tests and principal component analysis (PCA).
3.2 Traits Observed

The method for calculating a proxy for body size was determined using two measurements: glenoid fossa length (fl) and glenoid fossa breadth (fb). These values are used to calculate body size using the following formula:

Formula 1. Body size = √(fl x fb)

This formula came from Larson’s (1995) analysis of primate scapula as an indication of overall body size since body weights were unknown for the primate specimens used in this analysis.

I assessed the orientation of the glenoid fossa to different scapular landmarks several different ways using ImageJ software.

**Figures 5.** Angle of Glenoid Cavity to Scapular Spine, *H. sapiens*

**Figure 6.** Angle of Glenoid Cavity to Medial Border, *H. sapiens*
Figure 7. Angle of Glenoid to Lateral Border, 

*H. sapiens*

Figure 8. Angle of Medial Border to Scapular Spine, 

*H. sapiens*

1. The orientation of the glenoid fossa and the spine determined by measuring the angle between the two structures, the angle between a line drawn across the length of the glenoid fossa (AB) and a line drawn along the scapular spine (CD) (Figure 5).

2. The orientation of the glenoid fossa and the medial (vertebral) scapular border determined using an angle between the two structures, the angle between a line drawn across the length of the glenoid fossa (AB) and a line drawn from the superior angle to the inferior angle (EF) (Figure 6).
3. The orientation of the glenoid fossa and the lateral (axillary) border determined by taking the angle between a line drawn along the length of the cavity (AB) and a line drawn along the lateral border of the scapula (AG) (Figure 7).

4. The orientation of the scapular spine to the medial border determined by taking the angle between a line drawn along the scapular spine (CD) and a line drawn from the superior angle to the inferior angle (EF) (Figure 8).

I used digital calipers to take direct measurements (5 - 11) for the following structures shown on Figure 9 and Figure 10.

5. Supraspinous fossa breadth - superior angle to base of scapular spine

6. Infraspinous fossa breadth - base of scapular spine to inferior angle
7. Perpendicular supraspinous fossa breadth - perpendicular measurement from spine to medial scapular border
8. Perpendicular Infraspinous Fossa Breadth to Spine - perpendicular measurement from spine to lateral scapular border
9. Minimum width of the infraspinous fossa - the lateral-most point at the base of the scapular spine to the nearest point (point A) along the lateral scapular border
10. Width of the lateral expansion at the scapular neck - point A to the shortest point (point B) on the ventral bar
11. Length of the lateral expansion at the scapular neck - point B to the medial end of the lateral expansion of the subscapular fossa
12. The width of the glenoid cavity taken at the widest horizontal width (or center part) of the cavity
13. The length of the glenoid cavity taken at the longest vertical length of the cavity
CHAPTER 4

RESULTS

I examined the scapular data through several statistical tests to better understand the interspecies and intraspecies relationships. The subadult data only showed the expected change due to growth and maturation, therefore I exclude subadults in any further analysis. Scatterplots were important in the examination of relationships in interspecies scapular anatomies. I compared the means of adult male and females of a species. I used principal component analysis (PCA) to simply and clarify variation among the species. The subsections are as follows: Scatterplots, Independent Sample T-tests, and Principal Component Analysis.

Table 1. Species means, standard deviation (in parenthesis) for scapular angles in degrees

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Angle Spine to Medial Scapular Border</th>
<th>Angle Spine to Glenoid Fossa</th>
<th>Angle Glenoid Fossa to Lateral Scapular Border</th>
<th>Angle Glenoid Fossa to Medial Scapular Border</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. sapiens (HT)</td>
<td>92.95 (6.12)</td>
<td>85.42 (2.80)</td>
<td>124.20 (1.85)</td>
<td>17.33 (3.65)</td>
</tr>
<tr>
<td>H. sapiens (LIB)</td>
<td>71.50 (2.19)</td>
<td>82.22 (1.62)</td>
<td>123.53 (3.14)</td>
<td>17.59 (3.24)</td>
</tr>
<tr>
<td>P. troglodytes</td>
<td>53.56 (3.21)</td>
<td>72.29 (1.65)</td>
<td>115.64 (3.21)</td>
<td>39.52 (5.18)</td>
</tr>
<tr>
<td>G. gorilla</td>
<td>78.94 (6.60)</td>
<td>80.18 (2.06)</td>
<td>119.18 (4.22)</td>
<td>30.04 (4.86)</td>
</tr>
<tr>
<td>Hylobates</td>
<td>27.61 (2.46)</td>
<td>66.35 (1.44)</td>
<td>108.76 (3.84)</td>
<td>37.76 (4.40)</td>
</tr>
</tbody>
</table>

HT= Hamman-Todd Collection    LIB= Libben Collection

The initial step in analyzing the data was to report species means for all scapular measurements (with standard deviations) as shown in Table 1 through Table 3. For the
statistical tests I separated *H. sapiens* from the Hamman-Todd specimens (denoted as HT) and the Libben Collection specimens (denoted as LIB). The separation of the two populations was crucial because they existed centuries apart, they had varying access to nutrition, shelter, and physical demands for survival, and the two populations had differing genetic backgrounds.

**Table 2.** Species means, standard deviations (in parenthesis) for supraspinous fossa and infraspinous fossa breadths in millimeters

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Supraspinous Fossa Breadth</th>
<th>Infraspinous Fossa Breadth</th>
<th>Perpendicular Supraspinous Fossa Breadth</th>
<th>Perpendicular Infraspinous Fossa Breadth</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. sapiens</em> (HT)</td>
<td>50.45 (9.11)</td>
<td>111.23 (10.32)</td>
<td>43.26 (7.61)</td>
<td>110 (10.00)</td>
</tr>
<tr>
<td><em>H. sapiens</em> (LIB)</td>
<td>46.30 (7.09)</td>
<td>117.54 (11.54)</td>
<td>31.50 (5.74)</td>
<td>105.53 (10.97)</td>
</tr>
<tr>
<td><em>P. troglodytes</em></td>
<td>81.96 (7.97)</td>
<td>83.43 (7.63)</td>
<td>48.73 (4.23)</td>
<td>70.39 (9.57)</td>
</tr>
<tr>
<td><em>G. gorilla</em></td>
<td>112.60 (14.68)</td>
<td>112.34 (21.04)</td>
<td>77.43 (12.80)</td>
<td>106.31 (21.90)</td>
</tr>
<tr>
<td><em>Hylobates</em></td>
<td>46.84 (3.94)</td>
<td>22.79 (3.43)</td>
<td>15.46 (3.77)</td>
<td>24.67 (2.32)</td>
</tr>
</tbody>
</table>

HT= Hamman-Todd Collection  LIB= Libben Collection

**Table 3.** Species means, standard deviation (in parenthesis) for the lateral expansion of the subscapular fossa in millimeters

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Minimum Width of the Infraspinous Fossa</th>
<th>Width of the Lateral Expansion at the Neck of the Scapula</th>
<th>Length of the Lateral Expansion at the Neck of the Scapula</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. sapiens</em> (HT)</td>
<td>25.83 (2.11)</td>
<td>14.30 (2.29)</td>
<td>71.69 (10.17)</td>
</tr>
<tr>
<td><em>H. sapiens</em> (LIB)</td>
<td>23.08 (2.46)</td>
<td>14.45 (1.67)</td>
<td>78.19 (8.73)</td>
</tr>
<tr>
<td><em>P. troglodytes</em></td>
<td>18.86 (4.06)</td>
<td>15.87 (1.69)</td>
<td>88.29 (12.54)</td>
</tr>
<tr>
<td><em>G. gorilla</em></td>
<td>29.38 (4.93)</td>
<td>21.14 (5.11)</td>
<td>111.34 (16.96)</td>
</tr>
<tr>
<td><em>Hylobates</em></td>
<td>10.57 (1.06)</td>
<td>8.47 (1.25)</td>
<td>41.34 (2.99)</td>
</tr>
</tbody>
</table>

HT= Hamman-Todd Collection  LIB= Libben Collection
4.1 Scatterplots.

After gaining an overall view of the data by observing the means and standard deviations for each species, scatterplots allowed for a graphical interpretation of the data. I used scatterplots to visualize relationships between variables and species. Also I used the scatterplots to obtain the coefficient of determination (R² Linear) (Glantz and Slinker, 1990). This reports the percentage of the variation that is due to the independent variable the proxy for body size (See Formula 1).

Figure 11. Scatterplot: Angle, Scapular Spine to Medial Border with Proxy for Body Size

The first scatterplot was for the angle between the scapular spine and medial scapular border against body size (Fig. 11). The graph showed a difference between the two populations of *H. sapiens*, and there is a degree of overlap between *H. sapiens* and *G. gorilla*. The result of R² Linear for this scatterplot showed that body size caused variation in the angle between the scapular spine and medial scapular border: *Hylobates* 0.5%, *H. sapiens* (HT) 2.4%, *H. sapiens* (Lib) 13.1%, *P. troglodytes* 5.9%, and *G. gorilla* 13.1%.

Next, the analysis of the scatterplot (Fig. 12) for the angle between the glenoid cavity and the lateral scapular border against body-size proxy. Overall, the scatterplot showed that HT *H. sapiens*, LIB *H. sapiens* and *G. gorilla* showed a degree of overlap. Interestingly, in both populations of the adult *H. sapiens*, the larger individuals had slightly smaller angles between the lateral scapular border and the glenoid cavity. R² values for the second scatterplot showed that body size explained variation in the angle between the glenoid cavity the lateral border: *Hylobates* 32.7%, *H. sapiens* (HT) 54.2%, *H. sapiens* (Lib) 13.6%, *P. troglodytes* 8.4%, and *G. gorilla* 15.4%. For this measurement, body size had the biggest impact in *H. sapiens* (HT) and hyllobatids.
The third scatterplot (Fig. 13) depicted the relationship of the angle between the glenoid cavity and the medial scapular border on body-size proxy. The larger spread on the scatterplot for *G. gorilla* compared to *P. troglodytes* was likely the result of sexual dimorphism. Despite being the least sexually dimorphic species, the hylobatids also had a larger spread. The $R^2$ values for the third scatterplot showed that body size explained variation in the angle between the glenoid cavity and the medial border: *Hylobates* 1.1%, *H. sapiens* (HT) 39.5%, *H. sapiens* (Lib) 0% (as reported $4.856 \times 10^{-8}$), *P. troglodytes* 0.4%, and *G. gorilla* 2.5%.

**Figure 12.** Scatterplot: Angle, Glenoid Cavity to Lateral Border with Proxy for Body Size
The final scatterplot (Fig. 14) showed the angle between of the scapular spine to the glenoid cavity against the proxy for body size. Here, the angle between the glenoid cavity and the scapular spine showed overlap between *H. sapiens* and *G. gorilla*.

The $R^2$ values for the fourth scatterplot showed that body size explained variation in the angle between the scapular spine and the glenoid cavity: *Hylobates* 18.6%, *H. sapiens* (HT) 19.1%, *H. sapiens* (Lib) 11.9%, *P. troglodytes* 7.1%, and *G. gorilla* 15.2%.
Figure 14. Scatterplot: Angle, Scapular Spine to Glenoid Cavity with Proxy for Body Size

4.2 Comparison of Means

I performed independent sample t-tests to examine a variety of hominoid relationships to explore trends observed in the scatterplots. Table 5 reports the first t-tests between males and females for all species. The level of significance was denoted by asterisks, with $p \leq .05$ (*), $p \leq .01$ (**) and $p \leq .001$ (**). 

For all the independent sample t-tests, I used Levene’s Test to assess homogeneity of variance, and each species had some measurements that were significant for this test.
A result with a significance at 0.05 indicated that the variance of the two groups were unequal (Levene, 1960). When this occurred, I consulted the second set of results under “equal variance not assumed” in the SPSS output to accommodate for the unequal variance.

I used the independent sample t-tests to further explore the relationship between hominoid sexes. The majority of the findings were as expected, with the largest differences between male and female *G. gorilla*. There were a number of significant differences between male and female *P. troglodytes* for the supraspinous and infraspinous fossae breadths, as well as the angle between the glenoid cavity and the lateral scapular border. All species males and females showed a degree of significance in the size of the infraspinous fossa breadth. For the generally mono-morphic *Hylobates* there were significant differences between the sexes for the supraspinous and infraspinous fossae breadths, as well as the perpendicular fossae breadth measurements. *H. sapiens*, a moderately sexual dimorphic species, had a number of measurements that significantly differed between the sexes, differences reflected that the pattern seen in *G. gorilla* more than in the other hominoids. *P. troglodytes* was the only species to show significant difference for an angle measurement (angle between the glenoid cavity and lateral scapular border).

Based on the mean comparisons that were significant the degrees of sexual dimorphism in these hominoid species were assessed. The standardized difference (d) is an effective statistical tool used to measure the effect size between groups (Cohen, 1988). In this study, I used standardized difference as a way of comparing intraspecies sexual
dimorphism as reported in Table 6. The standardized difference was calculated using the formula:

Formula 2: \[ d = (\bar{x}_1 - \bar{x}_2)/s \]

Where \( \bar{x}_1 \) and \( \bar{x}_2 \) were the means for males (\( \bar{x}_1 \)) and females (\( \bar{x}_2 \)) respectively and \( s \) was the pooled within-sex standard deviations for the species. A negative indices denotes females reported larger measurements for that variable.

According to Cohen (1988): a small effect has an index < 0.2; a medium effect, which is visible to the observer, has an index < 0.5; a large effect has an index ≥ 0.8. For \( G. \) gorilla, the most sexually dimorphic species in the study, all but one measurement had a medium or large effect. For \( P. \) troglodytes, there was a mixture of sexual dimorphic characteristics in the scapula, with the majority of measurements being of a small or medium effect. Surprisingly, for the hylobatids there were a number of traits that had large standardized difference indices. The cause of this is unclear, but morphological differences may have been amplified because of hylobatids small scapulae. Last, \( H. \) sapiens, a moderately sexually dimorphic species, appeared to follow trends observed in \( G. \) gorilla. Both species scored large indices on a number of measurements, conversely, \( P. \) troglodytes showed sexual dimorphism for many of the same measurements.
Table 4. Adult means standard deviations (in parenthesis), and t-tests by sex

<table>
<thead>
<tr>
<th>Measurements</th>
<th>P. troglodytes</th>
<th>G. gorilla</th>
<th>H. sapiens</th>
<th>Hylobates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glenoid Height (mm)</td>
<td>33.27 (1.57)</td>
<td>32.36 (2.16)</td>
<td>53.88*** (4.46)</td>
<td>41.12*** (3.04)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>24.10 (1.48)</td>
<td>23.22 (2.10)</td>
<td>36.27*** (2.10)</td>
<td>28.46*** (1.16)</td>
</tr>
<tr>
<td>Proxy for Body Size</td>
<td>28.25 (1.41)</td>
<td>27.39 (1.90)</td>
<td>44.18*** (2.67)</td>
<td>34.19*** (1.77)</td>
</tr>
<tr>
<td>Glenoid Height (mm)</td>
<td>52.35 (3.46)</td>
<td>54.50 (2.95)</td>
<td>81.69 (5.64)</td>
<td>75.88 (6.50)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>24.10 (1.48)</td>
<td>23.22 (2.10)</td>
<td>36.27*** (2.10)</td>
<td>28.46*** (1.16)</td>
</tr>
<tr>
<td>Proxy for Body Size</td>
<td>28.25 (1.41)</td>
<td>27.39 (1.90)</td>
<td>44.18*** (2.67)</td>
<td>34.19*** (1.77)</td>
</tr>
<tr>
<td>Glenoid Height (mm)</td>
<td>72.31 (2.13)</td>
<td>72.25 (1.30)</td>
<td>80.83 (2.13)</td>
<td>79.52 (1.86)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>52.35 (3.46)</td>
<td>54.50 (2.95)</td>
<td>81.69 (5.64)</td>
<td>75.88 (6.50)</td>
</tr>
<tr>
<td>Glenoid Height (mm)</td>
<td>117.81* (1.34)</td>
<td>114.00** (3.27)</td>
<td>120.39 (2.32)</td>
<td>118.11 (5.31)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>117.81* (1.34)</td>
<td>114.00** (3.27)</td>
<td>120.39 (2.32)</td>
<td>118.11 (5.31)</td>
</tr>
<tr>
<td>Glenoid Height (mm)</td>
<td>38.80 (7.01)</td>
<td>40.09 (3.54)</td>
<td>29.94 (4.17)</td>
<td>30.13 (5.63)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>38.80 (7.01)</td>
<td>40.09 (3.54)</td>
<td>29.94 (4.17)</td>
<td>30.13 (5.63)</td>
</tr>
<tr>
<td>Glenoid Height (mm)</td>
<td>83.64 (7.54)</td>
<td>80.28 (8.47)</td>
<td>125.12*** (7.80)</td>
<td>100.08*** (6.78)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>87.54* (5.60)</td>
<td>79.29* (7.36)</td>
<td>129.52*** (13.58)</td>
<td>95.16*** (9.70)</td>
</tr>
<tr>
<td>Glenoid Height (mm)</td>
<td>51.11* (3.34)</td>
<td>46.34* (3.76)</td>
<td>88.14*** (8.90)</td>
<td>66.74*** (3.57)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>51.11* (3.34)</td>
<td>46.34* (3.76)</td>
<td>88.14*** (8.90)</td>
<td>66.74*** (3.57)</td>
</tr>
<tr>
<td>Glenoid Height (mm)</td>
<td>74.88* (8.49)</td>
<td>65.87* (8.78)</td>
<td>123.41*** (17.28)</td>
<td>89.20*** (7.99)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>18.55 (1.92)</td>
<td>19.17 (5.58)</td>
<td>33.17*** (2.48)</td>
<td>25.17*** (3.15)</td>
</tr>
<tr>
<td>Glenoid Height (mm)</td>
<td>15.68 (1.35)</td>
<td>16.06 (2.04)</td>
<td>24.92*** (3.82)</td>
<td>16.95*** (2.18)</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>15.68 (1.35)</td>
<td>16.06 (2.04)</td>
<td>24.92*** (3.82)</td>
<td>16.95*** (2.18)</td>
</tr>
<tr>
<td>Minimum Width of Infraspinous Fossa (mm)</td>
<td>90.17 (7.72)</td>
<td>86.40 (16.33)</td>
<td>123.24*** (14.80)</td>
<td>98.11*** (5.21)</td>
</tr>
</tbody>
</table>

* Significance (p ≤ .05) ** Significance (p ≤ .01) ***Significance (p ≤ .001)
Table 5. Hominoid standardized difference indices, adults

<table>
<thead>
<tr>
<th>Measurements</th>
<th><em>P. troglodytes</em></th>
<th><em>G. gorilla</em></th>
<th><em>H. sapiens</em></th>
<th><em>Hylobates</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Glenoid Height (mm)</td>
<td>0.15</td>
<td>3.34</td>
<td>1.34</td>
<td>0.49</td>
</tr>
<tr>
<td>Glenoid Width (mm)</td>
<td>0.18</td>
<td>4.59</td>
<td>2.32</td>
<td>0.76</td>
</tr>
<tr>
<td>Proxy for Body Size</td>
<td>0.16</td>
<td>4.40</td>
<td>1.97</td>
<td>0.75</td>
</tr>
<tr>
<td>Angle of Spine to Medial Border (degrees)</td>
<td>-0.38</td>
<td>0.96</td>
<td>-0.10</td>
<td>-0.56</td>
</tr>
<tr>
<td>Angle of Spine to Glenoid Cavity (degrees)</td>
<td>0.35</td>
<td>0.66</td>
<td>-0.59</td>
<td>1.97</td>
</tr>
<tr>
<td>Angle of Glenoid to Lateral Border (degrees)</td>
<td>0.01</td>
<td>0.54</td>
<td>-0.22</td>
<td>-0.80</td>
</tr>
<tr>
<td>Angle of Glenoid to Medial Border (degrees)</td>
<td>-0.24</td>
<td>-0.24</td>
<td>0.87</td>
<td>0.25</td>
</tr>
<tr>
<td>Supraspinous Fossa Breadth (mm)</td>
<td>0.19</td>
<td>3.43</td>
<td>0.99</td>
<td>1.73</td>
</tr>
<tr>
<td>Infraspinous Fossa Breadth (mm)</td>
<td>0.44</td>
<td>2.91</td>
<td>3.01</td>
<td>-1.025</td>
</tr>
<tr>
<td>Perpendicular Supraspinous Fossa Breadth to Spine(mm)</td>
<td>0.48</td>
<td>3.16</td>
<td>0.50</td>
<td>0.01</td>
</tr>
<tr>
<td>Perpendicular Infraspinous Fossa Breadth to Spine(mm)</td>
<td>0.60</td>
<td>2.54</td>
<td>1.97</td>
<td>-1.01</td>
</tr>
<tr>
<td>Minimum Width of Infraspinous Fossa (mm)</td>
<td>-0.16</td>
<td>2.84</td>
<td>0.44</td>
<td>0.13</td>
</tr>
<tr>
<td>Width of Lateral Expansion of Neck of Scapula (mm)</td>
<td>-0.10</td>
<td>2.52</td>
<td>1.32</td>
<td>0.86</td>
</tr>
<tr>
<td>Length of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.22</td>
<td>2.22</td>
<td>1.24</td>
<td>-0.07</td>
</tr>
</tbody>
</table>
4.3 Multivariate Analysis

Principal Component Analysis (PCA) was used to better understand the variation in the data set, by means of dimensional reduction (Anderson, 1984). Due to the age and condition of some of the scapulae, not all measurements were available for every specimen, most notably the Libben Collection adult *H. sapiens* specimens. However, so many of the specimens in the study were missing values that the PCAs could not be run with pairwise deletions or listwise deletions without severely reducing the sample size.

To make the data set as useful as possible for the PCAs, I calculated means by species and by sex, and then filled in the missing data.

The initial PCA (PCA-1) included all specimens. Subsequent PCAs (PCA-2 to PCA-4) contained different species groupings. These statistical tests used a correlation matrix for all of the PCAs because of the different variations and scales: millimeters and degrees. Running the correlation matrix standardized the variables, and the total variance equaled the number of variables in the analysis (Kachigan, 1991).

This portion of statistical examination used several tests to check for unique variables and to determine the validity of the PCA for this data set: Bartlett’s test of sphericity, the Kaiser-Meyer-Olkin Measure of Sampling Adequacy, and the Kasier’s Measure of Sampling Adequacy.

Bartlett’s test of sphericity tests the null hypothesis that the matrix is an identity matrix (Silva and Stam; 1998). For PCA-1, Bartlett’s test of sphericity was at .000 significance, this test rejected the null for this sample. Bartlett’s test of sphericity has
been reported as being highly sensitive, and widely used in conjunction with other statistical tests, which was done for this study (Silva and Stam; 1998).

The Kaiser-Meyer-Olkin measure of sampling adequacy (KMO) tests whether there appears to be some underlying (latent) structure in the data, or the Factorability of R (Kachigan, 1991). The KMO should be ≥ .6, a result lower than this should be considered unreliable. The KMO for the initial PCA was .868, exceeding the required value for factor analysis.

The PCA relied on the Kaiser’s Measure of Sampling Adequacy (MSA) on the Anti-image Matrices to determine the existence of partial correlations in the data set (Kachigan, 1991). Low values for the MSA (≤.5) indicate high partial correlation between two variables, which means that these variables share variance with one another, and not with the remaining variables (Kachigan, 1991). Low values of MSA are problematic because they indicate that the variance between two variables is unique, and therefore not useful in the PCA (Kachigan, 1991). Higher values of MSA signify low partial correlation between variables, which was needed for the PCA (Kachigan, 1991). In this data set the MSA ≥ .770 for all variables, permitting all variables to be included in PCA-1 with low partial correlation. With all three initial tests passed for the data set, further examination of PCA-1 could continue with increased reliability. Each subsequent PCA relied on these three tests and were only reported when a condition failed to meet the requirements of the PCA.

Extracting of the principle components was the next step in PCA-1. The rule for the selection of the principal components was: retain a component if eigenvalues ≥ 1
(Silva and Stam, 1998). A component with the eigenvalue < 1 captured less than one variable’s worth of variance (Kachigan, 1991; Silva and Stam, 1998). The PCA-1 suggested that a 2-factor solution best explained the data set. PC 3 and PC 4 were included to further explore any information in the data set. The variance explained by the solution was 88.24%, and the first two factors individually accounted for 70.34% and 20.99% of the variance, respectively. PC3 and PC4 contributed 2.20% and 1.80% of the variation. The scree test also supported a two-factor solution. The purpose of the scree test was to plot the incremental variance accounted for by each factor (Kachingan, 1991). The actual plot, called the scree curve, gave a visual confirmation of proper dimensional reduction (Kachigan, 1991).

After determining the number of principle components, the next step was to do an analysis of the component matrix. The entries in the matrix, the component loadings, showed correlations between the components and the variables.

It can be said that PC1 reflected overall body size differences between the species, and was named Body Size. It is common when dealing with data from specimens of greatly varying body size, the largest portion of the variance will be allotted to body size. PC2 represented a much more specific understanding of the variation, PC2 was named Glenoid Cavity and Scapular Spine Orientation to Medial Border. PC2 appeared to indicate that the second most cause of variation amongst all the species was orientation of the glenoid cavity and scapular spine to the overall scapula “length” (or the longest point on the scapula from top to bottom). The high loading of the Supraspinous Fossa Breadth and the Perpendicular Supraspinous Fossa Breadth to Spine on PC2 also contributed to
the orientation of the glenoid in relation to the scapular “length” because these two measurements expressed the most superior portion of the scapula, which the overall area varied greatly between species. PC3 had a moderately high negative loading on the glenoid angle to lateral border, which indicated an inverse impact on that component. PC4 failed to add any further insight into the variation.

A PCA scores plot of PC1 and PC2 proved beneficial for a visual examination of species and sex on the components. Fig. 15 illustrated the relationship between hominoid scapulae. PC1, as a reflection of body size, reported the spread of the hominoid species, with males and females of each species clustered together. The more sexually dimorphic species were more variable across PC1, with \textit{G. gorilla} being the most dispersed hominoid.

\textbf{Table 6.} Component Matrix PCA-1, all species

<table>
<thead>
<tr>
<th>Measurements</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
<th>PC 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glenoid Height</td>
<td>0.972</td>
<td>0.185</td>
<td>-0.003</td>
<td>-0.032</td>
</tr>
<tr>
<td>Glenoid Width</td>
<td>0.981</td>
<td>0.109</td>
<td>0.021</td>
<td>-0.075</td>
</tr>
<tr>
<td>Proxy for Body Size</td>
<td>0.983</td>
<td>0.147</td>
<td>0.009</td>
<td>-0.052</td>
</tr>
<tr>
<td>Angle of Spine to Medial Border</td>
<td>0.856</td>
<td>-0.403</td>
<td>0.187</td>
<td>0.161</td>
</tr>
<tr>
<td>Angle of Spine to Glenoid Cavity</td>
<td>0.727</td>
<td>-0.572</td>
<td>0.288</td>
<td>0.022</td>
</tr>
<tr>
<td>Supraspinous Fossa Breadth</td>
<td>0.551</td>
<td>0.840</td>
<td>0.020</td>
<td>0.184</td>
</tr>
<tr>
<td>Infraspinous Fossa Breadth</td>
<td>0.936</td>
<td>-0.228</td>
<td>-0.071</td>
<td>-0.162</td>
</tr>
<tr>
<td>Perpendicular Supraspinous Fossa Breadth to Spine</td>
<td>0.808</td>
<td>0.503</td>
<td>0.046</td>
<td>0.274</td>
</tr>
<tr>
<td>Perpendicular Infraspinous Fossa Breadth to Spine</td>
<td>0.934</td>
<td>-0.261</td>
<td>0.012</td>
<td>-0.068</td>
</tr>
<tr>
<td>Minimum Width of Infraspinous Fossa (mm)</td>
<td>0.950</td>
<td>-0.035</td>
<td>0.044</td>
<td>-0.033</td>
</tr>
<tr>
<td>Width of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.838</td>
<td>0.426</td>
<td>-0.090</td>
<td>-0.113</td>
</tr>
<tr>
<td>Length of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.852</td>
<td>0.426</td>
<td>-0.090</td>
<td>-0.150</td>
</tr>
<tr>
<td>Angle of Glenoid to Lateral Border</td>
<td>0.693</td>
<td>-0.545</td>
<td>-0.407</td>
<td>0.198</td>
</tr>
<tr>
<td>Angle of Glenoid to Medial Border</td>
<td>-0.441</td>
<td>0.840</td>
<td>0.037</td>
<td>-0.026</td>
</tr>
</tbody>
</table>
A PCA scores plot of PC1 and PC2 proved beneficial for a visual examination of species and sex on the components Fig. 15 illustrated the relationship between hominoid scapulae. PC1, as a reflection of body size, reported the spread of the hominoid species, with males and females of each species clustered together. The more sexually dimorphic species were more variable across PC1, with G. gorilla being the most dispersed hominoid.

**Figure 15.** PC1 with PC2, all hominoid species
The component PC2 could be viewed as a means of interpreting the position of the glenoid and spine in relation to scapular shape. PC2 discriminated \textit{H. sapiens} from the other hominoids, most notably from \textit{P. troglodytes} and \textit{Hylobates}. \textit{H. sapiens} scored lower on PC2 compared to \textit{P. troglodytes} and \textit{Hylobates}. Looking at the PCA plot, \textit{H. sapiens} fall in a cluster exclusive of any other hominoids. Referring back to the independent sample t-tests between sexes, the orientation of the scapular spine to the medial border, the scapular spine to the glenoid cavity and the glenoid cavity to the medial border were not significantly different for any of the hominoids, despite body size, perhaps angle measurements are the result of function rather than a dependent upon size. These findings are further evaluated in Chapter 5.

\textbf{Table 7.} Component Matrix PCA-2, \textit{H. sapiens} and \textit{G. gorilla}

<table>
<thead>
<tr>
<th>Measurements</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glenoid Height</td>
<td>0.968</td>
<td>0.018</td>
</tr>
<tr>
<td>Glenoid Width</td>
<td>0.956</td>
<td>0.176</td>
</tr>
<tr>
<td>Proxy for Body Size</td>
<td>0.983</td>
<td>0.091</td>
</tr>
<tr>
<td>Angle of Spine to Medial Border</td>
<td>-0.028</td>
<td>0.588</td>
</tr>
<tr>
<td>Angle of Spine to Glenoid Cavity</td>
<td>-0.513</td>
<td>0.560</td>
</tr>
<tr>
<td>Supraspinous Fossa Breadth</td>
<td>0.925</td>
<td>-0.215</td>
</tr>
<tr>
<td>Infraspinous Fossa Breadth</td>
<td>0.468</td>
<td>0.637</td>
</tr>
<tr>
<td>Perpendicular Supraspinous Fossa Breadth to Spine</td>
<td>0.912</td>
<td>-0.042</td>
</tr>
<tr>
<td>Perpendicular Infraspinous Fossa Breadth to Spine</td>
<td>0.464</td>
<td>0.787</td>
</tr>
<tr>
<td>Minimum Width of Infraspinous Fossa (mm)</td>
<td>0.798</td>
<td>0.268</td>
</tr>
<tr>
<td>Width of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.894</td>
<td>-0.009</td>
</tr>
<tr>
<td>Length of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.894</td>
<td>-0.122</td>
</tr>
<tr>
<td>Angle of Glenoid to Lateral Border</td>
<td>-0.458</td>
<td>0.456</td>
</tr>
<tr>
<td>Angle of Glenoid to Medial Border</td>
<td>0.816</td>
<td>-0.344</td>
</tr>
</tbody>
</table>

After completing the first PCA with all species included, I ran subsequent PCAs between different species to better understand the variation between them on a more
species-specific level. The same format was used for each PCA, and each PCA followed the same statistical guidelines to ensure reliability.

The second PCA included all *H. sapiens* and *G. gorilla* specimens. PCA-2 suggested a 2-factor solution best explained the data set. The variance explained by the solution was 82.66%, and the two factors individually accounted for 65.82% and 16.83% of the variance, respectively.

Again, PC1 was essentially a reflection overall body size differences, so I named PC2 Glenoid Cavity Orientation to Scapular Expanse. The variation between *H. sapiens* and *G. gorilla* appeared most notably in the location of the glenoid cavity to the overall expanse of the scapula, meaning that *G. gorilla* scapulae expand out more in relation to the glenoid cavity than observed in *H. sapiens*. This was not completely unexpected, since *G. gorilla* scapulae are significantly larger than that of *H. sapiens*, especially the male *G. gorilla* specimens. A high negative loading on the angle of the glenoid cavity to the medial border most likely is a consequence of growth differential between the species. A larger body requires a large shoulder girdle, thus the *G. gorilla* scapula must have a large area for muscle attachment, increasing the angle between the glenoid and medial border (See Figures 1 and 2). *H. sapiens* has a more compact scapulae, decreasing the angle between the glenoid and medial border. The high loading in the angle between the glenoid and the lateral border is most likely another consequence of size, especially in the subscapular area.

The next PCA consisted of all *H. sapiens* and *P. troglodytes* specimens. PCA-3 suggested a 2-factor solution best explained the data set. The variance explained by the
solution was 88.79%, and the two factors individually accounted for 62.92% and 25.87% of the variance, respectively.

Again, PC1 was essentially a reflection overall body size differences between *H. sapiens* and *P. troglodytes*, and named Body Size. I named PC2 Scapular Spine and Subscapular Fossa Orientation because the variation between *H. sapiens* and *P. troglodytes* appeared most notably in the orientation of the scapular spine, in conjuncture with shape and size of the subscapular fossa and supraspinous fossa. There were high negative loadings on PC2 of the angle of the spine to the glenoid cavity and the spine to the medial border. *P. troglodytes* have elongated supraspinous fossa, extending the scapula out more horizontally than in *H. sapiens*. This shifts all the scapular landmarks, which in turn influences scapular angles (See Figures 2 and 3).

Table 8. Component Matrix PCA-3, *H. sapiens* and *P. troglodytes*

<table>
<thead>
<tr>
<th>Measurements</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glenoid Height</td>
<td>0.972</td>
<td>0.082</td>
</tr>
<tr>
<td>Glenoid Width</td>
<td>0.957</td>
<td>0.055</td>
</tr>
<tr>
<td>Proxy for Body Size</td>
<td>0.974</td>
<td>0.066</td>
</tr>
<tr>
<td>Angle of Spine to Medial Border</td>
<td>0.689</td>
<td>-0.628</td>
</tr>
<tr>
<td>Angle of Spine to Glenoid Cavity</td>
<td>0.438</td>
<td>-0.817</td>
</tr>
<tr>
<td>Supraspinous Fossa Breadth</td>
<td>0.365</td>
<td>0.877</td>
</tr>
<tr>
<td>Infraspinous Fossa Breadth</td>
<td>0.935</td>
<td>-0.172</td>
</tr>
<tr>
<td>Perpendicular Supraspinous Fossa Breadth to Spine</td>
<td>0.751</td>
<td>0.514</td>
</tr>
<tr>
<td>Perpendicular Infraspinous Fossa Breadth to Spine</td>
<td>0.927</td>
<td>-0.214</td>
</tr>
<tr>
<td>Minimum Width of Infraspinous Fossa (mm)</td>
<td>0.941</td>
<td>-0.142</td>
</tr>
<tr>
<td>Width of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.846</td>
<td>0.445</td>
</tr>
<tr>
<td>Length of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.772</td>
<td>0.510</td>
</tr>
<tr>
<td>Angle of Glenoid to Lateral Border</td>
<td>0.822</td>
<td>-0.268</td>
</tr>
<tr>
<td>Angle of Glenoid to Medial Border</td>
<td>-0.181</td>
<td>0.942</td>
</tr>
</tbody>
</table>
Again, PC1 was essentially a reflection overall body size differences between *H. sapiens* and *P. troglodytes*, and named Body Size. I named PC2 Scapular Spine and Subscapular Fossa Orientation because the variation between *H. sapiens* and *P. troglodytes* appeared most notably in the orientation of the scapular spine, in conjuncture with shape and size of the subscapular fossa and supraspinous fossa. There were high negative loadings on PC2 of the angle of the spine to the glenoid cavity and the spine to the medial border. *P. troglodytes* have elongated supraspinous fossa, extending the scapula out more horizontally than in *H. sapiens*. This shifts all the scapular landmarks, which in turn influences scapular angles (See Figs. 2 and 3).

**Table 9.** Component Matrix PCA-4, *H. sapiens* and *Hylobates*

<table>
<thead>
<tr>
<th>Measurements</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glenoid Height</td>
<td>0.979</td>
<td>-0.028</td>
</tr>
<tr>
<td>Glenoid Width</td>
<td>0.965</td>
<td>0.016</td>
</tr>
<tr>
<td>Proxy for Body Size</td>
<td>0.978</td>
<td>-0.006</td>
</tr>
<tr>
<td>Angle of Spine to Medial Border</td>
<td>0.849</td>
<td>-0.409</td>
</tr>
<tr>
<td>Angle of Spine to Glenoid Cavity</td>
<td>0.707</td>
<td>-0.614</td>
</tr>
<tr>
<td>Supraspinous Fossa Breadth</td>
<td>0.434</td>
<td>0.805</td>
</tr>
<tr>
<td>Infraspinous Fossa Breadth</td>
<td>0.957</td>
<td>-0.110</td>
</tr>
<tr>
<td>Perpendicular Supraspinous Fossa Breadth to Spine</td>
<td>0.884</td>
<td>0.237</td>
</tr>
<tr>
<td>Perpendicular Infraspinous Fossa Breadth to Spine</td>
<td>0.969</td>
<td>-0.028</td>
</tr>
<tr>
<td>Minimum Width of Infraspinous Fossa (mm)</td>
<td>0.968</td>
<td>0.044</td>
</tr>
<tr>
<td>Width of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.874</td>
<td>0.355</td>
</tr>
<tr>
<td>Length of Lateral Expansion of Neck of Scapula (mm)</td>
<td>0.862</td>
<td>0.289</td>
</tr>
<tr>
<td>Angle of Glenoid to Lateral Border</td>
<td>0.831</td>
<td>0.211</td>
</tr>
<tr>
<td>Angle of Glenoid to Medial Border</td>
<td>-0.488</td>
<td>0.829</td>
</tr>
</tbody>
</table>

Next, PCA-4 included all *H. sapiens* and *Hylobates* specimens. PCA-4 suggested that a 2-factor solution best explained the data set. The variance explained by the solution
was 89.07%, and the two factors individually accounted for 73.32% and 15.75% of the variance, respectively.

Again, the PC1 was essentially a reflection overall body size differences between *H. sapiens* and *Hylobates*, and named Body Size as in the other PCAs. I named the PC2 Glenoid Orientation to Medial Scapular Border. PC2 it was very similar to that of the initial PCA. The second largest difference between *H. sapiens* and *Hylobates* was the orientation of the glenoid cavity to the overall scapula length, or the longest distance on the scapula between in the superior and inferior angles. As in PCA-3, the high loading of the supraspinous fossa breadth on PC2 also indicated the orientation of the glenoid on the scapula. Hylobatid scapulae are also elongated like that of *P. troglodytes*, shifting scapular angles and landmarks in a more horizontal direction (See Figs. 2 and 4).

Multivariate analysis have provide a clearer view of the differences among hominoid species. Data reductions have allowed for a better understanding of the underlying inter- and intraspecies similarities and difference. The statistical tests of this study helped evaluate a complex and multifaceted area of study. Hominoid scapular morphology offers a diverse field of exploration, where the interplay of function and form can have consequence on species ability to thrive in an environment.
CHAPTER 5

DISCUSSION

Scapular morphology, as observed in these hominoids, showed a considerable amount of variation, as expected. However, I found no notable scapular morphology indicative of knuckle-walking in any of the hominoids included in this study. A few scapular dissimilarities between *P. troglodytes* and *G. gorilla* suggests that knuckle-walking, although an important locomotor behavior, does not have any significant impact on scapular form, at least addressed in the scope of this study. The biggest impact on scapular morphology appears to be the role of suspensory behaviors in the hominoid locomotor repertoire.

Body size was an important factor when evaluating scapular morphology variation amongst the hominoids. Because of the degree of variation in overall body size of these hominoids, which contributed the majority of differences observed, the angle measurements between scapular landmarks provided a clearer view of scapular structures and their orientation. Based on the findings of the statistical tests, *G. gorilla* and *H. sapiens* had several similar morphological features, the most important being the orientation of the scapular spine and the glenoid cavity in relation to the medial border. In Scatterplot 1 and Scatterplot 4, both species show a degree of overlap. Table 4 reports the average angle of the scapular spine to the medial border for *G. gorilla* for the sexes $\checkmark = 81.69$, $\checkmark = 75.88$ and for *H. sapiens* for the sexes $\checkmark = 82.59$, $\checkmark = 83.74$. The $R^2$ value
showed that body size explains variation in this angle at \textit{H. sapiens} (HT) 2.4\%, \textit{H. sapiens} (Lib) 13.1\%, and \textit{G. gorilla} 13.1\%. The angle of the glenoid cavity to the scapular spine also showed a high degree of similarity, \textit{G. gorilla} for the sexes $\delta = 80.83$, $\varphi = 79.52$ and \textit{H. sapiens} for the sexes $\delta = 82.77$, $\varphi = 84.35$. The $R^2$ values show that body size explains variation in this angle at \textit{H. sapiens} (HT) 19.1\%, \textit{H. sapiens} (Lib) 11.9\%, and \textit{G. gorilla} 15.2\%. Also, the angle between the glenoid cavity and the medial border had lower averages for \textit{G. gorilla} and \textit{H. sapiens} than in the other two hominoid species. The $R^2$ values showed that body size caused variation in this angle at \textit{H. sapiens} (HT) 39.5\%, \textit{H. sapiens} (Lib) 0\% (as reported $4.856 \times 10^{-8}$), and \textit{G. gorilla} 2.5\%. \textit{H. sapiens}, however, has a more acute angle than \textit{G. gorilla}, a possible reason for this may be related to just overall body-size discrepancy between the two species.

The PCA for \textit{H. sapiens} and \textit{G. gorilla} showed the largest difference between the two species and this was largely due to body size. The PCA plot for all hominoid species (Fig. 15), placed \textit{G. gorilla} and \textit{H. sapiens} on the same sector of PC1, and opposite sectors for PC2. These placements reflected the differences in shape of the superior anterior portion of the scapula. These difference are likely driven by the need for a larger support structure in \textit{G. gorilla}. Also, \textit{H. sapiens} no longer utilizes suspensory behaviors. The lack of this behavior in the hominin lineage could also be a factor in the differences in the species. Sexual dimorphism may be a contributing factor to the difference in these angle measurements. For the standardized difference indices (Table 5), \textit{G. gorilla} has a large angle of the spine relative to the medial border, \textit{H. sapiens} has a large angle of the glenoid cavity to the medial border.
A similar case could be argued for *Hylobates* and *P. troglodytes*, these species showed marked similarities in the angle of the glenoid cavity to the medial border. Scatterplot 3 displayed a range for these two species that would overlap if not for the difference in body size. Body size explains hardly any variation in this angle at *Hylobates* ($R^2 = 1.1\%$) and *P. troglodytes* ($R^2 = 0.4\%$). The direct angle measurements between the sexes show little inter- and intraspecie variation (Table 4). Also the angle between the spine to medial border, and the angle between the spine and glenoid cavity were more acute in *Hylobates* and *P. troglodytes* than in the other two species. The angle measurements were not the same, however size discrepancy may also play a role here. The PCA score plot showed that the hylobatids and chimpanzees were in the same quadrant, meaning they were very alike in scapular shape. Subsequent PCAs showed these two groups have very different scapular shape than *H. sapiens*; moreover, *Hylobates* and *P. troglodytes* differed from *H. sapiens* in very similar ways.

The two distinct groupings of the hominoids, based on the orientation and shape of the scapular spine and glenoid cavity to the medial border suggest that they have different morphological adaptations for suspensory behaviors. The glenoid cavity and scapular spine play vital roles in upper-arm function, and variation in this morphology may indicate that these two hominoid groups depend on varying anatomical features to perform suspensory locomotion. This could also mean that these hominoids use suspension for varying behaviors, which would influence the anatomical framework needed to perform the behavior. Further analysis of muscles and other soft-tissues, in addition to analysis of muscle-firings during specific behaviors would be needed to
elaborate this idea. The cause of this scapular variation is unable to be determined in the scope of this study, but reliance on suspension in these hominoids ancestry likely played a key role in dictating the scapular morphology seen in extant hominoids.

Lastly, I would like to address some points found during the process of this study that did not fit with ideas in the literature review.

First, the view by Hunt (1991) and Pontzer and Wrangham (2004) that primates with both knuckle-walking and suspensory behaviors in their locomotor repertoire should have scapulae designed for the more “energy efficient” suspensory behaviors was not supported by my findings. *G. gorilla* and *P. troglodytes*, which both utilize knuckle-walking and suspensory locomotion during their life, showed marked differences in scapular form. These differences were not only in the size of the scapula, but also in scapular landmarks shown to be related to function. For the angle between the glenoid cavity and medial border, and the angle of the scapular spine to the glenoid cavity, these species were significantly different from each other. If knuckle-walking had proved “less-efficient” or a constraint of scapular morphology, the scapular form of *G. gorilla* should have been more like *P. troglodytes* and *Hylobates*, the dedicated brachiators, and it was not.

Also, findings from this study did not support Roberts (1974) classification of the hominoid scapulae. Robert divided the hominoids based on the shape of the supraspinous fossa and infraspinous fossa, which he believed vary considerable between locomotor repertoires. Roberts placed the knuckle-walkers *G. gorilla* and *P. troglodytes* together because of their broad scapula, with large fossa. This study showed that, in this case, *G.*
*gorilla* and *P. troglodytes* significantly differed in both sets of measurements for supraspinous fossa and infraspinous fossa magnitudes; therefore, grouping them based on the shapes of these fossa seemed inadequate. Also, Roberts concluded that the bipedal hominoids would have a less developed supraspinous fossa due to the arm habitually held below shoulder level (Roberts, 1974). The results of this study showed that although *H. sapiens* had a smaller average supraspinous fossa than *G. gorilla* or *P. troglodytes*, *H. sapiens* had a larger average infraspinous fossa than *P. troglodytes*. 
CHAPTER 6

CONCLUSION

This study appears to demonstrate that knuckle-walking did not have any noticeable impact on the form of the scapula. Suspensory behaviors appear to be the driving force behind scapular morphology. I did find some evidence that the hominoid’s way of suspension may be correlated to scapular shape. How suspensory behaviors dictate the varying morphology (for example suspensory locomotion vs. arm-hanging behaviors) remain undetermined and need further examination. One could easily place the four hominoids into two distinct groups based on scapular shape: *G. gorilla* and *H. sapiens* in one and *P. troglodytes* and *Hylobates* in the other.

Further analysis of the primate scapula could include more species of dedicated brachiators, primates that exhibit any suspensory behaviors, primates that use arm positions above the head, would give a much more detailed understanding the impact of suspensory behaviors on scapular morphology across the primate genera. Gathering behavioral data in conjuncture with anatomical data would help determine the relationship between varying suspensory activities and scapular shape. Including scapulae from extant hominid species might help address the role of suspension in the hominid line.

This study opens up a range of questions, including these two: What suspensory behaviors are more important in dictating scapular form? Are there any other behaviors,
such as vertical climbing or other movements that cause the arm to move above the head that could be the cause of these scapular differences? Future studies of primate scapulae, in relation to form and function, can only be beneficial to the ever-expanding knowledge of the far-reaching story that is hominoid evolution.
BIBLIOGRAPHY


