

# Geometric Morphometrics of *Gorilla* and *Pan* Scapulae

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## Abstract:

Understanding the morphology of the scapula of *Gorilla* and *Pan* is crucial to scientists who find fossil ape scapulae and need to assign them to taxa and interpret the functional significance of their morphology. While differences between the shapes of *Gorilla* and *Pan* scapulae are known, a morphological link between locomotor patterns and scapular shape has yet to be determined. Using geometric morphometrics and a large sample of *Gorilla* and *Pan* scapulae, the differences between the genera were investigated.

Fifteen three-dimensional landmarks were collected from *Gorilla* (n=150) and *Pan* (n=210) adult scapulae and analyzed using Procrustes analysis and principle components analysis. An analysis of *Pan* vs. *Gorilla* showed that *Pan* has a narrow scapula with a cranially tilted glenoid fossa and acromion process, which coupled with its smaller size, are features that previous researchers have predicted to be adapted for arboreal behavior. *Gorilla* has large muscle attachment sites such as a large supraspinous fossa and has an acromion process that extends farther laterally over the glenoid fossa, which are more suitable for stabilizing the shoulder joint when this larger animal climbs. Among the subspecies of *Gorilla*, *Gorilla gorilla gorilla* has the largest muscle attachment sites, which are consistent with its more arboreal behavior. *Gorilla beringei beringei*, on the other hand, does not climb to find food and consequently was found to have smaller muscle attachment sites. *Gorilla beringei graueri*, being intermediate in habitat and behavior, was found to be intermediate in scapular shape.

While previous research has searched for a continuum of scapular shape ranging from *Pan paniscus*, as the most arboreal African ape, to *G. b. beringei*, as the least arboreal African ape, this research showed that such a continuum does not exist, probably due to the great size dimorphism between the two genera, which results in different biomechanical demands on each ape when climbing. Instead, researchers should focus on the relationship between morphology and locomotor behavior within each genus.

## Introduction:

The main objective of my project was to determine whether and how the differing locomotor patterns of *Gorilla* (gorillas) and *Pan* (chimpanzees and bonobos) are reflected in their scapulae. To do this I used three-dimensional (3D) geometric morphometrics, which is a method used to analyze the shape of objects and is discussed further in the Methods section of this paper. Studies such as mine are important when interpreting fossils of apes and hominins (human relatives after the split with chimpanzees). If a scientist finds a fossil scapula, studies like mine can help the scientist reconstruct the locomotor patterns of the fossil individual. As scientists are still debating whether the genus *Gorilla* is made up of one species or two, my study can contribute to the study of gorilla taxonomy by showing how subspecies separate based on their scapulae and whether certain subspecies are different enough to be classified as their own

species. Finally, not much work has been done with 3D data from ape scapulae, and not much is known about one of the subspecies included in my study (*G. beringei graueri*).

For years, researchers have classified apes based on their locomotor patterns as either more terrestrial or more arboreal (Shea, 1986, Taylor, 1997, Taylor & Slice, 2005). However, the locomotion of apes is much more complicated than that, as engaging in more arboreal locomotion does not necessarily mean less terrestrial locomotion. For this reason, it is more meaningful to look at arboreal and terrestrial locomotion separately rather than as two ends of a continuum. This study focuses on relative amounts of arboreal locomotion, because climbing and suspensory behaviors (hanging and swinging from branches and vines) are distinctively arboreal and require distinctive muscle actions, while quadrupedal walking is characteristic of both terrestrial and arboreal behavior and does not involve such distinctive muscle actions.

Chimpanzees are considered to be more specialized frugivores, whereas gorillas are considered to be more generalist folivore-frugivores. Gorillas have longer guts, allowing them to fall back on vegetation when fruit is scarce, while chimpanzees do not have these adaptations (Marshall & Wrangham, 2007). Therefore it would be more advantageous for chimpanzees to spend more time foraging for fruit in trees, even when fruit is scarce, because they do not have adaptations for fall back foods (Marshall & Wrangham, 2007). Therefore *Pan* will be predicted to have a greater expression of adaptations for climbing and suspensory behaviors.

Within *Gorilla*, *G. g. gorilla* (western lowland gorilla) is the most arboreal subspecies because it has the tallest trees with the most fruit within its habitat. Data indicates that western lowland gorillas, inhabiting portions of tropical west and central Africa, are both more frugivorous, relying on seasonal fruit as well as fibrous plant material, herbs and vines, and more arboreal, incorporating a higher frequency of arboreal behaviors including tree climbing (Tutin & Fernandez, 1985; Williamson, 1988; Remis, 1994, 1995). Scapular features, in combination with shorter limbs, short pedal digits, a thick, strong big toe and broad heel, led Schultz (1927) to conclude that, compared with lowland gorillas, *G. b. beringei* (mountain gorilla) was less adapted to an arboreal way of life. *Gorilla beringei graueri* (eastern lowland gorilla) is seen as an intermediate between western lowland and mountain gorillas because its habitat is intermediate.

#### Background:

Although to date no conclusive findings regarding a functional link with the morphology of the African ape scapula have been published, no one has had a sample that included *G. b. graueri* individuals along with *G. b. beringei* and *G. g. gorilla* individuals in conjunction with the 3D geometric morphometrics method, which hasn't been widely used.

Previous work by Taylor and Slice (2005) compared *P. troglodytes*, *G. b. beringei*, and *G. g. gorilla*. Their sample sizes included 5 male and 2 female *G. g. gorilla*, 8 male and 5 female *G. b. beringei*, and 7 male and 10 female *P. troglodytes*. They used 10 two-dimensional landmarks, and a statistical computing program called R was used to analyze shape changes between taxa.

Taylor and Slice (2005) found that the two subspecies of *Gorilla* they examined do not differ in size of scapula based on centroid size but, unsurprisingly, they both differ in size from chimpanzees. Between *G. g. gorilla* and *G. b. beringei*, both subspecies share similar scapular and infraspinous fossa lengths but have minor shifts in the positioning of the acromial and glenoid fossa landmarks. *G. b. beringei* seems to have a slightly shorter spine length. Comparing gorilla scapulae to chimpanzee scapulae, they found that *Gorilla* has a relatively longer superior scapular border, scapula, and spine, a mediolateral expansion and a superior-inferior compression of the inferior portion of the infraspinous fossa, and a wider acromion process. However, the authors conclude that there is no apparent systematic or consistent pattern of differentiation across taxa that fits the predictions that have been widely used when comparing ape suspensory or vertical climbing behaviors (*Pan* being the most arboreal, then *G. g. gorilla* then *G. b. beringei*).

Taylor and Slice (2005) note that a well-developed scapular spine and acromion process, which usually means longer and wider, have been hypothesized to be mechanically advantageous in both arm swinging and vertical climbing behaviors. While the gorilla subspecies follow this trend, the opposite is found when gorillas are compared to chimpanzees. Chimpanzees should have more climbing behaviors and therefore a longer spine and acromion process, but results show that gorillas have longer spines and acromion processes than chimpanzees.

In primates, a well-developed scapular spine and acromion process, even though this idea of “well developed” is rarely explicitly defined, have been linked to arm-swinging and vertical climbing behaviors because these features are presumed to improve the mechanical leverage for the trapezius and deltoid muscles (Roberts, 1974).

Taylor (1997) compared the scapulae of *G. b. beringei* and *G. g. gorilla* but did not include *G. b. graueri*. She compared adult and non-adult gorillas and used linear dimensions measured with a digital caliper. These measurements included length, breadth, medial border length, supraspinous fossa length, and others. Taylor found no significant difference between these two subspecies of gorilla in scapular length. But interestingly, she found that if superior border length is a measure of supraspinous fossa size, then the more arboreal western lowland gorillas would exhibit larger supraspinous fossa. Larson and Stern (1989) found that western lowland gorillas had larger supraspinous fossa as well. If the medial border along the supraspinous fossa is longer then Taylor found the supraspinous fossa to be larger as well. Her paper finishes with the statement that perhaps superior border length would be interesting for further studies to investigate. In my own study, I had the ability to observe the supraspinous fossa.

Research into previous studies undertaken on the ape scapula taught me that many times researchers have not been able to find a link between what little is known about the morphology of the scapula and the ecology of the ape from which it came. I entered into writing my procedures knowing that they would serve as a starting point and that the ability to know the characteristics of a typical arboreal scapula was perhaps out of our reach as the behavior of each type of ape was slightly different and very complex.

Materials

In this project, two species of *Gorilla* (n=150) were analyzed: *Gorilla beringei* (n=36) and *Gorilla gorilla* (n=114). Subsequently two subspecies of *G. beringei*, *G. b. beringei* and *G. b. graueri*, were analyzed and one subspecies of *G. gorilla*, *G. g. gorilla*, was analyzed. Two species of *Pan* (n=210) were analyzed: *Pan paniscus* and *Pan troglodytes*. Complete sample sizes can be seen in Table 1. Fifteen three-dimensional landmarks were collected from the scapula of each specimen. Specimens were only included if they had been deemed adult based on whether or not epiphyses were fused (Jabbour, 2008) and included a complete set of landmarks. Specimens with missing or damaged landmarks were not included for *G. g. gorilla* while only some slight extrapolations of landmarks were included for *G. b. beringei* and *G. b. graueri* due to small sample sizes. Landmarks were extrapolated in the case of slight damage or presence of cartilage rather than bone. If the right scapula was damaged, the left scapula was used instead.

## Methods

Data were collected by Rebecca Jabbour. Fifteen three-dimensional landmarks were collected from each scapula with a MicroScribe 3DX digitizer. Landmarks were selected in order to best represent the overall shape of the scapula and are defined in Table 2. Landmark coordinates were recorded for each individual in an Excel spreadsheet. The contents of the Excel spreadsheets were compiled into a large text file, following specific protocols, and a computer program called Morphologika was used to run Generalized Procrustes Analysis and Principle Components Analysis (PCA). A Generalized Procrustes Analysis is used to translate, rotate, reflect, and scale the set of landmarks from each scapula so that the size and position differences are taken out and only the shape differences remain. A Principle Components Analysis is then used to show the patterns of variation within the sample. A PCA works to find a weighted combination of the variables that accounts for the greatest amount of variance within the sample but is blind to group memberships (Jabbour, 2008), which would be taxonomic assignments in this case. The first component accounts for the most variance, and the second component accounts for the second most variance. Morphologika was used to perform a PCA on the data and show the graph accounting for the variance within the sample. The shape of each individual's scapula was then displayed using a wire frame I designed which tells the computer which of the 15 landmarks to connect based on what would resemble a real scapula.

## Predictions

Prediction 1) *Pan* will have a narrower scapula than *Gorilla*, which is predicted to have a wider scapula (as measured along the axis of the scapula spine).

- A narrower scapula is associated with moving the upper limbs more rapidly, and a wider scapula is associated with moving the upper limbs more slowly (Shea, 1986).

Prediction 2) *Pan* will have a larger supraspinous fossa than *Gorilla*.

- This is the attachment site for the supraspinatus muscle, which is important for stabilizing the shoulder joint and keeping the humerus from becoming dislocated from the glenoid fossa (Marieb, Wilhelm & Mallatt, 2011).

Prediction 3) *Pan* will have a more cranially tilted glenoid fossa and acromion process as compared to *Gorilla*.

- This shape lends itself to using the arm in a raised position (Preuschoft, Hohn, Scherf, Schmidt, Krause, & Witzel, 2010).

Prediction 4) *Pan* will have an acromion process that extends farther laterally over the glenoid fossa than *Gorilla*.

- The acromion process is the attachment site for the deltoid and trapezius, which play a role in abducting the arm (Marieb, Wilhelm & Mallatt, 2011).

Prediction 5) *Pan* will have a coracoid process that extends further out from the scapula than *Gorilla*.

- It is an attachment site for the coracobrachialis and the pectoralis minor, which are used in flexion and adduction of the humerus (Marieb, Wilhelm & Mallatt, 2011).

Prediction 6) *Pan* will have a more laterally placed inferior angle than *Gorilla*.

- It is the attachment site of the teres major, which adducts and extends the humerus (Marieb, Wilhelm & Mallatt, 2011).

Prediction 7) *Gorilla gorilla gorilla* will have a wider supraspinous fossa than *G. b. beringei*. *Gorilla beringei graueri* will have a supraspinous fossa that is intermediate in size between *G. g. gorilla* and *G. b. beringei*.

- This is the attachment site for the supraspinatus muscle, which is important for stabilizing the shoulder joint when using climbing behaviors. (Marieb, Wilhelm & Mallatt, 2011)

Prediction 8) *Gorilla gorilla gorilla* will have a more cranially tilted glenoid fossa and acromion process as compared to *G. b. beringei*. *Gorilla beringei graueri* will have a glenoid fossa that is intermediately angled between *G. g. gorilla* and *G. b. beringei*.

- This shape lends itself to arm use above the head (Preuschoft et al., 2010).

Prediction 9) *Gorilla gorilla gorilla* will have an acromion process that extends farther laterally over the glenoid fossa than *G. b. beringei*. *Gorilla beringei graueri* will have intermediate extension.

- This is the attachment site for the deltoid and trapezius, which play a role in abducting the arm. (Marieb, Wilhelm & Mallatt, 2011).

Prediction 10) *Gorilla gorilla gorilla* will have a coracoid process that extends further out from the scapula than *G. b. beringei*. *Gorilla beringei graueri* will have intermediate extension.

- This is an attachment site for the coracobrachialis and the pectoralis minor, which are used in flexion and adduction of the humerus (Marieb, Wilhelm & Mallatt, 2011).

Prediction 11) *Gorilla gorilla gorilla* will have a more medially placed inferior angle than *G. b. beringei*. *Gorilla beringei graueri* will have an intermediate placement of the inferior angle.

- This is the attachment site of the teres major, which adducts and extends the humerus (Marieb, Wilhelm & Mallatt, 2011).

## Results:

*Pan* and *Gorilla* show a definite shape and size difference in their scapulae. As seen in Figure 1, *Pan* and *Gorilla* separate based on the scapula.

As predicted, *Pan* has a narrower scapula as measured along the axis of the scapular spine, a cranially angled glenoid fossa and cranially angled acromion process. Contrary to prediction, gorillas have a wider supraspinous fossa, and their acromion process is longer and extends farther laterally over the glenoid fossa. Their coracoid process seems to extend farther laterally but it is hard to tell. There is definitely a difference in angle (the angle of the coracoid compared the rest of the scapula) between *Pan* and *Gorilla*. The way the angle of the gorilla coracoid sticks out compared to the rest of the scapula makes it extend farther out laterally. *Pan* has a more medially placed inferior point as the whole scapula seems to angle up cranially. Gorillas have a more laterally placed inferior point but this could be again due to the entire shape of the scapula being less angled.

Among the *Gorilla* subspecies, shown in Figure 2, *G. g. gorilla* loads in the lower left corner of the graph and is characterized by larger attachment sites for climbing muscles. *G. g. gorilla* has the largest supraspinous fossa, the acromion process that extends farthest over the glenoid fossa, and the most laterally placed inferior point. Moving diagonally up the graph, *G. b. graueri* loads intermediately for all predictions. *G. b. beringei* loads in the upper right hand corner of the graph and is characterized by a slender and lever-like shape, with the most cranially angled glenoid fossa but with small attachment sites for muscles as predicted.

## Discussion:

Only some of the predictions made at the start of this project were found to hold true for *Pan* and *Gorilla* scapulae. This is most likely due to the very different demands that a chimpanzee or bonobo faces when it climbs a tree versus a gorilla. While some predictions held true that support the more arboreal nature of a chimpanzee such as a narrow, angled scapula which lends itself to arm swinging through trees, some predictions like larger muscle attachment sites used for tree climbing were found in *Gorilla* and not in *Pan*. This can be explained by the much larger body size of gorillas, which would require not only absolutely larger muscles but proportionally larger muscles to climb a tree and walk long distances on the ground.

Based on the results from the first analysis between *Pan* and *Gorilla*, we know that in the gorilla subspecies, a wider supraspinatus muscle and a longer and wider acromion process are found in *G. g. gorilla*, which would be climbing trees the most due to its diet and habitat. These muscle attachment sites are important in stabilizing the shoulder and supporting the larger muscles, which allow the gorilla to climb and walk long distances. Roberts (1974) found that a well-developed supraspinous fossa has been linked to relatively large, heavy, powerful limbs, and the need for glenohumeral joint stabilization during humeral elevation.

*G. b. beringei*, *G. b. graueri*, and *G. g. gorilla* all have differently shaped scapulae, which are a different shape and size than *Pan*. Strangely, *G. b. beringei* looks the most similar to *Pan* having the narrowest and most angled scapula of the gorillas. However, it can be hypothesized that in gorillas that don't climb very much, shoulder stabilization and large climbing muscles are not as

highly selected for because the need to climb in search of fruit is not present in mountain gorillas and the adaptation is not present in the scapulae. *Pan* does not have the adaptations for the same large climbing muscles as *G. g. gorilla* but this is explained by its smaller body size and different demands when climbing and not for the same reasons as *G. b. beringei*. This is supported by the intermediacy of the *G. b. graueri* scapula as, within the gorilla subspecies, evidence of a gradient from the gorilla that climbs the most (*G. g. gorilla*) to the gorilla that climbs the least (*G. b. beringei*) can be seen on the graph. *G. b. graueri* has not been included in a geometric morphometric or any method of scapula comparison before and therefore it was unknown where exactly *G. b. graueri* would lie compared to the other subspecies.

The arboreal shape of a scapula for *Pan* cannot be immediately compared to the arboreal shape of a scapula for *Gorilla*, as demonstrated in this paper. Previous research has searched for a gradient between *Pan* and *Gorilla* that would place *Pan* with the most arboreally shaped scapula and *G. b. beringei* with the least arboreally shaped scapula. This paper has demonstrated that *Pan* and *Gorilla* are different sizes with different behaviors and demands on their skeletons and therefore the shape of their scapulae cannot be compared but instead should be compared within genera. What it means to be “arboreally” shaped for the scapula of *Pan* is different than the meaning of an “arboreal” scapula for *Gorilla*.

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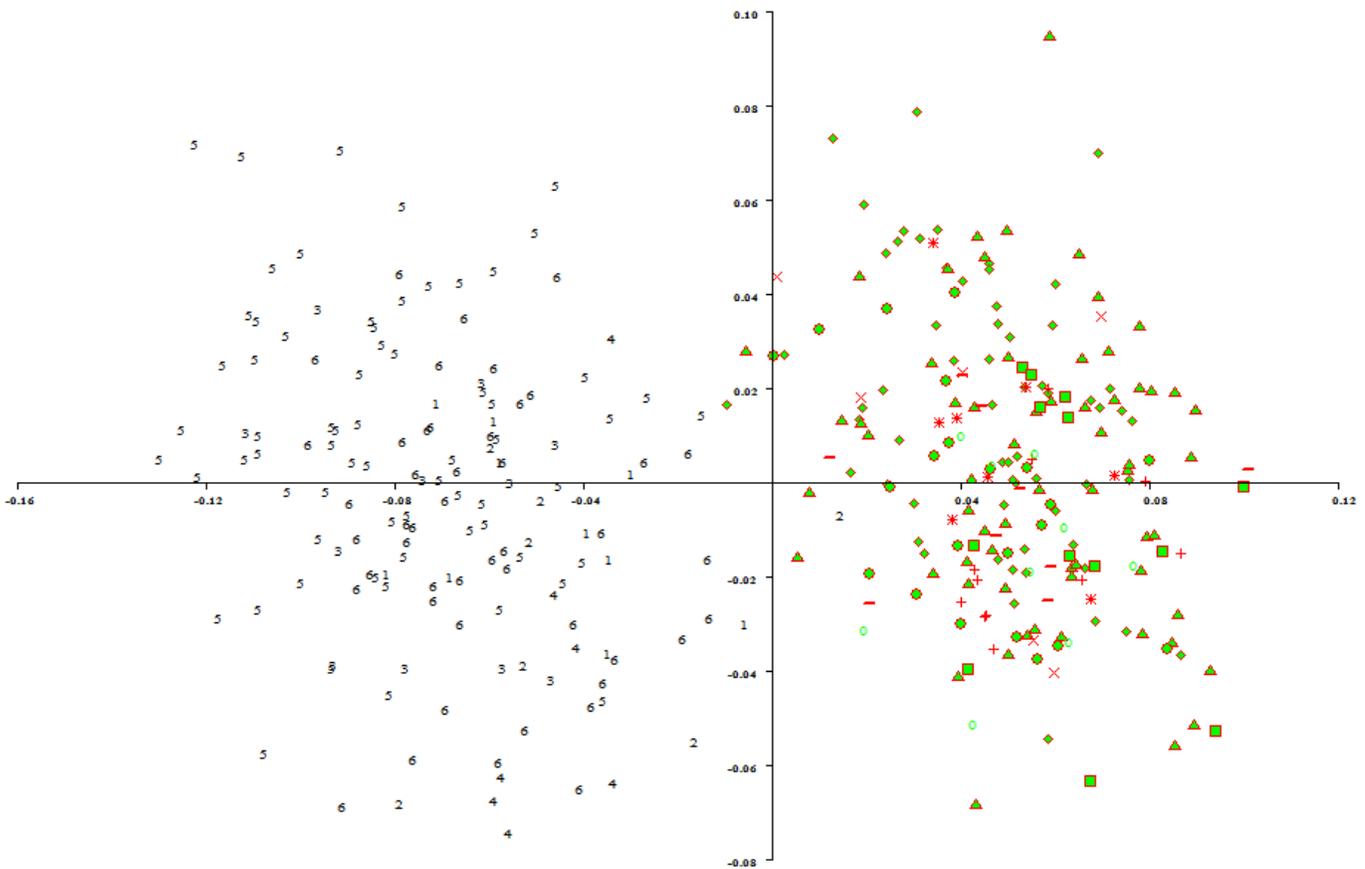


Figure 1. PCA graph of *Gorilla* vs. *Pan*. X-axis is component 1, which accounts for 38.8% of the total variance and the Y-axis is component 2, which accounts for 8.57% of the total variance. For *Gorilla* on the left side of the graph, 1's denote Male *G. b. beringei*, 2's denote Female *G. b. beringei*, 3's denote Male *G. b. graueri*, 4's denote Female *G. b. graueri*, 5's denote Male *G. g. gorilla*, and 6's denote Female *G. g. gorilla*. For *Pan*, on the right of the graph, diamonds denote Male *P. t. troglodytes*, triangles denote Female *P. t. troglodytes*, circles denote Male *P. t. schweinfurthii*, squares denote Female *P. t. schweinfurthii*, asterices denote Male *P. t. verus*, plus signs denote Female *P. t. verus*, crosses denote Female *P. t. elliotti* (no males), horizontal lines denote Male *P. paniscus* and open circles denote Female *P. paniscus*.

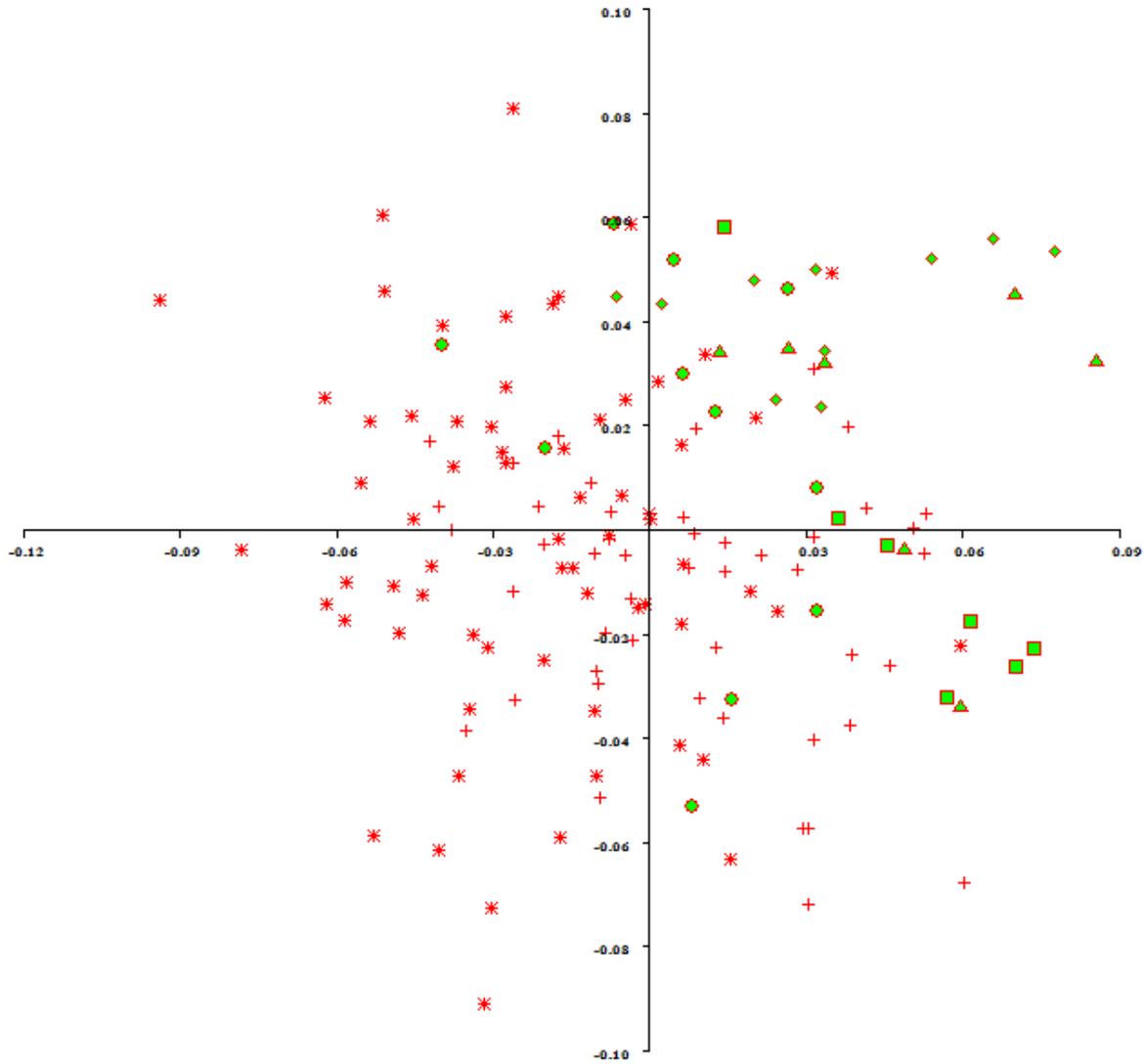


Figure 2. PCA graph of *G. g. gorilla*, *G. b. graueri*, and *G. b. beringei*. X-axis is component 1, which accounts for 17% of the total variance and the Y-axis is component 2, which accounts for 15% of the total variance. Diamonds denote Male *G. b. beringei*, triangles denote Female *G. b. beringei*, circles denote Male *G. b. graueri*, squares denote Female *G. b. graueri*, asterices denote Male *G. g. gorilla*, and plus signs denote Female *G. g. gorilla*.

**Table 1**

<b>Sample</b>	<b>Size</b>
<i>Pan</i>	210
Male <i>P. t. troglodytes</i>	62
Female <i>P. t. troglodytes</i>	66
Male <i>P. t. schweinfurthii</i>	22
Female <i>P. t. schweinfurthii</i>	13
Male <i>P. t. verus</i>	8
Female <i>P. t. verus</i>	15
Male <i>P. t. ellioti</i>	0
Female <i>P. t. ellioti</i>	6
Male <i>P. paniscus</i>	9
Female <i>P. paniscus</i>	9
<i>Gorilla</i>	150
Male <i>G. b. beringei</i>	11
Female <i>G. b. beringei</i>	7
Male <i>G. b. graueri</i>	11
Female <i>G. b. graueri</i>	7
Male <i>G. g. gorilla</i>	67
Female <i>G. g. gorilla</i>	47

**Table 2**

<b>Points</b>	<b>Description</b>
Superior angle	Most superior point of superior angle (on line of maximum scapular width).
Inferior angle	Most inferior point of inferior angle (on line of maximum scapular width).
Medial spine	Point where spine meets vertebral margin (extrapolated on straight line to border, if necessary).
Ventral acromion	Most ventro-superior point of acromion.
Posterior acromion	Dorsal most point on superior surface of acromion process (from glenoid perspective).
Dorso-lateral acromion	Dorso-lateral most point of acromion (overhanging the glenoid).
Spinoglenoid notch	Deepest point in spinoglenoid notch (greater scapular notch).
Suprascapular notch	Deepest point in suprascapular "notch", at base of coracoid.
Posterior coracoid	Most dorsal point of coracoid (from glenoid perspective).
Anterior coracoid	Most ventral point of coracoid (from glenoid perspective)
Superior glenoid	Most superior point of glenoid fossa (on outer border).
Inferior glenoid	Most inferior point of glenoid fossa (on outer border).
Deepest glenoid @ max width	Deepest point of glenoid fossa in plane of maximum glenoid width.
Ventral glenoid 1	Ventral outer border of glenoid fossa on line of max width perpendicular to long axis.
Dorsal glenoid 1	Dorsal outer border of glenoid fossa on line of maximum width perpendicular to long axis.