5-2012

Sizes of Joint Articular Surfaces in Homo sapiens and Pan paniscus and the Relevance to Locomotor Differences

Jacqueline Kenitz
University at Albany, State University of New York

Sizes of joint articular surfaces in Homo sapiens and Pan paniscus and the relevance to locomotor differences

A Thesis Presented to

The Faculty of the Anthropology Department

University at Albany

In Fulfillment

of the Requirements for

The Honors College

by

Jacqueline Kenitz

May 2012

Table Of Contents

Introduction:

Differences in locomotion have always presented interest in the anthropological field because of large differences found between similar species. By examining the proximal and distal femoral and humeral heads of *Homo sapiens* and *Pan paniscus***,** we are able to see the differential distribution of body weight, and how that compares to that particular species locomotion. Locomotion patterns of bonobos, *Pan paniscus*, include quadrupedal knuckle walking, suspensory movement under branches and occasional instances of bipedalism. However, humans, *Homo sapiens,* are known to be strictly bipedal using no other forms of locomotion. Many believe that habitual bipedalism evolved from an arboreal species like bonobos and chimpanzees that commonly used postural bipedalism when foraging or navigating through tree branches. Every type of locomotion has its own unique physical attributes that by simply examining bone samples one could determine what type of locomotion is present in that certain species. With further comparison of the bones of *Pan paniscus* and *Homo sapiens,* there is hope to find a correlation between the many proposed evolutionary theories.

In order to find differences in the locomotion patterns and joint articular surfaces of humans and bonobos, two predictions were tested. The first predication was that the human would have a much larger distal and proximal femoral and humeral head surfaces in comparison to the bonobo because the human is larger in size relative to the bonobo. This would also be true because most, if not all, of the weight is passed through the lower limbs while moving bipedally. The proximal and distal surfaces of the humeral head would be much smaller, because very little, if any mass is passed through the upper limbs in humans. The articular surfaces of humerus may not be as small as believed because humans carry large objects that would require having large bone surfaces to provide more space for muscle attachment. Overall, it is predicted that for

Homo sapiens at any given femur size they will have a smaller humeral head relative to *Pan paniscus.*

The second prediction is that *Pan paniscus* will have both smaller proximal and distal humeral and femoral heads with respect to the human because they have a smaller mass. Also, these two measurements may be very similar in size because while moving quadrupedally, as bonobos do, body weight is evenly distributed throughout both the upper and lower limbs. By scaling body size, it is possible that we will see bonobos having larger upper limb measurements, as they typically make use of these limbs for a greater amount of time compared to *Homo sapiens.* The study that has been done will relate *Homo sapiens and Pan paniscus* in order to account for the differences in body mass as well as locomotor differences and how the joint articular surfaces of the upper and lower limbs affect these differences.

Background Literature:

Locomotion is the act of moving from one place to another while keeping the body in equilibrium (Prost, 1967). Primates vary in locomotion patterns from arboreality, terresteriality, bipedalism, quadrupedalism, suspensory, vertical clinging and leaping, and just about everything in-between. Primates that are able to move freely about their habitat are able to participate in a variety of different kind of locomotor patterns, granted their bodies are adapted for it (Devine, 1985). Many times the locomotion pattern of the primate is dependent upon the behavior of primate such as the food it consumes, its environment, and its body size. When discussing locomotion, there are two parts, one is the particular activity and the second is where the activity takes place, or the substrate (Prost, 1967). For example, if a primate is an arboreal quadruped such as *Pan paniscus*, its locomotor activity is suspensory brachiation that occurs in the trees, and is predominately a knuckle-walker on the ground. Locomotion is also very dependent upon the physical makeup of the primate, such as the muscles, bone, and organs it is comprised of (Prost, 1967). Larger bones and muscles are required to move a larger bodied primate, while more restricted joints are necessary in quadrupedal primates as opposed to suspensory and brachiating primates. Locomotion has a wide range of variety across the primate spectra, but is dependent on many factors including environment, body adaptations, and behavioral patterns.

The first primate species that was researched was *Pan paniscus*, or the bonobo. In many ways, bonobos are quite similar to *Homo sapiens*, and may be thought of as the link to the evolutionary mystery of humans. They typically live in fission-fusion social groups which means, they are a large community that separates during the day into smaller groups for foraging and variety of other reasons and returns together in the eve, (Cawthon, 2010). “The bonobo can be characterized as a female-centered, equalitarian primate species that substitutes sex for aggression,” (De Waal, 1997, p. 1). Rates of sexual activity in this group of primates are very high; however, the rate of reproduction does not reflect the high sexual activity rate. Due to the high rates of sexual activity in the bonobo society, there is regularly paternal uncertainty when a female becomes pregnant (Cawthon, 2010). Typically, the bonobo is a habitual quadruped, or knuckle-walker, with some instances of postural bipedality (Videan and McGrew, 2002). Bonobos, once known as the pygmy chimpanzee on average weigh from 45 kg in males and 33.2 kg in females (Smith and Jungers, 1997). “To support their weight bonobos are skeletally created more for bipedalism than other ape relatives because of their longer femoral bones, larger tarsal and metatarsal bones, centrally positioned foramen magnum, and weight distribution, but typically move as knuckle-walkers,” (Cawthon, 2010, web pg.1). As compared to the common chimpanzee, bonobos act quite differently. The bonobos are sensitive and timid, physical violence is rarely seen, and bonobos are more vocal than chimpanzee and commonly raise and wave their hands while calling (De Waal, 1997). These behaviors are unique to bonobos, and are typically not even seen in sister taxa such as *Pan troglodytes.* Bonobo as well as the common chimpanzee is the closest extant relative to *Homo sapiens.* Analyses of the movement and bone structure of the bonobo may lead to missing pieces in the unsolved evolutionary puzzle of the bipedality of human beings.

Homo sapiens also have many characteristics that are unique to the species. To be human means to have enlarged brains, upright walking, extensive and versatile language, and a social life including many members (Koch, 2102). The brain began to increase in size when the early humans began using stone tools and walking bipedally. Then with a change in climate, brain size increased rapidly to allow for interaction and survival, (Koch, 2012). From extensive research that has been done we now can assume that hominids were present both in arboreal climbing settings, as well as terrestrial bipedalism (Thorpe, et al., 2007). The average weight of *Homo sapiens* ranges from 62.1-72.1 kg, with a wide variety across the species, (Smith and Jungers, 1997). To support this larger body and the locomotor adaptions, approximately "1.89 million years the development of the long thigh bone of *Homo erectus* allowed it to take long strides and therefore walk farther than earlier hominids," (Koch, n.d.). Bipedalism is one of the very important characteristics of present day humans as it unique to *Homo sapiens.* An enlarged brain and two-legged movement allowed this primate species to travel longer distances, freed their hands for food and infant carrying, and allowed them to scare of predators appearing bigger and more astounding. With these new characteristics that were developed, they were able to survive longer thus passing these traits on subsequent generations. Although it is unknown exactly how or why bipedalism evolved when it did, analysis of past and present day humans have led to further insight on the topic.

Quadrupedalism is a locomotor pattern striding with all four limbs placed on the ground. Bonobos typically use quadrupedalism as their main source of locomotion; however, studies have been done that prove they commonly use postural bipedalism when moving on branches and foraging for food. While locomoting quadrupedally, bonobos typically have a diagonal-sequence walk, seen in other primates (De Auot, et. al., 2004). When moving at a very brisk pace, bonobos appear to gallop, leading to a large amount of unnecessary stress on the fore and hindlimbs (De Auot, et al., 2004).This kind of walking experienced by bonobos and chimpanzees alike, is seemingly quite energetically inefficient, possibly leading to the development of bipedalism in early hominid species, (Sockol, et al., 2007). When moving arboreally, bonobos use a bent-hip, bent- knee posture that is less ineffective energetically than a human stance (Carey and Crompton, 2005). When walking quadrupedally, bonobos use larger steps and shorter frequency than when walking bipedally, using shorter steps but a greater frequency (De Auot et al., 2004). Many anthropologists of the past and present believe that the bipedalism of present day humans evolved from the gait of bonobos and chimpanzees.

Another form of locomotion practiced by *Pan paniscus* is suspensory movement in which the primate uses its forelimbs to swing below the branches as opposed to sitting on top of them. Although chimpanzees and bonobos alike most greatly rely on their hindlimbs to move them from place and their forelimbs solely as a prop, the forelimbs are adapted for general propelling behaviors, (Myatt et. al., 2012). These adaptations include a large range of motion in the shoulder joints, long extended phalanges to wrap around the branches, and opposable thumbs to name a few. Suspensory movement is not the most prominent movement since in only occurs in the trees, but should be accounted for as it may affect the size of the proximal and distal surfaces of the humerus.

Bipedalism is known as walking upright on two hind limbs for an extended period of time, practiced today by all modern humans as well as select primates and other animals. "Bipedalism is the defining feature of the earliest hominids, and marks the divergence from other apes," (Sockol et al., 2007). Many people have created hypotheses for the evolution of bipedalism from tool use to thermoregulation, and carrying to locomotor efficiency (Videan and McGrew, 2002). However, bipedalism developed far before the enlargement of the brain or any use of stone tools, told by the fossil record. It is important to make note that the "bipedalism" practiced by early hominids such as Lucy and other members *Australopithecus afarensis*, was not the same "bipedalism" practiced by modern *Homo sapiens.* Skeletal features such as a shorter hind limb in Lucy suggest that this species was not as fully adapted to walk on two limbs as are modern humans (Lewin, 1983). In order to be able to support to the body on only two limbs and walk upright, a variety of skeletal features must be demonstrated for structural and balance purposes. Some of these adaptions include the bicondylar angle, pelvic structure, and femoral attributes, and joint surfaces. Christopher Ruff stated the "modern adult humans are distinct from most other primates in having relatively very long and strong lower limb bones compared to upper limb bones," (Ruff, 2003). Research was done that found differences in the bicondylar angle of moderns, australopithecines, and chimpanzees. The angle in modern humans ranges from 8-11 degrees, 14-15 degrees in australopithecines, and from 1-5 degrees in chimpanzees (Shefelbine, et al., 2002). This can be accounted for by loading and locomotor patterns, and size of the rest of the body. These implications allow the modern human to not only stand upright, but also walk on two limbs while keepings its posture and balance. "While bipedalism may not be uniquely human, walking is," (Marks, 1987). Bipedalism has come a long way from our chimpanzee ancestors to early hominids and as advanced as walking and running in modern humans. While humans may be self-consciously bipedal today, it must have originated from sometime in the past (Devine, 1985).

The question you may be asking yourself is where does bipedalism evolve from? Or has it been practiced far longer than the fossil record suggests? While there is indeed an agreement between bipedalism characterizing earliest hominids, there is much less of an agreement about how it evolved, (Richmond et al., 2001). Measuring the articular joint surfaces of the bonobo and human may give better indication about the last common ancestor of the human, bonobo, and chimpanzee.

Methodology

Sample:

Bones of *Pan paniscus* and *Homo sapiens* were collected and photographs were taken by Adam Gordon, Ph.D. Each photograph was taken in a similar fashion, resting upon a flat surface with a ruler on the side of picture for scaling purposes. The *Pan panicus* bones were collected from the Royal Museum of Central Africa located in Tervuren, Belgium. Photographs were taken of the proximal femoral and humeral joint articular surfaces and also the distal femoral and humeral joint articular surfaces. The *Homo sapiens* bones were photographed from the Hamann-Todd Osteological Collection dated from 1960-1976 located in the The Cleveland Museum of Natural History.

Data Collection:

After the photographs were taken, the pictures were transferred on the laboratory computers for further analysis. Once the photographs were received, measurements began on the joint articulation surfaces using a program called Image J. First, I choose the straight line selection option was chosen from Image J and a scale was picked on the ruler, typically from about 10 mm to 80 or 90 mm, depending on the size of the bone. Then, the analyze function was chosen, set scale and the known distance box placed the “known distance” of typically about 70 or 80 mm (90/80 mm – 10mm), and selected OK. After zooming into the picture to get as close as possible, the measurements began. Using the polygon selection tool, points around the articulate surface were clicked to outline the bone as well as possible. Under the analyze tool was a function called measurement, that was chosen given the area of the joint articulation surface in mm^2. This was done for each bone and each specimen, and both the distal and proximal ends. After an initial run through was completed, the above process was done again a second and third time to ensure accuracy and precision of the data. A total of thirty-two *Homo sapiens* distal and proximal humeri were measured, not including two extra photographs that were taken to see other angles of the distal humerus. There were also thirty-two *Homo sapiens* distal and proximal femurs that were measured. For *Pan paniscus*, there were each a total of twenty-three distal and proximal humeral and femoral heads that were measured. However, MRAC 29048, MRAC 29056, and MRAC 29058 were removed from the analyses because they were previously determined to be juveniles, but will be included in the large sample size.

Analysis:

All data were collaborated into an Excel file, averages were taken for each specimen. After the average was taken, each of the three runs was compared to the average, for a percentage error, (((measured-actual)/actual) *100). If the percentage error was over 2%, the specimen was ultimately re-measured for a fourth data point to try to receive more accurate data. However, if the percent error was over 5%, that particular measurement was thrown away as it was too inaccurate to be considered in the data set. After the percentage errors were run on data, log values were run to better compare the bone sizes with differing body sizes. Finally, a simple regression was done to compare the distal femoral head and distal humeral head, and also the proximal femoral and humeral heads. On the same graph, plots were made of the log of the proximal femur to the log of the proximal humerus for both the human and bonobos. This was also done for the distal ends of the femur and humerus. Log ratios were found using techniques on Excel, log(proximal humerus/proximal femur) and log(distal humerus/distal femur) for both *Pan paniscus and Homo sapiens*. This value was graphed against either one or two to compare results of each species. Finally, a t-test was run on the data, a two sample test assuming equal variances, and the results were gathered for each articular surface of each species.

Results:

After measuring and analyzing the bone specimen of *Pan paniscus,* the minimum, maximum, and average absolute value of intra-observer error for each of the joint articular surfaces were calculated, and recorded in percentages. See table one below.

Pan paniscus	Bone	Average abs value	Minimum Error	Maximum Error
	Proximal Femur	0.28	-0.94	0.73
	Distal Femur	0.66	-2.31	2.61
	Proximal Humerus	0.51	-1.55	2.29
	Distal Humerus	0.36	-1.14	1.3

Table 1: Error for Articular Surfaces for *Pan paniscus*

Based upon the calculations of error, all of these values can be accepted and used for further analysis.

After the measurements were completed, these results were further analyzed using least squares regression. First, I compared log proximal femur to log of proximal humerus and found the following, see table 2.

	Coeff	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	0.585	0.462	1.266	0.222	-0.386	1.556	-0.386	1.556
LOG FP	0.839	0.161	5.220	0.000	0.501	1.177	0.501	1.177

Table 2: Least Squares Regression Analysis Comparing Proximal Femur to Proximal Humerus in *Pan paniscus*

The results have been graphed as seen in figure 1 below.

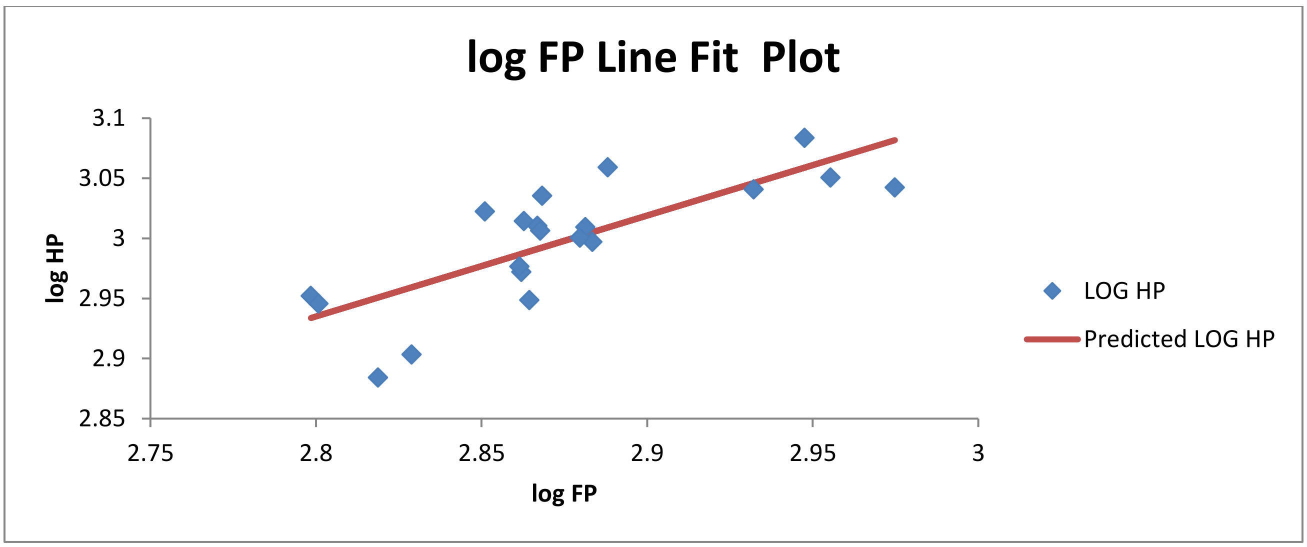

Figure 1: Least Squares Regression Comparing Proximal Femur and Humerus in *Pan paniscus*

Then, the distal femur and humerus were compared in a least squares regression analysis, and the results are show below in table three.

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	-0.121	0.237	-0.511	0.615	-0.614	0.372	-0.614	0.372
LOG FD	0.953	0.077	12.317	<0.001	0.792	1.114	0.792	1.114

Table 3: Least Squares Regression Analysis Comparing Distal Femur to Distal Humerus in *Pan paniscus*

The above information has been generated in to a graph by Excel and can be graphically viewed below in figure two.

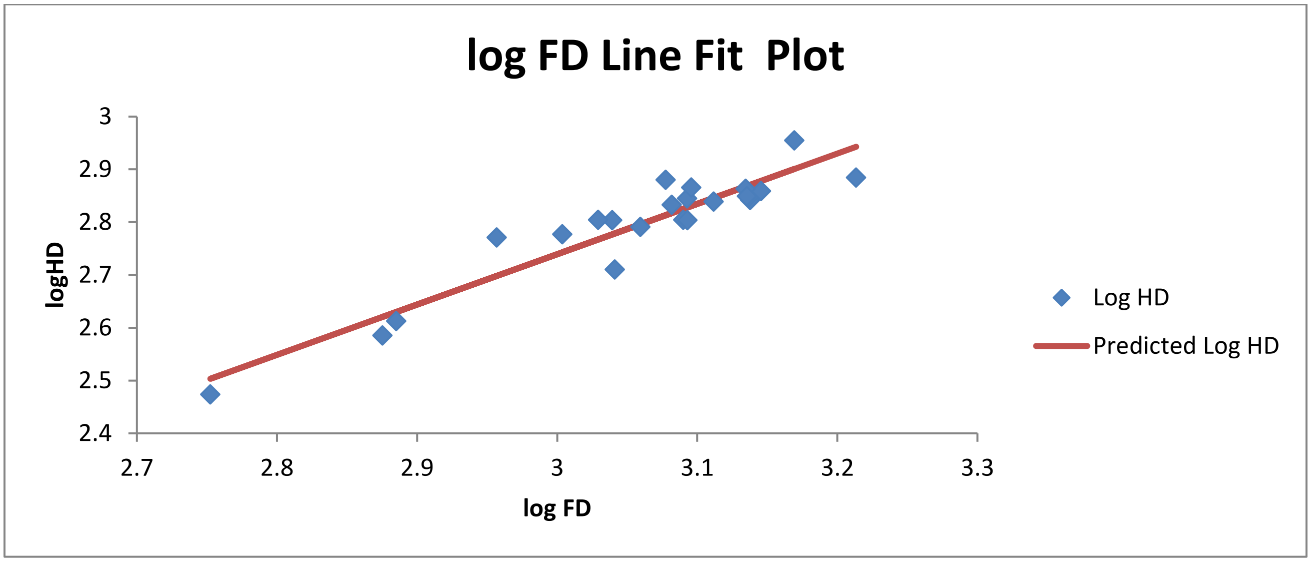

Figure 2: Least Squares Regression Comparing Distal Femur and Humerus in *Pan paniscus*

Intra-observer error was also found for *Homo sapiens* for each articular surfaces, proximal femur and humerus, and distal femur and humerus. Results can be seen below in table four.

Homo sapiens	Bone	Average abs value	Minimum Error	Maximum Error
	Proximal Femur	0.23	-0.86	0.61
	Distal Femur	0.5	-1.91	1.93
	Proximal Humerus	0.39	-1.32	1.72
	Distal Humerus	0.48	-1.5	2.01

Table 4: Error for Articular Surfaces for *Homo sapiens*

After reviewing the minimum, maximum, and average absolute value of errors for each surface, all of these values can be accepted and used again for further analysis. Again, a least squares regression analysis was run on the data, and the information below in table five was what was gathered.

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 80.0%*	*Upper 80.0%*
Intercept	0.191	0.181	1.056	0.299	-0.178	0.561	-0.046	0.428
Log FP	0.927	0.056	16.533	0.000	0.813	1.042	0.854	1.001

Table 5: Least Squares Regression Analysis Comparing Proximal Femur to Proximal Humerus in *Homo sapiens*

The above information can be found on figure three below, a graph generated by Excel.

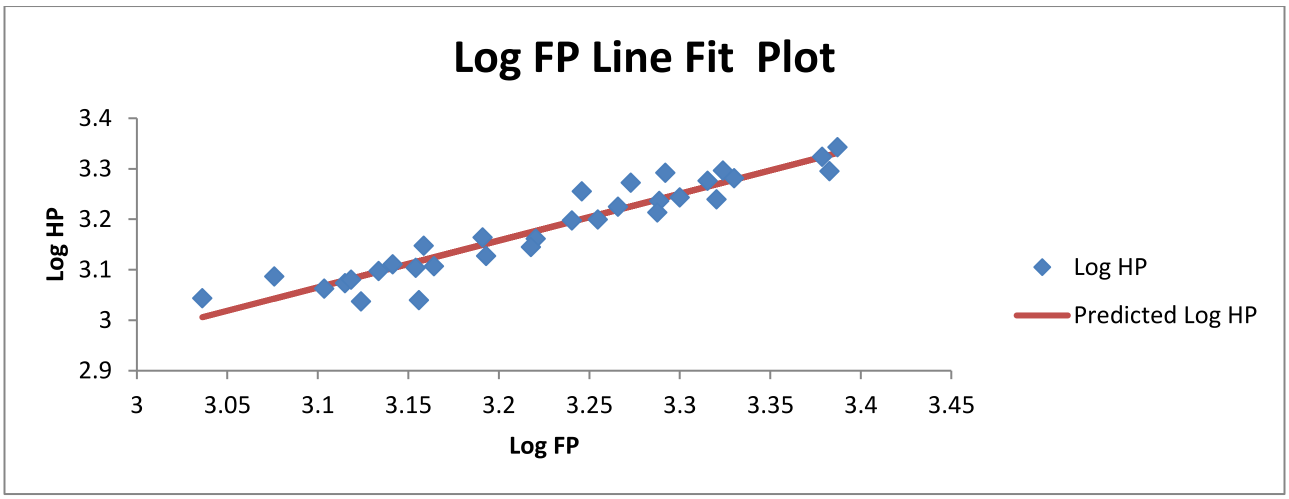

Figure 3: Least Squares Regression Comparing Proximal Femur and Humerus for *Homo sapiens*

Finally, one last regression was run on the distal femur and humerus of *Homo sapiens*, the information below in table six.

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 80.0%*	*Upper 80.0%*
Intercept	-0.820	0.258	-3.181	0.003	-1.346	-0.293	-1.157	-0.482
Log FD	1.066	0.073	14.515	0.000	0.916	1.217	0.970	1.163

Table 6: Least Squares Regression Analysis Comparing Distal Femur to Distal Humerus in *Homo sapiens*

This information above is further explained in the graph generated by Excel below in figure 4.

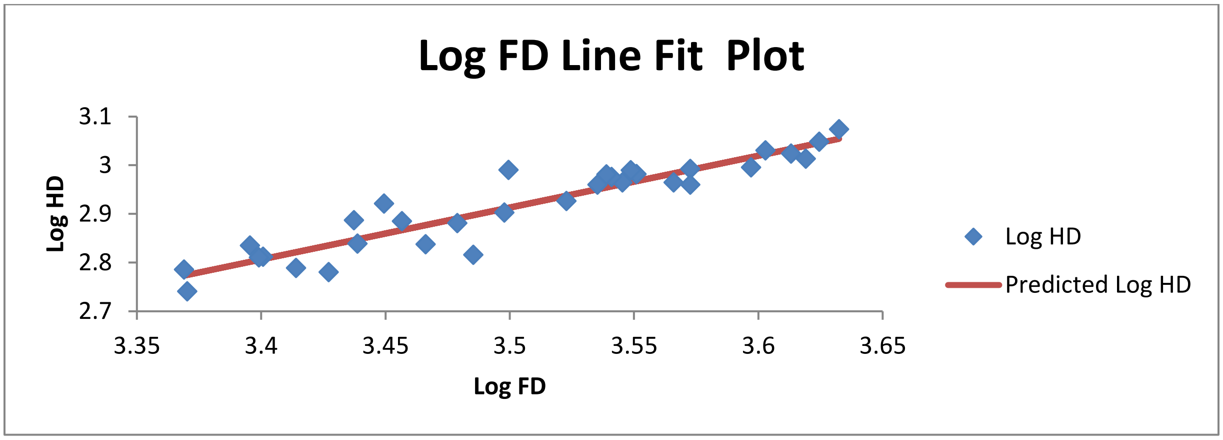

Figure 3: Least Squares Regression Comparing Distal Femur and Humerus for *Homo sapiens*

After the least squares regression was completed, a log function was run on each of the species, and log ratios were calculated, log (promixal humerus/proximal femur) for bonobos and humans, and log (distal humerus/distal femur) for bonobos and humans, as seen in tables nine-twelve in the appendix. Finally, a t-test assuming equal variances was run on the data. For the proximal femur and humerus ratio, the mean value for *Pan paniscus* is 0.123 and is -0.044 for *Homo sapiens*. The t-stat is 18.720 and the P one-tail is < 0.001. For the t-test comparing the distal femur and humerus the mean for *Pan paniscus* -0.261 and is -0.587 for *Homo sapiens*. The t-stat is 32.049 and the P one-tail is < 0.001, and can be referred to in table thirteen and fourteen in the appendix.

Finally, the log ratios of theproximal femur and proximal humerus for both *Pan paniscus* and *Homo sapiens* were compared and graphed together, below.

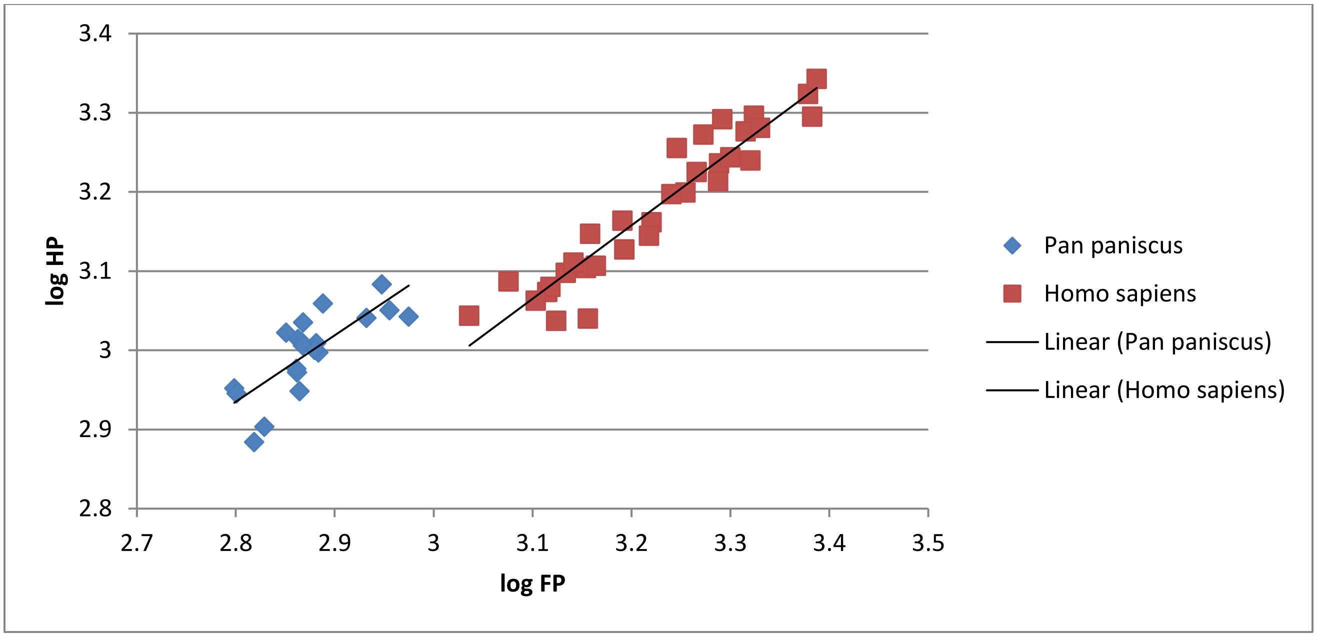

Figure 5: Comparing Log Ratios of Proximal Femur and Humerus for

Pan paniscus and *Homo sapiens*

The log ratios for the distal surfaces of the femur and humerus for *Pan paniscus* and *Homo sapiens* were also compared, seen below in figure six.

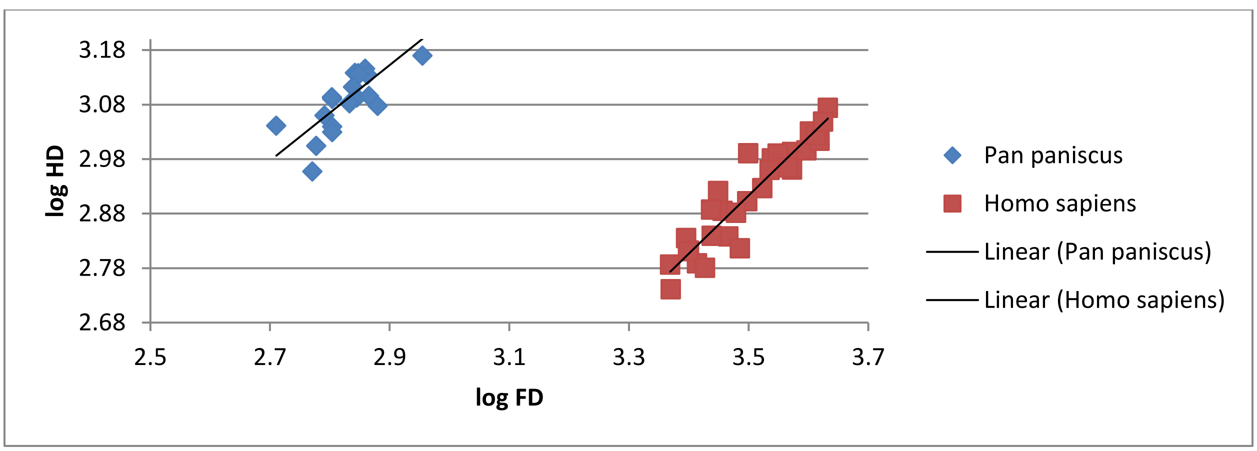

Figure 6: Comparing Log Ratios of Distal Femur and Humerus for *Pan paniscus* and *Homo sapiens*

The information provided to us by figures five and six will either support or not support the initial predictions.

Discussion:

The results found above are consistent with the initial prediction in that disregarding size of the primate, the forelimb in *Pan paniscus* is smaller in relationship to *Homo sapiens* because the body size of *Homo sapiens* is larger than the body size of *Pan paniscus*.

Further analysis of the least squares regression for proximal femur and proximal humerus of the *Pan paniscus*, it is seen that the slope does not differ significantly from isometry at alpha=0.05. For the distal femur and humerus for the same species, the slope also does not differ significantly from isometry at alpha =0.05. From this it can be gathered that, these values do not drastically change in retrospect to size, but rather stay constant to the size of the primate throughout the species. For the *Homo sapiens* species, similar results have been found. For both the distal and proximal femur and humeral articulation areas, the slope does not differ significantly from isometry at alpha = 0.05. This means the larger the human, the larger the femur and humeral heads of the person. For example, one would not see a 6’5’’ human with the same sized femoral heads as a 4’11’’ person. But, this also means that the ratio if proximal humerus to proximal femur doesn’t change within a given species, regardless of size (i.e, same ratio for 6’5’’ and 4’11’’.)

After discussing the isometry of the two species, valuable information has been uncovered. After comparing the log ratios for the proximal ends of the femur and humerus for both *Pan paniscus* and *Homo sapiens*, it has been noted for primates of similar sizes, *Pan paniscus* has both a larger proximal femur and humerus, which can been seen in figure 5.

Therefore, at any given proximal femur size, it can be expected that *Pan paniscus* will have a larger proximal humeral size.

This agrees with the initial prediction made since *Pan paniscus* pass more weight through their forelimbs while moving quadrupedally, it is expected they should have larger forelimb measurements in comparison to *Homo sapiens*, which only use their hind limbs for movement.

The same holds constant for the distal humerus and femur for *Pan paniscus* and *Homo sapiens.* It has been found that for any distal femur size, the distal humerus for *Pan paniscus* is much larger. This also agrees with the initial prediction in that primates who use all four limbs to move would be expected to have larger forelimb measurements, than primates who only use their hind limbs for locomotor purposes. The graph explaining the above data can be seen in figure six above.

The one-tailed t-test that was used as it compares two different populations. The information gathered from this test showed that these two species were definitely from two different populations. This information can be gathered due to the large value of the t-stat. It was found that the ratio between the distal humerus and the distal femur produced a greater t-statistic. This gives us the information that there is a greater separation in the sizes of the distal articulation surfaces in comparison to the proximal articular surfaces. Further work can be done to test why locomotion may affect the distal surfaces more significantly than the proximal surfaces of both the humerus and femur.

Conclusion:

In conclusion, my initial predication was supported that morphology does indeed reflect locomotion. This experiment has found that passing weight through four limbs makes for larger sized humeral heads to support the moving primate. On the opposing side, a primate must have larger femoral measurements if he/she is only passing weight through the hind limbs. The limbs must be large enough the support the weight passing through them, but not too large as to compromise the movement of the species.

All of the evidence supports the prediction that if a species uses forelimbs as well as hind limbs as in quadrupedal movement to locomote, they should indeed have larger forelimbs relative to hindlimbs than a species that does not use their forelimbs for the same purpose. Both *Pan paniscus* and *Homo sapiens* have specialized morphological details that effect their locomotor preferences as well as where and how it is performed.

References Cited:

1. Carey, T.S., Crompton, R.H. (2005). The metabolic costs of “bent-hip, bent-knee” walking in humans. *J of Hum Evo, 48(1),* 25-44.
2. Cawthon, Lang KA. 2010 December 1. Primate Factsheets: Bonobo (Pan paniscus) Behavior. http://pin.primate.wisc.edu/factsheets/entry/bonobo/20ehave. Accessed 2011 November 21.
3. D Auot, K., Vereecke, E.,Schooanaert, K., De Clercq, D., Van Elsacker, L., Aerts, P. (2004). Locomotion in bonobos (Pan paniscus): differences and similarities between bipedal and quadrupedal terrestrial walking, and a comparison with other locomotor modes. *J of Anat*, *204(5),* 353-361.
4. Devine, J. (1985). The versatility of human locomotion. *American anthropologist*, *87*(3), 550-70.
5. De Waal Frans. 1997. Bonobo: The Forgotten Ape. University of California Press Chapter 1. 1-1.
6. Harmon, E.H. (2007). The shape of the hominoid proximal femur: A geometric morphometric analysis. *J of Anat*., 210(2), 170-185.
7. Koch, D. H. (2012). *What does it mean to be human?* Retrieved from http://humanorigins.si.edu/human-characteristics. Accessed 2011 November 28.
8. Lewin, R. (1983). Do ape-size legs mean ape-like gait? *Science, 221,* 537-38.
9. Marks J. 1987. Bipedal Locomotion. Science 236: 1412.
10. Prost JH. 1967. A definitional system for the classification of primate locomotion. American Anthropologist 67: 1198-1214
11. Richmond, B., Begun, D.R., Strait, D.S., (2001). Origin of human bipedalism: the knuckle-walking hypothesis revisited. *Yearbook of Physical Anthropology*, 44, 70-105.

12. Ruff, C., (2003). Ontogenetic adaptions to bipedalism: age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. *Journal of Human Evolution, 45(4),* 317-349.

13. Shefelbine, S.J., Tardieu, C., Carter, D.R. (2002). Development of the femoral bicondylar angle in hominid bipedalism. *Bone, 30(5)*, 765-770

14. Smith, R., and Jungers, W. (1997). Body mass in comparative primatology, *Journal of Human Evolution, 32,* 523-559.

15. Sockol, M. D., Raichlen, D. A., & Pontzer, H. (2007). Chimpanzee locomotor energetics and the origin of human bipedalism. *PNAS*, *104*(30), 12265-12269.

16. Thorpe, S. S., Holder, R. L., & Crompton, R. H. (2007). Origin of human bipedalism: As an adaption for locomotion on flexible branches. *Science*, *316*, 1328-1331.

17. Videan E.N, McGrew W.C. 2002. Bipedality in Chimpanzee (*Pan tyoglodytes*) and Bonobo(*Pan paniscus*): Testing hypotheses on the Evolution of Bipedalism. American J of Phys Anthro 118: 184-190.

Appendix

Specimen	Ver.	Area (sq. mm) – 1st	Area (sq. mm) – 2nd	Area (sq. mm)	Mean Measurement	% Error 1	% Error 2	% Error 3
MRAC 13202		727.520	729.275	730.780	729.192	-0.23%	0.01%	0.22%
MRAC 15293		758.567	761.167	762.948	760.894	-0.31%	0.04%	0.27%
MRAC 15294		765.040	764.599	764.574	764.738	0.04%	-0.02%	-0.02%
MRAC 15295		736.838	736.533	734.403	735.925	0.12%	0.08%	-0.21%
MRAC 15296		904.828	900.661	901.821	902.437	0.26%	-0.20%	-0.07%
MRAC 27696		857.093	858.296	850.735	855.375	0.20%	0.34%	-0.54%
MRAC 27698		724.802	730.844	728.113	727.920	-0.43%	0.40%	0.03%
MRAC 27699		832.163	831.363	827.067	830.198	0.24%	0.14%	-0.38%
MRAC 29035		730.577	738.966	742.890	737.478	-0.94%	0.20%	0.73%
MRAC 29040		886.620	889.021	883.352	886.331	0.03%	0.30%	-0.34%
MRAC 29042		727.908	731.001	721.793	726.901	0.14%	0.56%	-0.70%
MRAC 29044		708.501	711.366	709.031	709.633	-0.16%	0.24%	-0.08%
MRAC 29045	2	775.557	774.005	769.034	772.865	0.35%	0.15%	-0.50%
MRAC 29045	3	771.190	778.349	775.974	775.171	-0.51%	0.41%	0.10%
MRAC 29045	1	765.714	770.748	770.325	768.929	-0.42%	0.24%	0.18%
MRAC 29047		944.029	947.864	939.188	943.694	0.04%	0.44%	-0.48%
MRAC 29048		336.267	339.147	336.644	337.353	-0.32%	0.53%	-0.21%
MRAC 29051	2	633.939	637.716	631.311	634.322	-0.06%	0.54%	-0.47%
MRAC 29051	3	638.064	639.702	643.686	640.484	-0.38%	-0.12%	0.50%
MRAC 29051	1	631.854	627.647	626.699	628.733	0.50%	-0.17%	-0.32%
MRAC 29052		758.299	760.230	755.608	758.046	0.03%	0.29%	-0.32%
MRAC 29053		670.706	676.537	675.982	674.408	-0.55%	0.32%	0.23%
MRAC 29054	2	732.145	732.094	728.145	730.795	0.18%	0.18%	-0.36%
MRAC 29054	1	733.501	728.487	733.873	731.954	0.21%	-0.47%	0.26%
MRAC 29056		455.127	457.014	456.375	456.172	-0.23%	0.18%	0.04%
MRAC 29057		662.190	659.989	654.386	658.855	0.51%	0.17%	-0.68%
MRAC 29058		491.649	491.775	496.451	493.292	-0.33%	-0.31%	0.64%
MRAC 29060		635.458	628.122	632.884	632.155	0.52%	-0.64%	0.12%
MRAC 29063		739.787	738.880	736.567	738.411	0.19%	0.06%	-0.25%
MRAC 84036		1075.914	1075.725	1072.441	1074.693	0.11%	0.10%	-0.21%
MRAC 84036		787.161	788.650	790.088	788.633	-0.19%	0.00%	0.18%
MRAC84036M		578.716	581.963	580.811	580.497	-0.31%	0.25%	0.05%

Table 1: Measurements of Proximal Femur for *Pan paniscus*

***MRAC 29048, 29056, and 29058 were removed in the analysis as they were identified as juveniles

Specimen	Area (sq. mm)	Area (sq. mm)	Area (sq. mm)	Mean Measurement	% Error 1	% Error 2	%Error 3
MRAC 13202	1643.184	1622.816	1638.300	1634.767	0.51%	-0.73%	0.22%
MRAC 15293	1372.690	1371.291	1377.389	1373.790	-0.08%	-0.18%	0.26%
MRAC 15294	1370.018	1371.863	1370.737	1370.873	-0.06%	0.07%	-0.01%
MRAC 15295	1193.628	1198.135	1194.681	1195.481	-0.16%	0.22%	-0.07%
MRAC 15296	1377.232	1397.835	1419.334	1398.134	-1.49%	-0.02%	1.52%
MRAC 27696	1362.732	1368.115	1358.592	1363.146	-0.03%	0.36%	-0.33%
MRAC 27698	1142.022	1144.011	1154.474	1146.836	-0.42%	-0.25%	0.67%
MRAC 27699	1224.168	1236.612	1230.256	1230.345	-0.50%	0.51%	-0.01%
MRAC 29035	1069.762	1100.504	1114.965	1095.077	-2.31%	0.50%	1.82%
MRAC 29040	1373.330	1359.688	1365.196	1366.071	0.53%	-0.47%	-0.06%
MRAC 29042	1233.015	1231.006	1227.890	1230.637	0.19%	0.03%	-0.22%
MRAC 29044	1236.555	1243.881	1236.133	1238.856	-0.19%	0.41%	-0.22%
MRAC 29045	1318.038	1270.671	1292.011	1293.573	1.89%	-1.77%	-0.12%
MRAC 29047	1484.534	1473.024	1472.359	1476.639	0.53%	-0.24%	-0.29%
MRAC 29048	554.590	572.358	569.552	565.500	-1.93%	1.21%	0.72%
MRAC 29051	1063.734	1077.618	1068.104	1069.819	-0.57%	0.73%	-0.16%
MRAC 29052	1261.662	1223.204	1230.111	1238.326	1.88%	-1.22%	-0.66%
MRAC 29053	1035.058	999.234	991.790	1008.694	2.61%	-0.94%	-1.68%
MRAC 29054	1205.216	1200.637	1215.781	1207.211	-0.17%	-0.54%	0.71%
MRAC 29056	769.033	773.969	759.772	767.591	0.19%	0.83%	-1.02%
MRAC 29057	894.901	908.697	913.002	905.533	-1.17%	0.35%	0.82%
MRAC 29058	762.391	749.114	740.314	750.606	1.57%	-0.20%	-1.37%
MRAC 29060	1090.153	1102.782	1104.913	1099.283	-0.83%	0.32%	0.51%
MRAC 29063	1259.648	1253.176	1227.730	1246.851	1.03%	0.51%	-1.53%
MRAC 84036M	1673.547	1686.165	1683.363	1681.025	-0.44%	0.31%	0.14%
MRAC 84036M	1251.534	1253.290	1235.056	1246.627	0.39%	0.53%	-0.93%
MRAC 84036M	1015.693	1030.983	1034.239	1023.338	-0.75%	0.75%	1.07%

Table 2: Measurements of the Distal Femur for *Pan paniscus*

***MRAC 29048, 29056, and 29058 were removed in the analysis as they were identified as juveniles

Specimen	Area (sq. mm)	Area (sq. mm)	Area (sq. mm)	Mean Meas	% Error 1	% Error 2	% Error 3
MRAC 13202	1033.667	1035.274	1031.292	1033.411	0.02%	0.18%	-0.21%
MRAC 15293	1017.986	1024.731	1021.261	1021.326	-0.33%	0.33%	-0.01%
MRAC 15294	994.114	1001.318	985.115	993.516	0.06%	0.79%	-0.85%
MRAC 15295	1015.565	1021.988	1034.518	1024.024	-0.83%	-0.20%	1.02%
MRAC 15296	1127.935	1130.687	1112.188	1123.603	0.39%	0.63%	-1.02%
MRAC 27696	1101.249	1094.115	1099.567	1098.310	0.27%	-0.38%	0.11%
MRAC 27698	939.712	935.626	937.654	937.664	0.22%	-0.22%	0.00%
MRAC 29035	1011.236	1020.965	1011.816	1014.672	-0.34%	0.62%	-0.28%
MRAC 29040	1196.029	1207.564	1232.384	1211.992	-1.32%	-0.37%	1.68%
MRAC 29042	933.228	955.667	952.824	947.240	-1.48%	0.89%	0.59%
MRAC 29044	1036.727	1077.182	1045.220	1053.043	-1.55%	2.29%	-0.74%
MRAC 29045	1137.420	1152.861	1147.875	1146.052	-0.75%	0.59%	0.16%
MRAC 29047	1097.602	1111.468	1098.447	1102.506	-0.44%	0.81%	-0.37%
MRAC 29048	309.126	307.470	306.966	307.854	0.41%	-0.12%	-0.29%
MRAC 29051	891.583	897.496	896.693	895.257	-0.41%	0.25%	0.16%
MRAC 29052	998.977	1002.859	1002.221	1001.352	-0.24%	0.15%	0.09%
MRAC 29053	802.495	798.785	800.530	800.603	0.24%	-0.23%	-0.01%
MRAC 29054	890.837	887.143	886.690	888.223	0.29%	-0.12%	-0.17%
MRAC 29056	412.613	411.156	408.412	410.727	0.46%	0.10%	-0.56%
MRAC 29057	761.616	758.109	777.603	765.776	-0.54%	-1.00%	1.54%
MRAC 29058	353.506	361.014	357.906	357.475	-1.11%	0.99%	0.12%
MRAC 29060	882.623	880.505	883.913	882.347	0.03%	-0.21%	0.18%
MRAC 29063	1076.715	1094.316	1083.268	1084.766	-0.74%	0.88%	-0.14%

Table 3: Measurements of the Proximal Humerus for *Pan paniscus*

Specimen	Area (sq. mm) – 1st	Area (sq. mm) – 2nd	Area (sq. mm)	Mean Measurement	% Error 1	% Error 2	% Error 3
MRAC 13202	768.341	769.184	763.068	766.864	0.19%	0.30%	-0.50%
MRAC 15293	693.331	697.570	694.540	695.147	-0.26%	0.35%	-0.09%
MRAC 15294	711.847	701.123	697.299	703.423	1.20%	-0.33%	-0.87%
MRAC 15295	759.019	762.107	754.209	758.445	0.08%	0.48%	-0.56%
MRAC 15296	723.946	726.431	718.576	722.984	0.13%	0.48%	-0.61%
MRAC 27696	728.878	728.969	731.102	729.650	-0.11%	-0.09%	0.20%
MRAC 27698	616.392	622.111	616.634	618.379	-0.32%	0.60%	-0.28%
MRAC 29035	644.927	629.375	635.646	636.649	1.30%	-1.14%	-0.16%
MRAC 29040	705.762	707.977	705.869	706.536	-0.11%	0.20%	-0.09%
MRAC 29042	638.469	636.134	636.247	636.950	0.24%	-0.13%	-0.11%
MRAC 29044	635.176	638.872	635.635	636.561	-0.22%	0.36%	-0.15%
MRAC 29045	688.173	687.638	694.896	690.236	-0.30%	-0.38%	0.68%
MRAC 29047	900.782	902.926	900.607	901.438	-0.07%	0.17%	-0.09%
MRAC 29048	296.689	296.560	299.275	297.508	-0.28%	-0.32%	0.59%
MRAC 29051	635.694	638.582	637.126	637.134	-0.23%	0.23%	0.00%
MRAC 29052	701.670	701.089	698.110	700.290	0.20%	0.11%	-0.31%
MRAC 29053	600.824	598.267	596.818	598.636	0.37%	-0.06%	-0.30%
MRAC 29054	676.969	682.392	682.031	680.464	-0.51%	0.28%	0.23%

MRAC 29056	405.406	408.964	414.389	409.586	-1.02%	-0.15%	1.17%
MRAC 29057	589.730	592.499	587.175	589.801	-0.01%	0.46%	-0.45%
MRAC 29058	385.315	384.610	385.391	385.105	0.05%	-0.13%	0.07%
MRAC 29060	515.176	517.610	507.614	513.467	0.33%	0.81%	-1.14%
MRAC 29063	736.920	731.972	732.890	733.927	0.41%	-0.27%	-0.14%

Table 4: Measurements of the Distal Humerus for *Pan paniscus*

Specimen	Area (sq. mm)	Area (sq. mm)	Area (sq. mm)	Mean Measurement	% Error 1	% Error 2	% Error 3	mean absolute error
CMNH HTH 0290	2093.179	2087.541	2091.060	2090.593	0.12%	-0.15%	0.02%	0.10%
CMNH HTH 0524	1939.604	1948.528	1943.317	1943.816	-0.22%	0.24%	-0.03%	0.16%
CMNH HTH 0538	1868.914	1882.773	1871.414	1874.367	-0.29%	0.45%	-0.16%	0.30%
CMNH HTH 0561	1298.348	1304.739	1306.416	1303.168	-0.37%	0.12%	0.25%	0.25%
CMNH HTH 0594	1950.682	1964.427	1961.111	1958.740	-0.41%	0.29%	0.12%	0.27%
CMNH HTH 0596	1839.945	1848.181	1845.483	1844.536	-0.25%	0.20%	0.05%	0.17%
CMNH HTH 0598	1797.923	1794.999	1799.430	1797.451	0.03%	-0.14%	0.11%	0.09%
CMNH HTH 0657	1326.228	1328.899	1334.941	1330.023	-0.29%	-0.08%	0.37%	0.25%
CMNH HTH 0658	2099.889	2113.214	2109.838	2107.647	-0.37%	0.26%	0.10%	0.25%
CMNH HTH 0666	2049.341	2079.785	2072.199	2067.108	-0.86%	0.61%	0.25%	0.57%
CMNH HTH 0704	1308.992	1310.220	1320.499	1313.237	-0.32%	-0.23%	0.55%	0.37%
CMNH HTH 0814	1551.001	1551.367	1554.644	1552.337	-0.09%	-0.06%	0.15%	0.10%
CMNH HTH 1062	2127.168	2143.825	2141.612	2137.535	-0.48%	0.29%	0.19%	0.32%
CMNH HTH 1103	1180.828	1197.639	1193.799	1190.755	-0.83%	0.58%	0.26%	0.56%
CMNH HTH 1152	2383.018	2387.916	2402.826	2391.253	-0.34%	-0.14%	0.48%	0.32%
CMNH HTH 1208	1362.969	1359.642	1357.923	1360.178	0.21%	-0.04%	-0.17%	0.14%
CMNH HTH 1214	1086.859	1085.764	1087.833	1086.819	0.00%	-0.10%	0.09%	0.06%
CMNH HTH 1270	1431.680	1433.051	1430.762	1431.831	-0.01%	0.09%	-0.07%	0.06%
CMNH HTH 1313	2406.228	2414.822	2420.758	2413.936	-0.32%	0.04%	0.28%	0.21%
CMNH HTH 1345	1651.685	1660.074	1671.141	1660.967	-0.56%	-0.05%	0.61%	0.41%
CMNH HTH 1361	1760.205	1762.733	1761.296	1761.411	-0.07%	0.08%	-0.01%	0.05%
CMNH HTH1415	1414.507	1430.298	1433.308	1426.038	-0.81%	0.30%	0.51%	0.54%
CMNH HTH 1419	1736.292	1740.591	1740.674	1739.186	-0.17%	0.08%	0.09%	0.11%
CMNH HTH 1427	1646.691	1649.631	1656.474	1650.932	-0.26%	-0.08%	0.34%	0.22%
CMNH HTH 1534	1453.043	1463.208	1460.880	1459.044	-0.41%	0.29%	0.13%	0.27%
CMNH HTH 1539	1560.728	1563.474	1553.568	1559.257	0.09%	0.27%	-0.36%	0.24%
CMNH HTH 1709	1267.900	1269.880	1269.004	1268.928	-0.08%	0.08%	0.01%	0.05%
CMNH HTH 1748	1382.286	1391.850	1380.454	1384.863	-0.19%	0.50%	-0.32%	0.34%
CMNH HTH 1778	1936.143	1939.863	1940.280	1938.762	-0.14%	0.06%	0.08%	0.09%
CMNH HTH 1903	2445.263	2444.503	2426.543	2438.770	0.27%	0.24%	-0.50%	0.33%
CMNH HTH 1961	1437.505	1442.476	1440.363	1440.115	-0.18%	0.16%	0.02%	0.12%

Table 5: Measurements of the Proximal Femur for *Homo sapiens*

Specimen	Ver.	Area (sq. mm)	Area (sq. mm)	Area (sq. mm)	Mean Measurement	% Error 1	% Error 2	% Error 3
CMNH HTH 0290		3482.968	3520.119	3526.280	3509.789	-0.76%	0.29%	0.47%
CMNH HTH 0524		3733.402	3777.362	3702.386	3737.717	-0.12%	1.06%	-0.95%
CMNH HTH 0538		3716.640	3745.487	3750.982	3737.703	-0.56%	0.21%	0.36%
CMNH HTH 0561		2606.417	2590.977	2585.290	2594.228	0.47%	-0.13%	-0.34%
CMNH HTH 0594		3933.533	3960.628	3968.287	3954.149	-0.52%	0.16%	0.36%
CMNH HTH 0596		3471.048	3478.054	3474.997	3474.700	-0.11%	0.10%	0.01%
CMNH HTH 0598		3163.785	3148.703	3162.565	3158.351	0.17%	-0.31%	0.13%
CMNH HTH 0657		2487.374	2538.285	2522.247	2515.969	-1.14%	0.89%	0.25%
CMNH HTH 0658		4038.307	3961.179	4021.154	4006.880	0.78%	-1.14%	0.36%
CMNH HTH 0666		3560.811	3552.280	3554.208	3555.766	0.14%	-0.10%	-0.04%
CMNH HTH 0704	1	2490.992	2492.340	2475.249	2486.194	0.19%	0.25%	-0.44%
CMNH HTH 0704	2	2422.364	2459.663	2432.119	2438.049	-0.64%	0.89%	-0.24%
CMNH HTH 0814		3335.002	3327.505	3334.897	3332.468	0.08%	-0.15%	0.07%
CMNH HTH 1062		4154.501	4175.860	4147.749	4159.370	-0.12%	0.40%	-0.28%
CMNH HTH 1103		2310.804	2364.213	2341.504	2338.840	-1.20%	1.08%	0.11%
CMNH HTH 1152		4268.484	4294.864	4308.041	4290.463	-0.51%	0.10%	0.41%
CMNH HTH 1208		2555.197	2458.956	2506.258	2506.804	1.93%	-1.91%	-0.02%
CMNH HTH 1214		2343.618	2327.951	2365.522	2345.697	-0.09%	-0.76%	0.85%
CMNH HTH 1270		2680.887	2660.390	2679.478	2673.585	0.27%	-0.49%	0.22%
CMNH HTH 1313		4098.447	4094.405	4116.675	4103.176	-0.12%	-0.21%	0.33%
CMNH HTH 1345		3151.295	3145.291	3141.238	3145.941	0.17%	-0.02%	-0.15%
CMNH HTH 1361		3474.054	3428.035	3471.699	3457.929	0.47%	-0.86%	0.40%
CMNH HTH 1389		3541.909	3504.878	3565.987	3537.591	0.12%	-0.92%	0.80%
CMNH HTH 1415		2929.154	2931.946	2913.352	2924.817	0.15%	0.24%	-0.39%
CMNH HTH 1419		3423.776	3450.980	3413.627	3429.461	-0.17%	0.63%	-0.46%
CMNH HTH 1427		2813.915	2831.950	2798.842	2814.902	-0.04%	0.61%	-0.57%
CMNH HTH 1534		3033.834	3089.670	3048.930	3057.478	-0.77%	1.05%	-0.28%
CMNH HTH 1539		2892.073	2845.291	2846.840	2861.401	1.07%	-0.56%	-0.51%
CMNH HTH 1709		2717.651	2746.922	2774.589	2746.387	-1.05%	0.02%	1.03%
CMNH HTH 1748		2689.790	2767.101	2755.216	2737.369	-1.74%	1.09%	0.65%
CMNH HTH 1778		3662.726	3692.966	3686.873	3680.855	-0.49%	0.33%	0.16%
CMNH HTH 1903		4206.056	4245.536	4182.454	4211.349	-0.13%	0.81%	-0.69%
CMNH HTH 1961		3009.904	2967.545	3060.578	3012.676	-0.09%	-1.50%	1.59%

Table 6: Measurements of Distal Femur of *Homo sapiens*

Specimen	Area (sq. mm)	Area (sq. mm)	Area (sq. mm)	Mean Measurement	% Error 1	% Error 2	% Error 3
CMNH HTH 0290	1754.336	1720.763	1733.446	1736.182	1.05%	-0.89%	-0.16%
CMNH HTH 0524	1725.005	1719.337	1722.922	1722.421	0.15%	-0.18%	0.03%
CMNH HTH 0538	1872.074	1876.289	1869.620	1872.661	-0.03%	0.19%	-0.16%
CMNH HTH 0561	1200.688	1171.858	1182.409	1184.985	1.33%	-1.11%	-0.22%
CMNH HTH 0594	1962.399	1957.862	1957.328	1959.196	0.16%	-0.07%	-0.10%
CMNH HTH 0596	1696.944	1674.245	1665.393	1678.861	1.08%	-0.27%	-0.80%
CMNH HTH 0598	1591.711	1585.611	1571.462	1582.928	0.55%	0.17%	-0.72%

CMNH HTH 0657	1089.107	1094.612	1084.384	1089.368	-0.02%	0.48%	-0.46%
CMNH HTH 0658	1983.238	1981.663	1971.842	1978.914	0.22%	0.14%	-0.36%
CMNH HTH 0666	1922.101	1878.902	1867.691	1889.565	1.72%	-0.56%	-1.16%
CMNH HTH 0704	1210.569	1198.826	1199.319	1202.905	0.64%	-0.34%	-0.30%
CMNH HTH 0814	1465.308	1455.282	1453.954	1458.181	0.49%	-0.20%	-0.29%
CMNH HTH 1062	1929.217	1903.464	1898.783	1910.488	0.98%	-0.37%	-0.61%
CMNH HTH 1103	1228.790	1216.076	1219.144	1221.337	0.61%	-0.43%	-0.18%
CMNH HTH 1152	2111.475	2100.760	2108.461	2106.899	0.22%	-0.29%	0.07%
CMNH HTH 1208	1256.384	1251.451	1249.495	1252.443	0.31%	-0.08%	-0.24%
CMNH HTH 1214	1097.837	1109.923	1108.745	1105.502	-0.69%	0.40%	0.29%
CMNH HTH 1270	1098.283	1093.203	1097.264	1096.250	0.19%	-0.28%	0.09%
CMNH HTH 1313	1975.910	1967.537	1977.122	1973.523	0.12%	-0.30%	0.18%
CMNH HTH 1345	1449.661	1451.129	1452.291	1451.027	-0.09%	0.01%	0.09%
CMNH HTH 1361	1804.221	1796.220	1801.769	1800.737	0.19%	-0.25%	0.06%
CMNH HTH 1389	1751.875	1754.055	1751.052	1752.327	-0.03%	0.10%	-0.07%
CMNH HTH 1415	1274.207	1272.328	1264.629	1270.388	0.30%	0.15%	-0.45%
CMNH HTH 1419	1573.135	1562.296	1591.700	1575.710	-0.16%	-0.85%	1.01%
CMNH HTH 1427	1395.315	1393.782	1398.161	1395.753	-0.03%	-0.14%	0.17%
CMNH HTH 1534	1279.460	1279.821	1277.207	1278.829	0.05%	0.08%	-0.13%
CMNH HTH 1539	1342.370	1328.717	1352.920	1341.336	0.08%	-0.94%	0.86%
CMNH HTH 1709	1151.464	1151.241	1164.632	1155.779	-0.37%	-0.39%	0.77%
CMNH HTH 1748	1295.404	1291.034	1287.149	1291.196	0.33%	-0.01%	-0.31%
CMNH HTH 1778	1613.167	1644.610	1646.611	1634.796	-1.32%	0.60%	0.72%
CMNH HTH 1903	2203.022	2191.412	2210.054	2201.496	0.07%	-0.46%	0.39%
CMNH HTH 1961	1408.329	1390.494	1413.071	1403.965	0.31%	-0.96%	0.65%

Table 7: Measurements of Proximal Humerus for *Homo sapiens*

Specimen	Ver.	Area (sq. mm)	Area (sq. mm)	Area (sq. mm)	Mean Measurement	% Error 1	% Error 2	% Error 3
CMNH HTH 0290		919.223	922.049	923.511	921.594	-0.26%	0.05%	0.21%
CMNH HTH 0524	1	981.988	979.065	989.177	983.410	-0.14%	-0.44%	0.59%
CMNH HTH 0524	2	964.211	959.772	967.049	963.677	0.06%	-0.41%	0.35%
CMNH HTH 0538		907.152	920.029	910.427	912.536	-0.59%	0.82%	-0.23%
CMNH HTH 0561		611.178	616.606	616.493	614.759	-0.58%	0.30%	0.28%
CMNH HTH 0594		991.373	990.193	989.953	990.506	0.09%	-0.03%	-0.06%
CMNH HTH 0596		940.202	951.061	948.694	946.652	-0.68%	0.47%	0.22%
CMNH HTH 0598		979.544	978.415	977.783	978.581	0.10%	-0.02%	-0.08%
CMNH HTH 0657		649.799	646.753	650.253	648.935	0.13%	-0.34%	0.20%
CMNH HTH 0658		1071.332	1072.214	1074.862	1072.803	-0.14%	-0.05%	0.19%
CMNH HTH 0666		978.533	954.247	945.018	959.266	2.01%	-0.52%	-1.49%
CMNH HTH 0704		685.773	686.063	680.596	684.144	0.24%	0.28%	-0.52%
CMNH HTH 0814		839.659	852.134	840.536	844.110	-0.53%	0.95%	-0.42%
CMNH HTH 1062		1037.868	1028.196	1027.770	1031.278	0.64%	-0.30%	-0.34%
CMNH HTH 1103		605.238	610.457	616.626	610.774	-0.91%	-0.05%	0.96%
CMNH HTH 1152		1181.875	1194.385	1181.970	1186.077	-0.35%	0.70%	-0.35%
CMNH HTH 1208		652.353	641.159	647.471	646.994	0.83%	-0.90%	0.07%
CMNH HTH 1214		555.241	548.972	548.273	550.829	0.80%	-0.34%	-0.46%

CMNH HTH 1270		604.972	604.087	600.491	603.183	0.30%	0.15%	-0.45%
CMNH HTH 1313		1065.312	1051.647	1054.358	1057.106	0.78%	-0.52%	-0.26%
CMNH HTH 1345		802.438	799.563	795.274	799.092	0.42%	0.06%	-0.48%
CMNH HTH 1361		968.423	953.498	951.075	957.665	1.12%	-0.44%	-0.69%
CMNH HTH 1389		963.700	983.816	983.500	977.005	-1.36%	0.70%	0.66%
CMNH HTH 1415		688.927	688.169	688.417	688.504	0.06%	-0.05%	-0.01%
CMNH HTH 1419		919.072	905.256	912.307	912.212	0.75%	-0.76%	0.01%
CMNH HTH 1427		834.18	834.927	832.202	833.770	0.05%	0.14%	-0.19%
CMNH HTH 1534		655.986	645.818	661.461	654.422	0.24%	-1.31%	1.08%
CMNH HTH 1539	1	762.924	769.769	769.288	767.327	-0.57%	0.32%	0.26%
CMNH HTH 1539	2	789.818	774.006	774.166	779.330	1.35%	-0.68%	-0.66%
CMNH HTH 1709		686.104	697.098	686.408	689.870	-0.55%	1.05%	-0.50%
CMNH HTH 1748		772.005	775.341	766.337	771.228	0.10%	0.53%	-0.63%
CMNH HTH 1778		916.094	925.154	925.439	922.229	-0.67%	0.32%	0.35%
CMNH HTH 1903		1123.451	1130.087	1101.552	1118.363	0.45%	1.05%	-1.50%
CMNH HTH 1961		757.436	764.162	761.250	760.949	-0.46%	0.42%	0.04%

Table 8: Measurements of the Distal Humerus of *Homo sapiens*

Name	HP	FP	LOG HP	LOG FP	log (HP/FP)
Pan Paniscus MRAC 13202	1033.411	729.192	3.014	2.863	0.151
Pan Paniscus MRAC 15293	1021.326	760.894	3.009	2.881	0.128
Pan Paniscus MRAC 15294	993.516	764.738	2.997	2.884	0.114
Pan Paniscus MRAC 15295	1024.024	735.925	3.010	2.867	0.143
Pan Paniscus MRAC 15296	1123.603	902.437	3.051	2.955	0.095
Pan Paniscus MRAC 27696	1098.31	855.375	3.041	2.932	0.109
Pan Paniscus MRAC 27698	937.664	727.92	2.972	2.862	0.110
Pan Paniscus MRAC 29035	1014.672	737.478	3.006	2.868	0.139
Pan Paniscus MRAC 29040	1211.992	886.331	3.084	2.948	0.136
Pan Paniscus MRAC 29042	947.24	726.901	2.976	2.861	0.114
Pan Paniscus MRAC 29044	1053.043	709.633	3.022	2.851	0.171
Pan Paniscus MRAC 29045	1146.052	772.865	3.059	2.888	0.171
Pan Paniscus MRAC 29047	1102.506	943.694	3.042	2.974	0.067
Pan Paniscus MRAC 29051	895.257	628.733	2.951	2.798	0.153
Pan Paniscus MRAC 29052	1001.352	758.046	3.000	2.879	0.120
Pan Paniscus MRAC 29053	800.603	674.408	2.903	2.828	0.074
Pan Paniscus MRAC 29054	888.223	731.954	2.948	2.864	0.084
Pan Paniscus MRAC 29057	765.776	658.855	2.884	2.818	0.065
Pan Paniscus MRAC 29060	882.347	632.155	2.945	2.800	0.144
Pan Paniscus MRAC 29063	1084.766	738.411	3.035	2.868	0.167

Table 9: Log and Log Ratios for Proximal Surfaces of *Pan paniscus*

Name	HP	FP	Log HP	Log FP	Log (HP/FP)
Homo sapiens CMNH HTH 0290 FP	1736.182	2090.593	3.239	3.320	-0.080
Homo sapiens CMNH HTH 0524 FP	1722.421	1943.816	3.236	3.288	-0.052
Homo sapiens CMNH HTH 0538 FP	1872.661	1874.367	3.272	3.272	0.000
Homo sapiens CMNH HTH 0561 FP	1184.985	1303.168	3.073	3.115	-0.041
Homo sapiens CMNH HTH 0594 FP	1959.196	1958.74	3.292	3.291	0.000
Homo sapiens CMNH HTH 0596 FP	1678.861	1844.536	3.225	3.265	-0.04
Homo sapiens CMNH HTH 0598 FP	1582.928	1797.451	3.199	3.254	-0.055
Homo sapiens CMNH HTH 0657 FP	1089.368	1330.023	3.037	3.123	-0.086
Homo sapiens CMNH HTH 0658 FP	1978.914	2107.647	3.296	3.323	-0.027
Homo sapiens CMNH HTH 0666 FP	1889.565	2067.108	3.276	3.315	-0.039
Homo sapiens CMNH HTH 0704 FP	1202.905	1313.237	3.080	3.118	-0.038
Homo sapiens CMNH HTH 0814 FP	1458.181	1552.337	3.163	3.190	-0.027
Homo sapiens CMNH HTH 1062 FP	1910.488	2137.535	3.281	3.329	-0.048
Homo sapiens CMNH HTH 1103 FP	1221.337	1190.755	3.086	3.075	0.011
Homo sapiens CMNH HTH 1152 FP	2106.899	2391.253	3.323	3.378	-0.054
Homo sapiens CMNH HTH 1208 FP	1252.443	1360.178	3.097	3.133	-0.035
Homo sapiens CMNH HTH 1214 FP	1105.502	1086.819	3.04	3.036	0.007
Homo sapiens CMNH HTH 1270 FP	1096.250	1431.831	3.03	3.155	-0.115
Homo sapiens CMNH HTH 1313 FP	1973.523	2413.936	3.295	3.382	-0.087
Homo sapiens CMNH HTH 1345 FP	1451.027	1660.967	3.161	3.220	-0.058
Homo sapiens CMNH HTH 1361 FP	1800.737	1761.411	3.25	3.245	0.009
Homo sapiens CMNH HTH 1389 FP	1752.327	1994.742	3.243	3.299	-0.056
Homo sapiens CMNH HTH 1415 FP	1270.388	1426.038	3.103	3.154	-0.050
Homo sapiens CMNH HTH 1419 FP	1575.710	1739.186	3.197	3.240	-0.042
Homo sapiens CMNH HTH 1427 FP	1395.753	1650.932	3.144	3.217	-0.072
Homo sapiens CMNH HTH 1534 FP	1278.829	1459.044	3.106	3.164	-0.057
Homo sapiens CMNH HTH 1539 FP	1341.336	1559.257	3.127	3.192	-0.068
Homo sapiens CMNH HTH 1709 FP	1155.779	1268.928	3.062	3.103	-0.040
Homo sapiens CMNH HTH 1748 FP	1291.196	1384.863	3.110	3.141	-0.030
Homo sapiens CMNH HTH 1778 FP	1634.796	1938.762	3.213	3.287	-0.074
Homo sapiens CMNH HTH 1903 FP	2201.496	2438.77	3.342	3.387	-0.044
Homo sapiens CMNH HTH 1961 FP	1403.965	1440.115	3.147	3.158	-0.011

Table 10: Log and Log Ratios for Proximal Surfaces of *Homo sapiens*

Name	HD	FD	Log HD	LOG FD	log (HD/FD)
Pan Paniscus MRAC 13202	766.864	1634.767	2.884718	3.213456	-0.32874
Pan Paniscus MRAC 15293	695.147	1373.79	2.842077	3.13792	-0.29584
Pan Paniscus MRAC 15294	703.423	1370.873	2.847217	3.136997	-0.28978
Pan Paniscus MRAC 15295	758.445	1195.481	2.879924	3.077543	-0.19762
Pan Paniscus MRAC 15296	722.984	1398.134	2.859129	3.145549	-0.28642
Pan Paniscus MRAC 27696	729.65	1363.146	2.863115	3.134542	-0.27143
Pan Paniscus MRAC 27698	618.379	1146.836	2.791255	3.059501	-0.26825
Pan Paniscus MRAC 29035	636.649	1095.077	2.8039	3.039445	-0.23554
Pan Paniscus MRAC 29040	706.536	1366.071	2.849134	3.135473	-0.28634
Pan Paniscus MRAC 29042	636.95	1230.637	2.804105	3.09013	-0.28602

Pan Paniscus MRAC 29044	636.561	1238.856	2.80384	3.093021	-0.28918
Pan Paniscus MRAC 29045	690.236	1293.573	2.838998	3.111791	-0.27279
Pan Paniscus MRAC 29047	901.438	1476.639	2.954936	3.169274	-0.21434
Pan Paniscus MRAC 29048	297.508	565.5	2.473499	2.752433	-0.27893
Pan Paniscus MRAC 29051	637.134	1069.819	2.804231	3.02931	-0.22508
Pan Paniscus MRAC 29052	700.29	1238.326	2.845278	3.092835	-0.24756
Pan Paniscus MRAC 29053	598.636	1008.694	2.777163	3.003759	-0.2266
Pan Paniscus MRAC 29054	680.464	1207.211	2.832805	3.081783	-0.24898
Pan Paniscus MRAC 29056	409.586	767.591	2.612345	2.88513	-0.27278
Pan Paniscus MRAC 29057	589.801	905.533	2.770706	2.956904	-0.1862
Pan Paniscus MRAC 29058	385.105	750.606	2.585579	2.875412	-0.28983
Pan Paniscus MRAC 29060	513.467	1099.283	2.710513	3.04111	-0.3306
Pan Paniscus MRAC 29063	733.927	1246.851	2.865653	3.095815	-0.23016

Table 11: Log and Log Ratios for Distal Surfaces of *Pan paniscus*

Name	HD	FD	Log HD	Log FD	log (HD/FD)
Homo sapiens CMNH HTH 0290 FD	921.594	3509.789	2.964	3.545	-0.580
Homo sapiens CMNH HTH 0524 FD	983.41	3737.717	2.992	3.572	-0.579
Homo sapiens CMNH HTH 0538 FD	912.536	3737.703	2.960	3.572	-0.612
Homo sapiens CMNH HTH 0561 FD	614.759	2594.228	2.788	3.414	-0.625
Homo sapiens CMNH HTH 0594 FD	990.506	3954.149	2.995	3.597	-0.601
Homo sapiens CMNH HTH 0596 FD	946.652	3474.7	2.976	3.540	-0.564
Homo sapiens CMNH HTH 0598 FD	978.581	3158.351	2.990	3.497	-0.508
Homo sapiens CMNH HTH 0657 FD	648.935	2515.969	2.812	3.400	-0.588
Homo sapiens CMNH HTH 0658 FD	1072.803	4006.88	3.030	3.602	-0.572
Homo sapiens CMNH HTH 0666 FD	959.266	3555.766	2.981	3.550	-0.568
Homo sapiens CMNH HTH 0704 FD	684.144	2486.194	2.831	3.395	-0.560
Homo sapiens CMNH HTH 0814 FD	844.11	3332.468	2.926	3.522	-0.596
Homo sapiens CMNH HTH 1062 FD	1031.278	4159.37	3.013	3.619	-0.605
Homo sapiens CMNH HTH 1103 FD	610.774	2338.84	2.785	3.369	-0.583
Homo sapiens CMNH HTH 1152 FD	1186.077	4290.463	3.074	3.632	-0.558
Homo sapiens CMNH HTH 1208 FD	646.994	2506.804	2.810	3.399	-0.588
Homo sapiens CMNH HTH 1214 FD	550.829	2345.697	2.741	3.370	-0.629
Homo sapiens CMNH HTH 1270 FD	603.183	2673.585	2.780	3.427	-0.646
Homo sapiens CMNH HTH 1313 FD	1057.106	4103.176	3.024	3.613	-0.589
Homo sapiens CMNH HTH 1345 FD	799.092	3145.941	2.902	3.497	-0.595
Homo sapiens CMNH HTH 1361 FD	957.665	3457.929	2.981	3.538	-0.557
Homo sapiens CMNH HTH 1389 FD	977.005	3537.591	2.989	3.548	-0.558
Homo sapiens CMNH HTH 1415 FD	688.504	2924.817	2.837	3.466	-0.628
Homo sapiens CMNH HTH 1419 FD	912.212	3429.461	2.960	3.535	-0.575
Homo sapiens CMNH HTH 1427 FD	833.77	2814.902	2.921	3.449	-0.528
Homo sapiens CMNH HTH 1534 FD	654.422	3057.478	2.815	3.485	-0.669
Homo sapiens CMNH HTH 1539 FD	767.327	2861.401	2.884	3.456	-0.571
Homo sapiens CMNH HTH 1709 FD	689.87	2746.387	2.838	3.438	-0.599
Homo sapiens CMNH HTH 1748 FD	771.228	2737.369	2.887	3.437	-0.550
Homo sapiens CMNH HTH 1778 FD	922.229	3680.855	2.964	3.565	-0.601

Homo sapiens CMNH HTH 1903 FD	1118.363	4211.349	3.048	3.624	-0.575
Homo sapiens CMNH HTH 1961 FD	760.949	3012.676	2.881	3.478	-0.597

Table 12: Log and Log Ratios for Distal Surfaces of *Homo sapiens*

t-Test: Two-Sample Assuming Equal Variances		
	Pan paniscus ratio	*Homo sapiens ratio*
Mean	0.122	-0.0440
Variance	0.001	0.00089
Observations	20	32
Pooled Variance	0.0010	
Hypothesized Mean Difference	0	
df	50	
t Stat	18.7197	
P(T<=t) one-tail	<0.001	
t Critical one-tail	1.6759	
P(T<=t) two-tail	<0.001	
t Critical two-tail	2.009	

Table 13: T-Test Table for Proximal Surfaces of *Pan paniscus and Homo sapiens*

t-Test: Two-Sample Assuming Equal Variances		
	Pan paniscus ratio	*Homo sapiens ratio*
Mean	-0.2609	-0.5865
Variance	0.0016	0.0011
Observations	20	32
Pooled Variance	0.0013	
Hypothesized Mean Difference	0	
df	50	
t Stat	32.0492	
P(T<=t) one-tail	<0.001	
t Critical one-tail	1.6760	
P(T<=t) two-tail	<0.001	
t Critical two-tail	2.009	

Table 14: T-Test Table for Distal Surfaces of *Pan paniscus and Homo sapiens*