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**Estimating load distribution across the radius and ulna in humans and non-
human primates**

A Thesis Presented

by

Molly Elmer

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Abstract of the Thesis

Estimating load distribution across the radius and ulna in humans and non-human primates

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The hominoid wrist joint has changed substantially during the course of primate evolution. One of these changes is the retraction of the ulna from direct contact with the carpals and the insertion of a triangular fibrocartilaginous disc. This change permits a greater degree of mobility at the wrist in apes and is functionally linked to suspensory behaviors. However, the implications of this more mobile wrist joint on how loads are distributed from the hand to the forearm across the wrist joint remains unclear. The goal of this study is to investigate forearm loading by estimating how loads may be distributed into and between the radius and ulna in primates that have different wrist joints morphologies (i.e., with and without ulnar-carpal contact). Cortical area was used as a proxy to estimate stress in several points throughout the length of the radius and ulna in both humans and non-human primates. Results indicate that although significant differences are found in the cortical area distribution of gibbons and humans, great apes and monkeys do not differ in initial values or trends. This suggests that the more mobile wrist joint evolved by great apes as a consequence of fully retracting the ulna from the carpals may not have significant effects on how these groups are loading their forearms.

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Introduction

The morphology of the wrist joint in living apes and humans is unlike that of most other living and fossil primates (e.g. Lewis, 1965; 1969; 1972; Cartmill and Milton, 1977; Sarmiento, 1988). One anatomical specialization found in living hominoids is a reduced ulnar styloid process and the consequential lack of direct bony contact between the ulna and proximal row of carpals. This difference has received a lot attention from physical anthropologists and functional morphologists because it implies a much greater degree of mobility at the wrist which is necessary for the unique hand postures adopted by extant hominoids during brachiation and allows the power grips needed by humans when using tools (Lewis, 1971; O'Connor, 1975; Aiello and Dean, 2006).

The generalized mammalian condition demonstrates a wrist joint that contains a direct articulation between the distal end of the ulna and the triquetrum and pisiform bones (Lewis, 1965). The non-hominoid primate condition mimics this general mammalian pattern despite the variety of locomotor repertoires within primates (Lewis et al., 1970; Lewis, 1972). Within hominoids, there is variation in the degree of ulnar retraction and the development of an interposing meniscus between the ulna and carpals. Both the great apes (orangutans, chimpanzees, and gorillas) and humans show a marked reduction of the ulnar styloid process, but only African apes and humans demonstrate a fully developed fibrocartilaginous triangular disc interposed between the ulna and carpals (Lewis, 1965; Sarmiento, 1988). The lesser apes (gibbons and siamangs) possess a wrist joint morphology intermediate between that of great apes and monkeys with the ulnar styloid process articulating

with the triquetrum and an additional bony element called the os daubentonii, to the exclusion of the pisiform (Lewis, 1965; 1969; Sarmiento, 1988). Hence, this modification is not as derived as the morphology seen in the great apes (Sarmiento, 1988). These changes in wrist morphology throughout hominoid evolution have likely allowed for increased mobility at the wrist. Specifically, the removal of the ulna from direct articulation with the proximal row of carpals allows hominoids a greater range of wrist adduction and nearly double the range of pronation and supination, as compared to monkeys, which is argued to be necessary for true brachiation (Lewis, 1965; Tuttle, 1969a,b; Lewis et al., 1970; Lewis, 1971; 1972; Jouffroy and Medina, 2002; Moya-Sola et al., 2004; Richmond, 2006).

Although the comparative morphology of the hominoid wrist has been well documented, the possible functional consequences of forelimb loading associated with a more mobile wrist joint have yet to be investigated. It has been suggested that there may be a trade-off in joint structure between allowing mobility and resisting the loads that pass through it, with increased mobility accompanied by a decrease in strength (Swartz, 1989). Because there is no longer any direct bony contact between the ulna and carpals in the great apes and humans, the way in which loads (derived from ground reaction forces [GRF] acting at the supporting hand, joint reaction forces [JRF] arising from the contraction of muscles crossing the joints, etc.) are transferred to the radius and ulna through the wrist could vary from the loading pattern experienced by non-hominoid primates.

In order to understand how different wrist morphologies impact forearm loading in general, knowledge of how both the radius and ulna are loaded is needed.

Unfortunately, direct (i.e., *in vivo* experimental) studies of limb loading using bone strain gauges have typically been conducted on one long bone at a time whereas the simultaneous loading of multiple bones in a limb segment is not as well researched (e.g. Rabinowitz et al., 1993; Birkbeck et al., 1997; Markolf et al., 1998; Markolf et al., 2000). This is not surprising because strain gauge studies are highly invasive and may disrupt an animal's normal performance (see review in Demes, 1998). Accordingly, the results of studying only one bone individually in a distal limb segment is not sufficient because the way in which one bone is loaded may very well be dependent on the loading of the other.

One way that has been proposed to indicate how much force is transmitted through one bone in comparison to another is by quantitatively comparing relative joint surface area in a multi-bone joint complex. For example, the bone with the relatively larger surface area at a joint should experience a greater share of the force being transmitted through that joint (Swartz, 1989). In fact, Swartz (1989) quantified articular surface areas in both the proximal and distal radius and ulna in a large sample of primates and she found that relative joint surface areas of bones at the wrist and elbow joints differ among primate taxa. At the wrist joint, the distal radius of all primates has a larger articular surface area than its corresponding distal ulna. This similarity among primate wrists was not observed for the elbow. At the elbow joint, the proximal ulna of great apes has a larger articular surface area than the proximal radius, whereas in all other primates included in her study, the ulna had a relatively smaller joint surface area than its corresponding radius. Because it is expected that a greater surface area would help transfer a greater proportion of

stress through a bone, these differing patterns of joint surface area should be reflected in the transfer of load into and between the bones of the forearm, and ultimately into the humerus at the elbow joint. It could be predicted by joint size alone that a transfer of load must occur somewhere along the shafts of the radius and ulna as forces move proximally along the diaphyses of both bones in great apes. However, it is unknown if this prediction would remain the same if elements are completely removed from direct bony contact with one another at a joint, as in the hominoid wrist.

In the human bone biology literature, several studies have tested load distribution across the two bones of the forearm, but they have returned very contradictory results. The primary aim of these studies was to test how the interosseous membrane acts as a pathway for force transfer between the radius and ulna. These studies measured *in vitro* loading of cadaveric forearms using strain gauges to evaluate force transmission from the hand to the elbow. One study found that 70% of load is transmitted through the radius and only 30% through the ulna (Rabinowitz et al., 1994). Another found that the interosseous membrane played no role in weight transfer at all, with over 90% of the load transmitted directly through the radius from distal to proximal (Markolf et al., 2000). A study by Birkbeck et al. (1997) found that the interosseous membrane plays a large role in load distribution such that the majority of load was transmitted initially through the radius distally but the ulna proximally at the elbow. This last study indicates that at some point force was being transferred from the radius to the ulna via the membranous connection between the shafts of the bones. However, with these inconclusive results, neither

the loading regime of the forelimb in humans nor the role of the interosseous membrane in regulating load distribution can be understood with any certainty.

Another approach to estimate limb loading behavior is to quantify cortical bone area (CA). Because CA reflects a bone's ability to resist compressive and tensile forces and is thus an indirect measure of its strength (e.g., Demes and Jungers, 1993; Carter and Beaupre, 2001; Lieberman et al., 2004; Marchi and Borgognini-Tarli, 2004), CA can be used as a proxy to measure the relative amount of load a long bone experiences in an axial direction (Currey, 2006). The distribution of cortical bone between both bones of the forelimb is therefore a potential source of valuable information about how compressive and tensile forces are transmitted into and between the radius and ulna. Whether the radius or ulna will be disproportionately loaded in comparison to each other, and how exactly the morphology of the wrist joint could contribute to that unequal loading could therefore be estimated by comparing the ratio of cortical bone in the radius to the ulna.

The aim of this study was to use primates as a natural experiment to investigate load distribution in and between the radius and ulna in species with and without direct ulna-carpal contact. Specifically, cortical area distribution along the diaphyses of the radius and ulna was examined to detect differences in trends between different groups of primates with different wrist joint morphology. Several predictions were made. First, it was predicted that all primates will show more cortical area in the radius compared to the ulna in the distal end of the forearm near the wrist joint, and that this radius-to-ulna (R/U) cortical area proportion will decrease proximally towards the elbow in all taxa. Second, it was predicted that monkeys who

retain full ulna-carpal contact will have an absolutely lower R/U value when compared to great apes in the distal end of the forearm. In contrast, great apes and humans who have a retracted ulna will show larger R/U values distally. Gibbons with their intermediate wrist morphology will be intermediate in this measure at the distal end of the forearm. Third, it was predicted that gorillas and chimpanzees will show similar R/U patterns to orangutans because of similar wrist morphology and have similar patterns of articular surface areas both distally and proximally, even though they load their forelimbs differently during locomotion. Fourth, it was predicted that great apes and humans will have lower R/U values in the proximal end of the forearm compared to monkeys and gibbons because they have relatively larger articular surfaces in their proximal ulna compared to their proximal radius, whereas the opposite should be seen in gibbons and monkeys.

Methods

Comparative Sample

A radius and ulna from 29 non-human primate individuals were used in this study. The sample includes quadrupedal and suspensory great apes (*Gorilla*, *Pan*, and *Pongo*), suspensory lesser apes (*Hylobates*), and terrestrial and arboreal quadrupedal monkeys (*Papio* and *Nasalis*, respectively). The sample was borrowed from the American Museum of Natural History's Department of Mammalogy (New York, NY) and from the private collection of Dr. Randall L. Susman (Stony Brook, NY). Only non-pathological, wild-shot specimens with fully-fused epiphyses were included in this study. Human osteological material was obtained from the Norris

Farms #36 archaeological skeletal collection belonging to the Illinois State Museum and temporarily housed at Pennsylvania State University. Individuals (n=8) were non-pathological, adult males between the ages of 25 and 40 years old. All human remains were part of the Oneota population excavated from a late Prehistoric cemetery in the central Illinois River Valley dating to about 1300 AD (Ryan and Krovitz, 2006) (Table 1).

CT scanning procedure

To assess cortical bone area throughout the length of both bones, computer-assisted tomography (CT) scans were taken of each set of radii and ulnae. All scans of the non-human primate material were taken on a GE LightSpeed VCT scanner located in the Department of Radiology, Stony Brook University Medical Center (Stony Brook, NY). Serial cross-sections were taken with a minimum possible field of view (FOV) with a slice thickness of 0.625 mm. This resulted in a pixel resolution of 5.333 pixels/mm and between 350 and 657 slices per specimen depending on the size and length of the bones. Other relevant scanning parameters include a kV of 120, mA of 70, and scan time of 1 sec. Human specimens were scanned at the Center for Quantitative Imaging, Pennsylvania State University (State College, PA) using a Universal Medical Systems medical CT scanner. Serial cross-sections were taken with a minimum possible field of view (FOV) with a slice thickness of 1.0 mm. This resulted in a pixel resolution of 4.267 pixels/mm and between 250 and 300 slices per specimen depending on the size and length of the bones. Other relevant scanning parameters include a kV of 120, mA of 65, and scan time of 1 sec.

The paired radius and ulna from each individual were scanned together and were positioned in an articulated, supinated position (Fig. 1). This standard human anatomical position was used to create a repeatable set-up that is applicable for all taxa. Although the forearms of many primate species included in this study may be loaded in a pronated position (e.g., quadrupedal apes and monkeys), other taxa such as the suspensory apes and bipedal humans, may not have a typical forearm orientation when loaded, and thus it is unclear at this time if there is an ideal orientation to measure cortical area. Since this study is investigating only cortical bone area present in the radius and ulna at different cross-sectional levels, and not shape of cross-sections themselves (i.e., a measure reserved for assessing bending moments), it was preferred to set up the bones in a standardized, repeatable position prior to scanning (e.g., Ruff, 2002). Evaluating other cross-sectional geometric properties, such as second and principal moments of area, are only effective on bones that can be modeled as a cylindrical beam. Moreover, because of the large interosseous crest on the radii, and their high degree of curvature (Patel, 2005), these measures may be inappropriate for this study (e.g., Lieberman et al. 2004).

The posterior surfaces of the bones were laid on a foam block to create a level surface. Both the proximal and distal ends of each bone were pressed onto a piece of clay for stability. The two bones were adjusted in the clay so that they both lay on an equal plane parallel to the surface of the foam block. The bones were oriented so that the sagittal plane was positioned to create a line through the middle of both the proximal and distal articular surfaces of the ulna. The transverse plane

was positioned through the midpoint of the shafts of the articulated bones. The coronal plane was positioned parallel to the bones, midway through the depth of the ulnar shaft.

Measurement and Analysis

Seven slices throughout the diaphyses of the paired ulna and radius were selected and their cortical area (CA) was measured. The seven slices were at the following locations in the bones: 5, 20, 35, 50, 65, 80, and 95 percent of a bone length, which was determined specifically for the purposes of this study. The 5% slice corresponded to a distal point in the bones and 95% slice was the most proximal slice measured. Bone length was determined by starting distally in a plane through the middle of the articular surface of the distal ulna, perpendicular to the long axis of the bone (0%) and ending at a proximal plane that was at a level through the middle of the radial head, also perpendicular to the shaft of the bone (100%) (Fig. 1). Because of variable lengths of the radius and ulna, it was preferable to use this biomechanical bone length over total length because it allowed for the comparison of slices in a similar plane in the articulated radius and ulna. All scans were reconstructed in Amira v5.2.0 software (Visage Imaging, Inc) using the isosurface function and the slices which corresponded to the selected distances were determined. Cortical area in each radial and ulnar slice was then measured in ImageJ v1.43u software using MomentMacroJ v1.3 (<http://www.hopkinsmedicine.org/fae/mmacro.htm>). Any trabecular bone, soft tissue remaining in the medullary cavity, and clay were erased if necessary before

measurement. The CA in the radius was divided by that of the ulna to create a proportion (R/U) at each distance. The R/U ratios were calculated for all slices for all individuals in the comparative sample.

To view the overall trends in R/U values from the distal to proximal ends of the forearm, a line graph was created displaying the mean values for each taxon across all slice locations. A second line graph was created which displayed the mean R/U values across all slice locations when individuals were grouped into monkeys (n=12), great apes (n=12), gibbons (n=5), and humans (n=8). In these graphs, a horizontal line equal to 1.0 was added to illustrate the point at which CA in the radius and ulna were equal (i.e., R/U of 1.0). Values above this line indicate that the radius had a greater proportion of CA than the ulna and with the opposite being true for values below the line.

In order to assess general overall patterns within each slice location along the length of the forearm, box-and-whiskers plots were generated displaying R/U values for each of the four groups at each distance. To test for significant differences between each group at each slice, non-parametric comparison of means tests were performed. Only non-parametric comparisons were performed because of small sample sizes and homogeneity of variance for this data of each group could not be assumed. First, Kruskal-Wallis tests were performed at each distance comparing all groups against one another. This test works well with small samples sizes (as low as n=5) down to a significance level of $\alpha=0.05$. (Sokal and Rohlf, 1995). If the Kruskal-Wallis tests returned significant values, a post-hoc Games-Howell test was performed to determine which groups were significantly different from one another.

This is a non-parametric test for pairwise comparisons and is effective with small and unequal sample sizes (Seaman et al., 1991). To keep the test-wide error rate at 0.05 in the all the pairwise comparison tests, all p-values were adjusted using the Bonferroni-Holm correction (Holm, 1979). All box-and-whiskers plots were created and all significance tests were performed using SPSS v. 14.0 (SPSS, Inc).

To test for differences within the great apes who have similar wrist morphology but load their forelimbs differently, gorillas and chimps were compared against orangutans. A line graph was generated using mean R/U values across all slices. Box-and-whisker plots were generated to make comparisons between the two groups at each distance.

An ordinary least squares (OLS) regression was performed to assess the relationship between slice location (independent variable) and R/U ratio (dependent variable). This was done using the values from all distances and then done a second time removing the R/U values at 5%. An analysis was then done to test for similar slopes across groups. Because the slopes in both tests were found to be significantly different from one another, a post-hoc multiple comparison of slopes among groups was conducted. Both tests were performed using SMATR: Standardized Major Axis Tests and Routines v. 2.0 (Falster, 2006). A scatter plot was produced to better visualize comparisons among all individuals across groups using SPSS v. 14.0 (SPSS, Inc). A line of best fit was added onto each group for visual comparison of trends across groups.

Error/Repeatability Study

Two separate tests were conducted to test for repeatability of the protocol and potential measurement error. The first was done to test for consistent alignment of the two bones prior to CT scanning and repeatable slice selection. A wild-shot adult male *Theropithecus gelada* specimen (n=1) was scanned five times on five separate days over five weeks to test for repeatability of set-up during scans. This individual was not included in the formal study. The specimen was borrowed from the Department of Anatomical Sciences' Museum of Anatomy at Stony Brook University (Stony Brook, NY). The slices for all five sets of scans were selected and measured following the methods outlined above. A second study was done to test for the implications of imprecision of slice selection and its impact on CA measurements. One *Pongo pygmaeus* individual (AMNH 200898) was reanalyzed using different slices that represented an increase and decrease of 2% from the original slice selected (e.g., 3% and 7% vs. 5%; 48% and 52% vs. 50%). This orangutan individual was chosen because it had the longest forearm bones in our comparative sample, meaning that a 2% change accounts for the greatest absolute change in slice number. Measurement errors were calculated following the method described by White and Folkiens (2005).

Results

Error/Repeatability Study

The study test for repeatability of alignment during scanning and slice selection returned an average measurement error across all slices of 4.9% and 3.5%

for the radius and ulna, respectively. We deemed this to be acceptable to continue with the study. The second test for error involved altering the original slice selections by two-percent of bone length in both distal and proximal directions. Average difference in CA was 4.7% and 5.1% for the radius and ulna respectively. For the radius, most of this difference was located in the most distal slice where the radius rapidly increases in size. Not surprisingly, for the ulna, the largest difference in CA was found in the proximal end where it becomes larger to articulate with the humerus. These findings indicate that any selection error of slice location affects measures of CA the most towards the ends of the bones, but not in the diaphyses. However, even when these larger differences at the ends are accounted for, average error is still within an acceptable limit. Moreover, these two error studies demonstrate that the CT scanning set-up and slice selection are consistent.

Cortical area analyses

All primate taxa in this study show a decrease in R/U cortical area values from distal to proximal (Fig. 2). The horizontal black line on each graph in Figure 2 represents the point at which CA in the radius and ulna are equal (i.e., R/U is equal to 1.0). Above this line, the radius has a greater CA than the ulna and below this line the opposite is true. What is seen in both graphs, but more clearly when comparing groups (Fig. 2b), is that gibbons, great apes and humans cross this line between the 50% and 65% slice locations indicating that at a point just proximal to midshaft these groups have shifted from having a greater proportion of CA in the radius to having more CA in the ulna. The monkeys cross the 1.0 threshold at a

distance closer to 80% indicating that CA is always greater in the radius compared to the ulna except in the most proximal region of the forearm. Although the two species of monkeys included do show slightly different patterns in the R/U values (Fig. 2a), they were combined together to form a common group mean for the rest of the statistical tests included in this study.

Results for non-parametric statistical tests comparing R/U ratios between different groups at all slice locations are summarized in Table 3 and Figure 3. Only at the 5% slice location do the gibbons have a significantly higher R/U ratio compared to all other taxa. For all other slice locations, the monkeys are significantly different by having larger R/U values compared to the hominoids.

Despite differences in how great ape forearms are loaded, a line graph showing only the African apes (collectively) and orangutans (Fig. 5) displays similar trends in R/U ratios from distal to proximal. Furthermore, box-and-whisker plots comparing African apes with orangutans show both groups overlapping in R/U values at each slice distance (Fig. 6). However, these visual assessments could not be supported with statistical significance because the sample size of orangutans was too small ($n=2$).

Regressions were performed to test for the relationship between slice location (independent variable) and R/U ratio (dependent variable) within each group. These regressions were performed using the data points for all individuals within a group across all distances. The relationship between slice location and R/U ratio was significant for each group (Table 4a). For all groups, the slopes were negative indicating that R/U decreases from distal to proximal (Table 4a). Because

regressions were significant, a test for homogeneity of group slopes was conducted (Table 4b). A p-value ($p=0.002$) lower than the critical value ($p=0.05$) indicates that the group slopes are heterogenous. To identify which slopes were different from one another, a post-hoc multiple comparison of slopes among groups was conducted (Table 4c). These results indicated that the slope of the humans was significantly different from all others and, additionally, the slope of the gibbons was significantly different from the great apes. The slopes of monkeys and great apes were not different from one another, nor was the slope of gibbons when compared to monkeys. A scatter plot including R/U values for all individuals with best fit lines fitted at group level was created to visually assess these slopes among groups (Fig. 4a).

Regressions were also performed testing distance (dependent variable) against R/U ratio (independent variable) within each group but with the R/U values at the 5% distance removed from the data set. The relationships were again significant for all groups (Table 5a). Because regressions were significant, a test for homogeneity of group slopes was conducted (Table 5b). This test returned a significant p value ($p = 0.001$) indicating group slopes were heterogenous. A post-hoc multiple comparison was conducted to identify which groups were differing from which others (Table 5c). This test indicated that the slope of the monkey groups was significantly different from all others. The slope of the human group was also significantly different from the great ape group. With the 5% slices removed, gibbons were no longer significantly different from the great apes.

Discussion

The greater range of motion allowed by the hominoid wrist is due in part to morphological changes in which a direct ulna-carpal contact has been reduced. This contrasts the condition seen in monkeys that exhibit the generalized mammalian condition. As a result, it is likely that the two bones that make up the forearm (i.e., radius and ulna) in hominoids may experience loading conditions that differ at the wrist joint, and consequently at the elbow joint (i.e., differences in distal vs. proximal load distribution) when compared to non-hominoid primates. Despite this possibility, actual magnitudes of loading of the forearm at the wrist and subsequently within the forearm are not well understood in any primate taxon because of the highly invasive nature to acquire true values of limb loading (e.g., from bone strain gauges).

If joint surface area is correlated with the amount of load a particular bone experiences, it would be expected that a greater proportion of the force traveling across a joint with multiple bony elements takes place in the larger one. At the wrist joint where forces can be transferred from the carpals into the radius and/or ulna, it is most likely that the radius bears most of the load because the distal radius is always larger in surface area compared to the distal ulna in primates (Swartz, 1989). This would be expected to be even further exaggerated in species that possess an ulna that is completely removed from the wrist joint, as is the case in humans, great apes, and to some extent, gibbons. Using cortical area (CA) as a proxy for bone strength, it was found that all primate taxa examined here do in fact show that the proportion of CA in the radius relative to the ulna is greater in the distal half of the forearm (i.e. R/U ratio greater than 1.0). These results supported the first prediction.

In contrast to this original prediction, however, great apes and humans that lack a direct ulna-carpal articulation did not have a significantly larger R/U ratio compared to monkeys (or gibbons) in the proximal half of the forearm. Thus it appears that wrist joint loading in all taxa may be similar despite the fundamental morphological differences between hominoids and non-hominoids.

Swartz (1989) found that monkeys and gibbons have a relatively larger articular surface area in the proximal radius compared to the corresponding proximal ulna. Accordingly, it was predicted that R/U ratios should be larger in monkeys and gibbons in the proximal half the forearm compared to great apes and humans. This, however, was not observed (Table 3, Fig. 2). These results suggest that the ulna, and not the radius, may distribute more of the load across the elbow joint in all primates. If this is true, then it contrasts Swartz's (1989) findings. In her measure of articular surface area of the proximal radius, she included the part of the head that articulates with the proximal ulna and suggested that this region would also help distribute forces across the elbow joint. The results of this study indicate that this may not be true and that it is the ulna that has a larger functional surface area at the elbow in terms of load transmission.

Although no specific predictions were made about the exact nature of the relationship between CA and slice location in the forearm, several interesting differences were observed between the different primate groups. Humans show a unique trend in R/U proportion throughout the two forearm bones from distal to proximal. Although their initial R/U ratio at the 5% slice location is not different from great apes or monkeys, the slope of their OLS regression line is significantly lower

than those of all non-human primates examined here when all distances are included. This is not unexpected because humans do not habitually load their forearms during locomotion and should therefore be expected to demonstrate a different pattern of CA distribution between the radius and ulna than any other species whose forelimbs are regularly being loaded in either compression and/or tension during locomotion.

A prediction was made about possible differences between R/U patterns in African apes and orangutans because of the different ways they may be loading their forelimbs. Although statistical significance was not assessed for differences between these groups because of the small sample sizes, their R/U values do not seem to differ when the data is assessed visually (Figs. 5 and 6). This supports the prediction that these two groups with similar wrist morphology may not differ from one another in spite of different ways of loading their forearms.

Although gibbons were predicted to be intermediate to great apes and monkeys in initial R/U values because of their intermediate wrist morphology, this was not observed. The high value initially found in gibbons and the significantly higher slope value they show when compared to monkeys and humans could be associated with the way in which their forearm is loaded, but this is unlikely since even when they brachiate their forearms are loaded in net compression (Swartz et al., 1989). Rather, it is possible that the high initial R/U value is a consequence of the expansion of the distal radius in comparison to the extremely slender diaphyses of the radius and ulna in gibbons. Because the radius expands distally at the radiocarpal joint, the amount of that expansion when compared to the shaft of the

radius could be driving the extremely high cortical area. Also, because the length of the diaphyses in comparison to the length of the distal and proximal ends may be skewing this initial value. What corresponds to 5% region in the gibbon radius and ulna may be different from that same location in another species that has shorter limbs (see Fig. 1). However, both these potential explanations need further testing to investigate if the high initial proportion and odd pattern is explained by differential loading of the bones or is potentially just consequence of the gracile and elongated morphology of their forearm bones.

On a similar note, when slope values of the regressions are compared (Table 4a), gibbons do show the largest negative slopes, followed by monkeys, great apes, and humans, respectively. This may suggest that forces transmitted from the radius to the ulna from a distal to proximal direction may occur more quickly in gibbons. However, because the R/U ratio crossing the 1.0 threshold did not differ from other hominoids (i.e., between 50% and 65%), it is likely that the large negative slope in gibbons is related to their very high R/U values at the 5% slice only. R/U values at the other slice locations are not significantly different among the hominoids (Table 3). The results of the second regression (Table 5), indicate that these differences in slope that were found in gibbons in the original regression may be driven by the 5% distance. When those values are removed, monkeys are found to be the group that differs from hominoids and gibbons are no longer different from the great apes. This may indicate that the initial loading of the bones of the forearm in gibbons is very different from great apes, but that the patterns are similar throughout the rest of the length of the bones.

An interesting observation in the results that was not expected is the patterns seen in R/U ratios between 35% and 65% of bone length. As noted above, it is seen in Figure 2b that the trend lines of gibbons, great apes, and humans separate from the line representing monkeys across these distances. The box-and-whiskers plots and statistical tests at these distances (Figs. 2c-e; Table 3) also confirm a separation of the higher R/U values of monkeys from those of the rest of the groups. Gibbons, great apes, and humans are not significantly different from one another at any of these slices. This distance range is also when the R/U values of the apes and humans drop below the line where R/U is equal to 1.0, indicating a greater proportion of cortical area is found in the ulna than in the radius. This implies that the monkey group is retaining a R/U value greater than one much further proximally than any of the other groups. However, why this would be the case is unclear. Although this pattern is clearly separating the groups based on wrist morphology, retaining a greater proportion of load in the radius after having similar initial values at the wrist does not seem to link to wrist morphology in any clear way. However, monkeys, especially *Papio*, have large interosseous crests on their radii. It may be that the presence of this crest is driving these high values. The other monkey species included (*Nasalis larvatus*) does not possess such extreme cresting of the radius and it has lower R/U values throughout bone length (Fig. 2a). Perhaps there is a mechanical reason related to weight support or muscle force that is concentrating more cortical area in the radius more proximally in monkeys than in apes. This pattern necessitates further investigation to explain the cortical area differences

seen along the shafts of the bones in monkeys and why a greater proportion would be retained in the radius more proximally than in other groups.

Although it was hypothesized that a loss of bony contact between the ulna and carpals would cause a greater proportion of load to be directed through the distal radius in hominoids, the results of this study demonstrate that there are no significant differences between CA ratios between the radius and ulna at the most distal end of the forearm among great apes and monkeys. Sarmiento (1988) suggests that with the addition of a true triangular disc, as seen in African apes and humans, the joint surface area between the ulna and carpals is actually increased and more weight can be transmitted than in a joint with true ulna-carpal contact. These results indicate that the fibrocartilaginous disc may indeed act as a mechanism for increased load transfer to the ulna in the great apes because, when compared to monkeys, they do show a slightly lower mean R/U value than monkeys distally, meaning that the cortical area in the radius is nearer to that of the ulna in great apes. However, statistical differences were not observed at 5% slice location between these groups (Table 3), so perhaps great apes are retaining a similar forearm loading pattern to monkeys even though they have drastic morphological differences at the wrist joint.

The results of this study suggest that the unusual morphology hominoids possess for increased mobility at the wrist may not alter how loads are experienced at this joint and how they are transferred into the bones of the forearm. Some authors have proposed that the hominoid wrist joint morphology is a unique functional compromise evolved by hominoids to enhance range of motion. Sarmiento

(1988) argued that the development of the true triangular articular disc that is found in African apes acts as a weight-bearing surface so that the ulna can support weight during pronation and supination. The more mobile joint of hominoid wrist has also been proposed as a compromise for large bodied hominoids who require a mobile wrist to climb and brachiate, but who also need to support their bodyweight on terrestrial substrates (Jouffroy and Medina, 2002). These viewpoints, and the results of this study, suggest that hominoids may have found a novel way to retain similar forelimb loading patterns to monkeys while evolving unique morphologies that permit more mobility at the wrist joint.

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Appendix

Table 1 Comparative sample

Species	Specimen No.	Wrist Morphology
<i>Nasalis lavartus</i>	AMNH 103667	D
<i>Nasalis lavartus</i>	AMNH 103670	D
<i>Nasalis lavartus</i>	AMNH 103671	D
<i>Nasalis lavartus</i>	AMNH 106272	D
<i>Nasalis lavartus</i>	AMNH 106275	D
<i>Papio ursinus</i>	AMNH 80771	D
<i>Papio ursinus</i>	AMNH 80774	D
<i>Papio ursinus</i>	AMNH 216247	D
<i>Papio ursinus</i>	AMNH 216250	D
<i>Papio ursinus</i>	R Susman collection (B)	D
<i>Papio ursinus</i>	R Susman collection (C)	D
<i>Papio ursinus</i>	R Susman collection (F)	D
<i>Hylobates hoolock</i>	AMNH 43065	P
<i>Hylobates hoolock</i>	AMNH 83416	P
<i>Hylobates hoolock</i>	AMNH 83419	P
<i>Hylobates hoolock</i>	AMNH 83420	P
<i>Hylobates hoolock</i>	AMNH 112676	P
<i>Pongo pygmaeus</i>	AMNH 140426	R
<i>Pongo pygmaeus</i>	AMNH 200898	R
<i>Pan troglodytes</i>	AMNH 51202	R
<i>Pan troglodytes</i>	AMNH 90191	R
<i>Pan troglodytes</i>	AMNH 167341	R
<i>Pan troglodytes</i>	AMNH 167344	R
<i>Pan troglodytes</i>	AMNH 167346	R
<i>Gorilla gorilla</i>	AMNH 54092	R
<i>Gorilla gorilla</i>	AMNH 54327	R
<i>Gorilla gorilla</i>	AMNH 54356	R
<i>Gorilla gorilla</i>	AMNH 81652	R
<i>Gorilla gorilla</i>	AMNH 167340	R
<i>Homo sapiens</i>	NF 819928	R
<i>Homo sapiens</i>	NF 819977	R
<i>Homo sapiens</i>	NF 819994	R
<i>Homo sapiens</i>	NF 820668	R
<i>Homo sapiens</i>	NF 820740	R
<i>Homo sapiens</i>	NF 821230	R
<i>Homo sapiens</i>	NF 819996	R
<i>Homo sapiens</i>	NF 821228	R

List of specimens included in the sample and where the bones were obtained from. AMNH = American Museum of Natural History, NF = Norris Farms #36 collection. Wrist morphology is designated D = direct contact between ulna and carpals, P = partial retraction of the ulna, R = ulna has retracted from direct carpal contact.

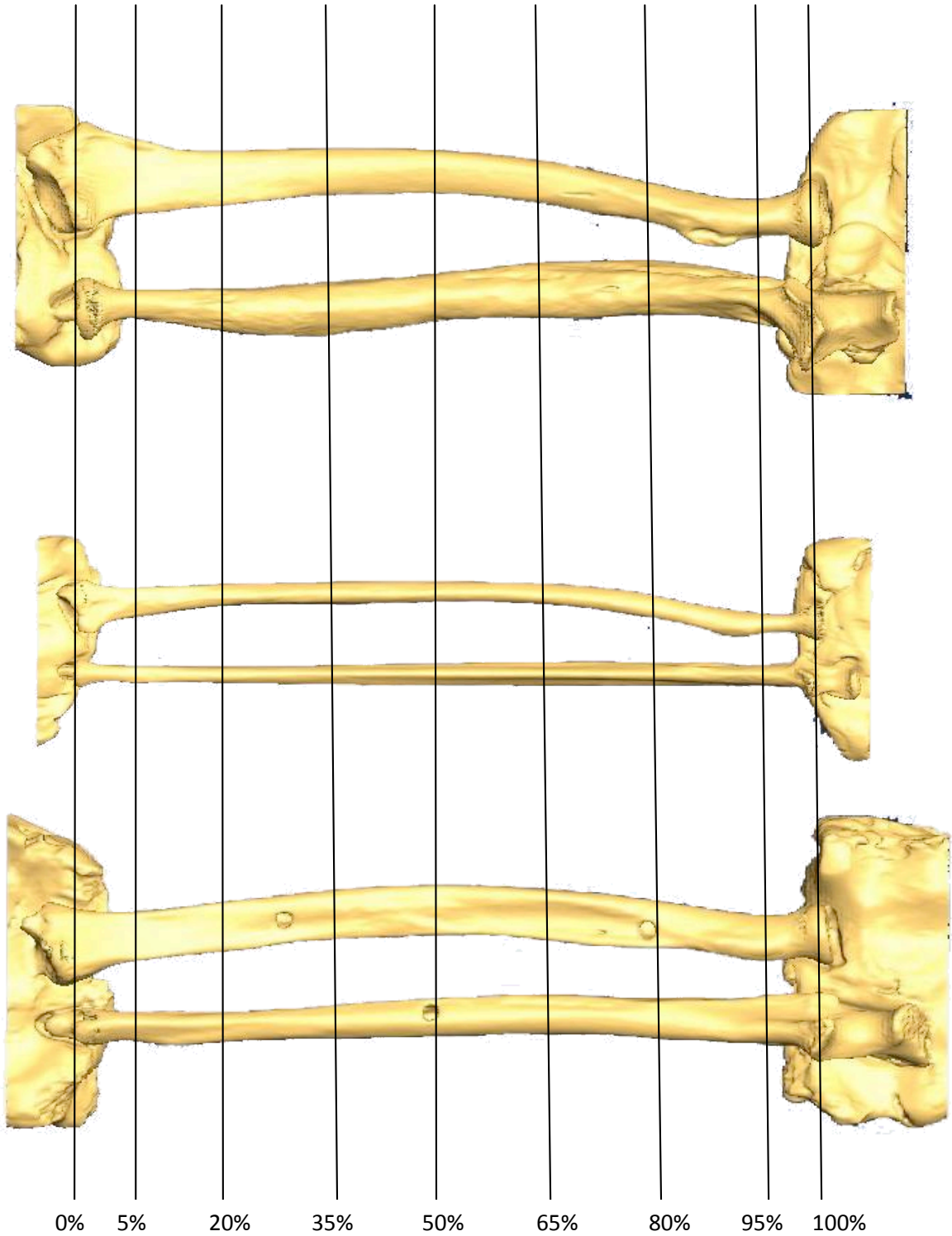


Figure 1 Bone alignment and slice selection in, from top to bottom, *Pan troglodytes*, *Hylobates hoolock*, and *Papio ursinus*. All bones have been scaled to the same length in order to show where corresponding points (5%, 20%, etc) are taken in one species as compared to another.

Table 2. Descriptive statistics for group R/U values

		Mean	St. Deviation	Minimum	Maximum
5%	Humans	1.862	0.936	0.988	3.434
	Great Apes	2.296	0.418	1.835	3.198
	Gibbons	3.757	0.486	3.044	4.380
	Monkeys	2.507	1.300	1.113	5.728
20%	Humans	1.563	0.318	1.077	1.992
	Great Apes	1.985	0.483	1.418	2.985
	Gibbons	1.788	0.257	1.459	2.143
	Monkeys	2.971	0.955	1.903	4.780
35%	Humans	1.241	0.350	0.753	1.767
	Great Apes	1.247	0.321	0.502	1.684
	Gibbons	1.229	0.182	0.926	1.410
	Monkeys	2.051	0.612	1.368	3.341
50%	Humans	1.079	0.330	0.540	1.410
	Great Apes	1.033	0.297	0.543	1.582
	Gibbons	0.877	0.162	0.688	1.104
	Monkeys	1.616	0.361	1.025	2.220
65%	Humans	0.849	0.214	0.597	1.205
	Great Apes	0.784	0.211	0.463	1.172
	Gibbons	0.782	0.177	0.597	1.052
	Monkeys	1.359	0.280	0.893	1.888
80%	Humans	0.774	0.171	0.531	0.956
	Great Apes	0.693	0.185	0.416	1.021
	Gibbons	0.636	0.058	0.599	0.736
	Monkeys	0.888	0.294	0.502	1.295

		Mean	St. Deviation	Minimum	Maximum
95%	Humans	0.465	0.177	0.264	0.707
	Great Apes	0.400	0.097	0.263	0.671
	Gibbons	0.512	0.124	0.386	0.711
	Monkeys	0.546	0.110	0.405	0.791
	Humans	1.862	0.936	0.988	3.434

Table 2 displays the mean, standard deviation, minimum and maximum R/U values for each group at each distance

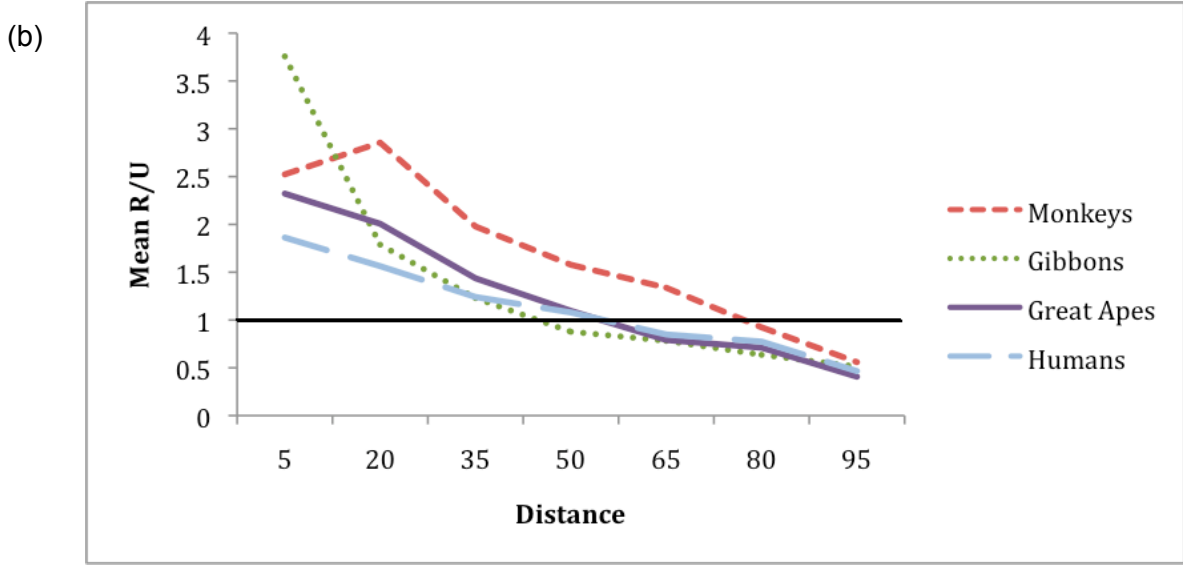
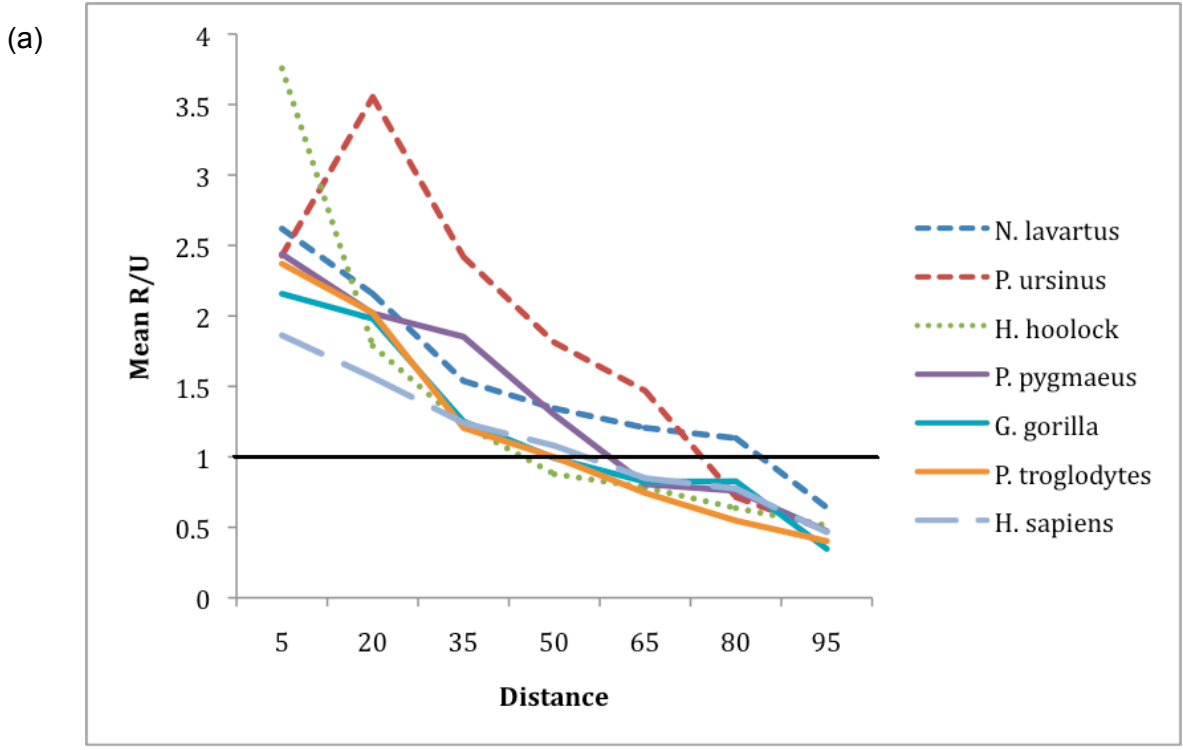


Figure 2. Line graph showing mean R/U values for (a) all taxa across all distances and (b) for all groups: monkeys, gibbons, great apes, and humans. Lower distance values equal more distal positions in the bone and larger numbers indicate more proximal distances. In Fig 2a, the taxa are represented by different patterned lines depending on which group they correspond to in Fig 2b. The horizontal black line in each image represents a point at which R/U is equal to 1.

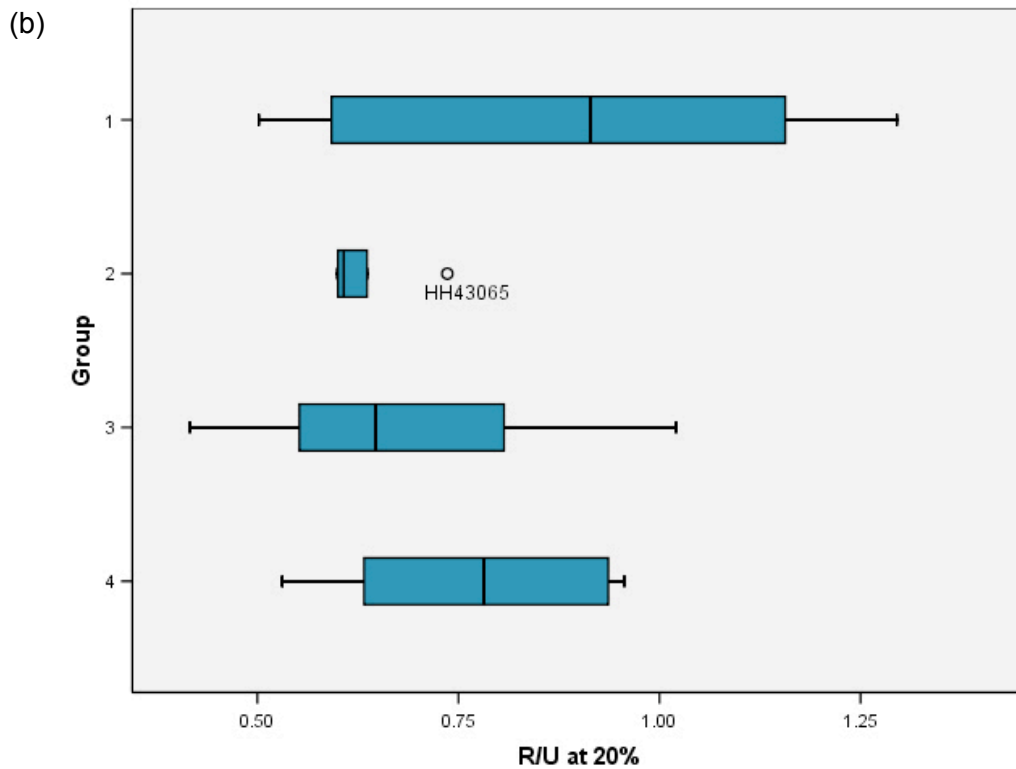
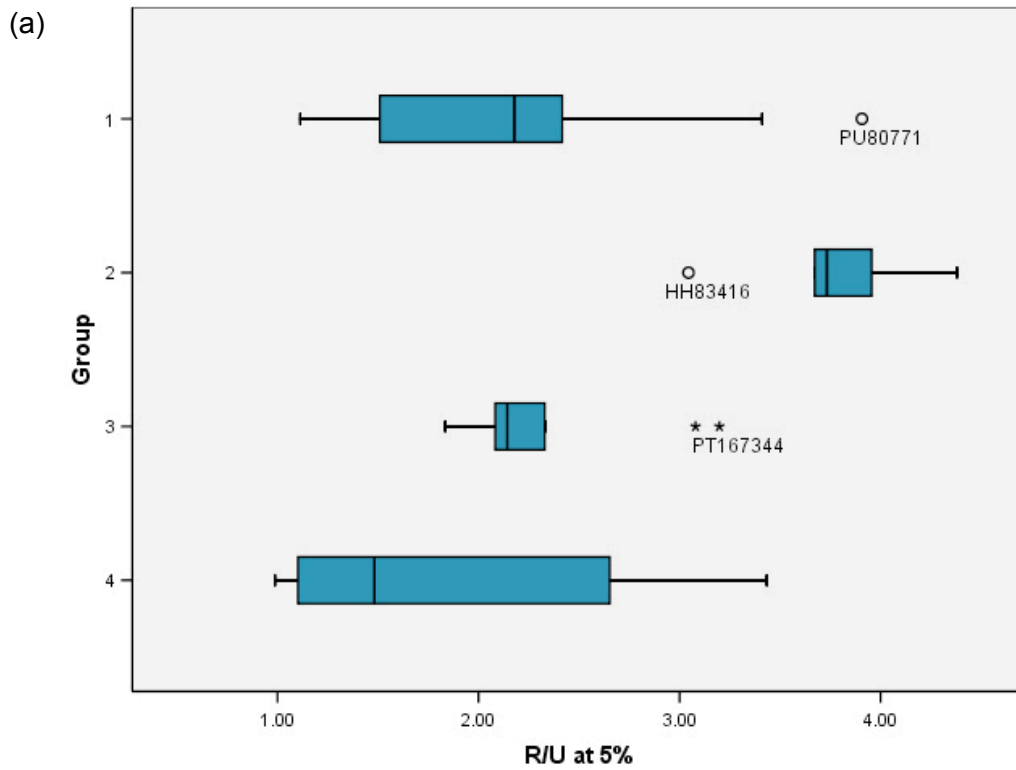


Figure 3. R/U values for all groups displayed as Box-and-Whisker plots at (a) 5% and (b) 20%. Outliers beyond the range of error are marked with the specimen number. Group: 1 = Monkeys, 2 = Gibbons, 3 = Great Apes, 4 = Humans. Black lines indicate the median value for each group.

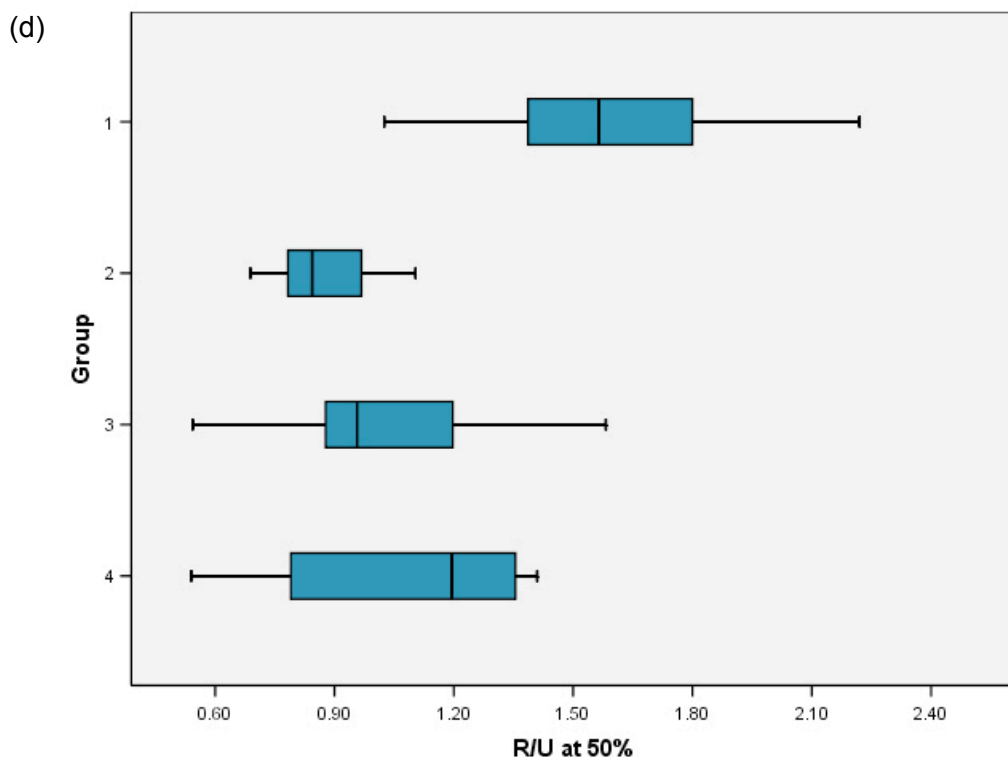
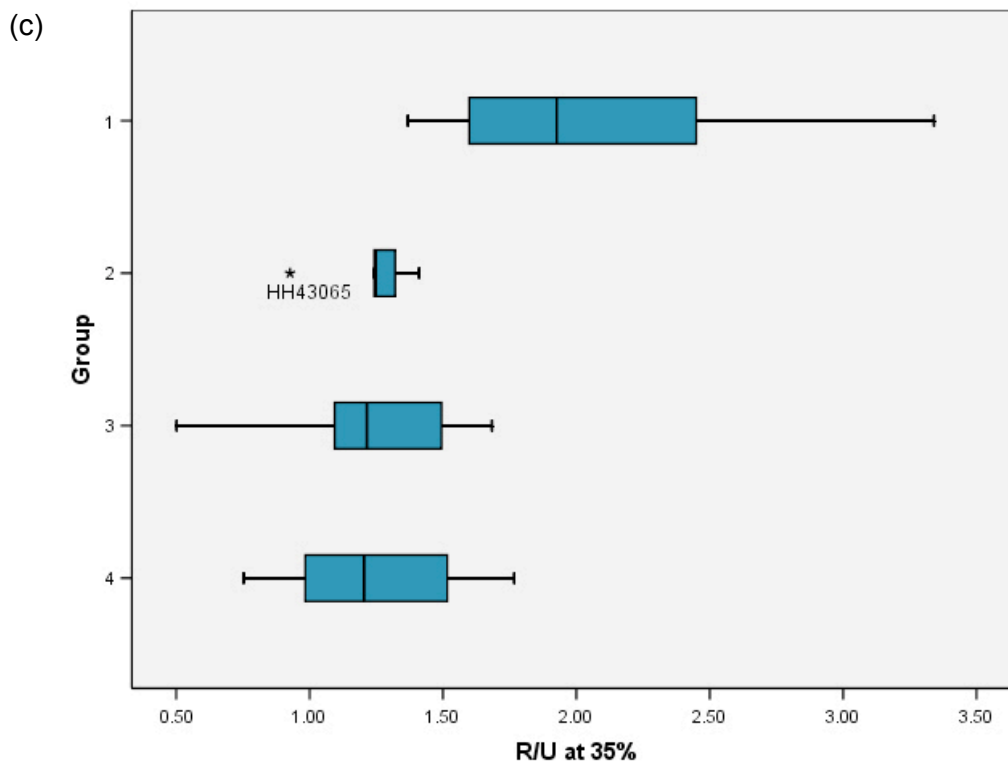


Figure 3. R/U values for all groups displayed as Box-and-Whisker plots at (c) 35% and (d) 50% of bone length. Outliers beyond the range of error are marked with the specimen number. Group: 1 = Monkeys, 2 = Gibbons, 3 = Great Apes, 4 = Humans. Black lines indicate the median value for each group.

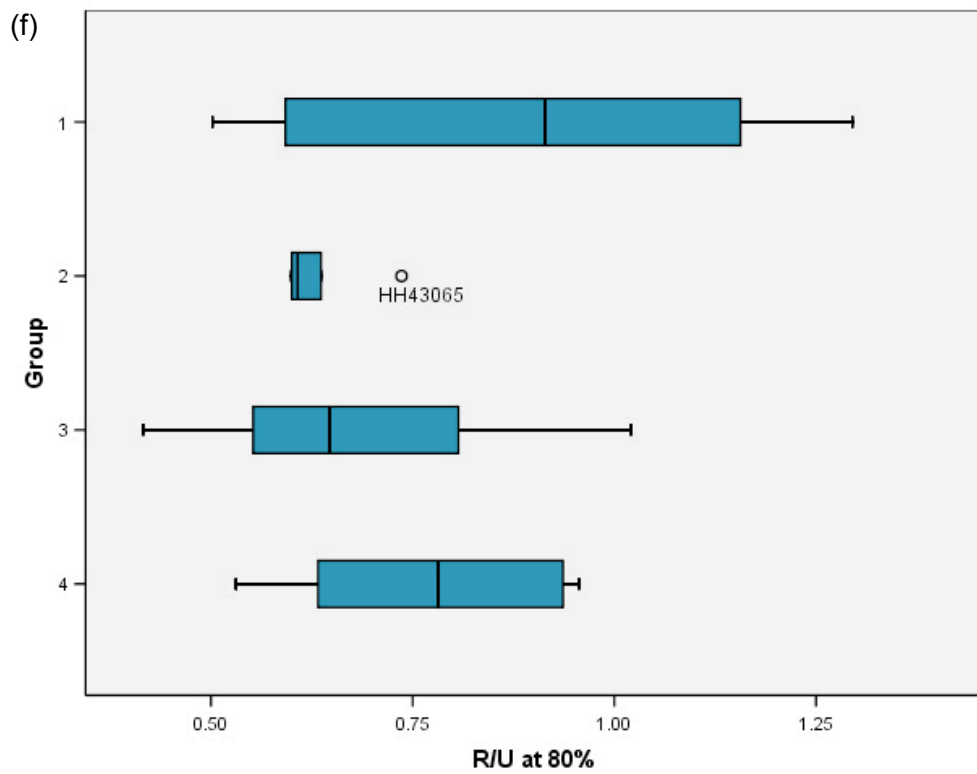
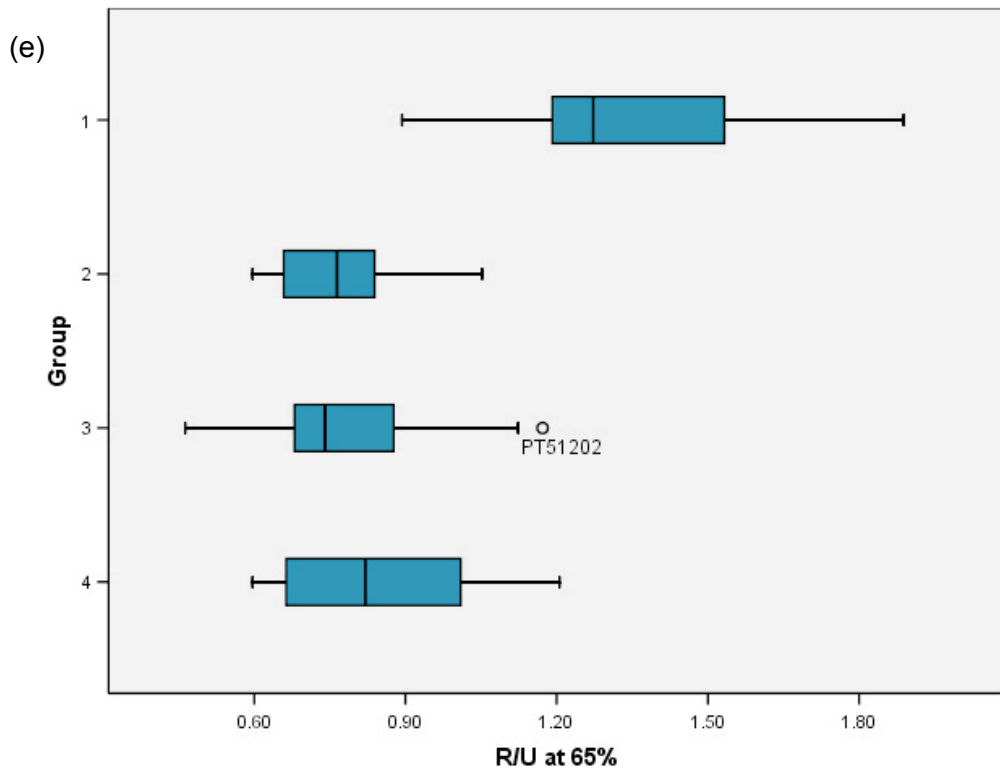


Figure 3. R/U values for all groups displayed as Box-and-Whisker plots at (e) 65% and (f) 80% of bone length. Outliers beyond the range of error are marked with the specimen number. Group: 1 = Monkeys, 2 = Gibbons, 3 = Great Apes, 4 = Humans. Black lines indicate the median value for each group.

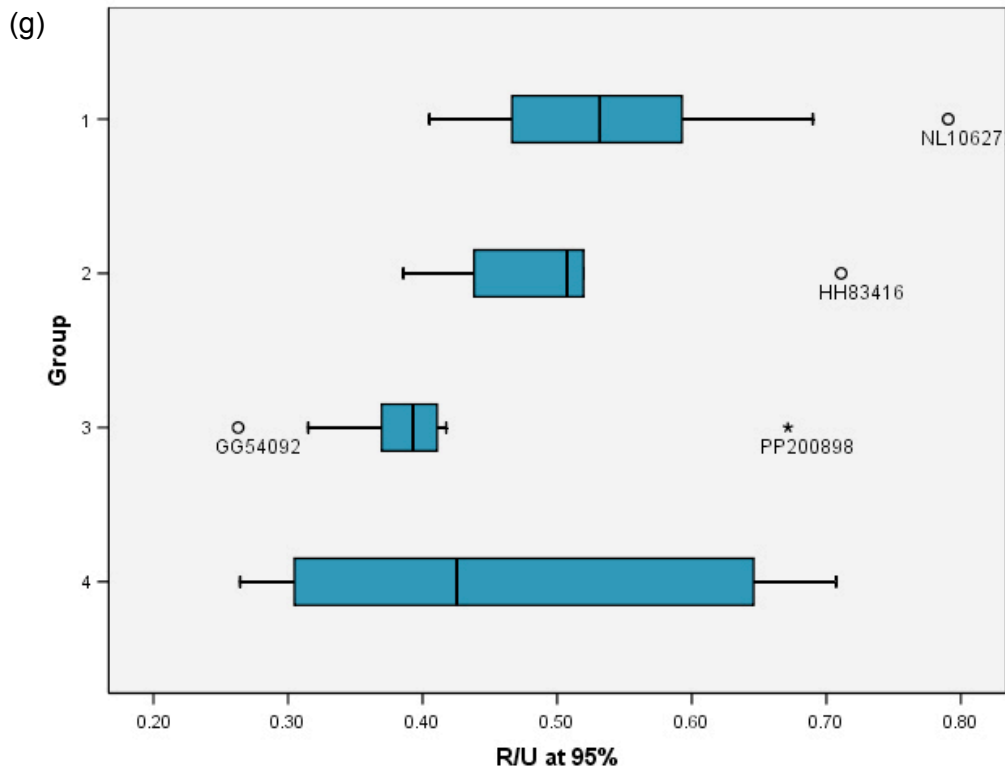


Figure 3. R/U values for all groups displayed as Box-and-Whisker plots at (g) 95% of bone length. Outliers beyond the range of error are marked with the specimen number. Groups: 1 = Monkeys, 2 = Gibbons, 3 = Great Apes, 4 = Humans. Black lines indicate the median value for each group.

Table 3 Results of Kruskal-Wallis and Games-Howell tests

Distance	Kruskal-Wallis Result	Games-Howell Result
5	p=0.009*	Gibbons different from all other groups (M: p=0.0014; GA: p=0.0032; H: p=0.0028)
20	p=.343	
35	p=0.001*	Monkeys different from all other groups (Gib: p=0.004; GA: p=.0045; H: p=0.0073)
50	p=0.001*	Monkeys different from gibbons and apes (Gib: p=0.0002; GA: p=0.0016)
65	p=0.000*	Monkeys different from all other groups (Gib: p=0.0013; GA: p=0.0001; H: p=0.0012)
80	p=0.343	
95	p=0.010*	No groups different from one another with correct p-values

Significant differences found in Kruskal-Wallis tests are marked by an *. If the p-value was significant, Games-Howell tests were performed using a Bonferroni-Holm correction (see text for further explanation). Results of those tests are summarized and groups which were significantly different from one another with corrected p-values are listed. Groups are abbreviated as follows: Gib = gibbons, GA = great apes, M = monkeys, H = humans.

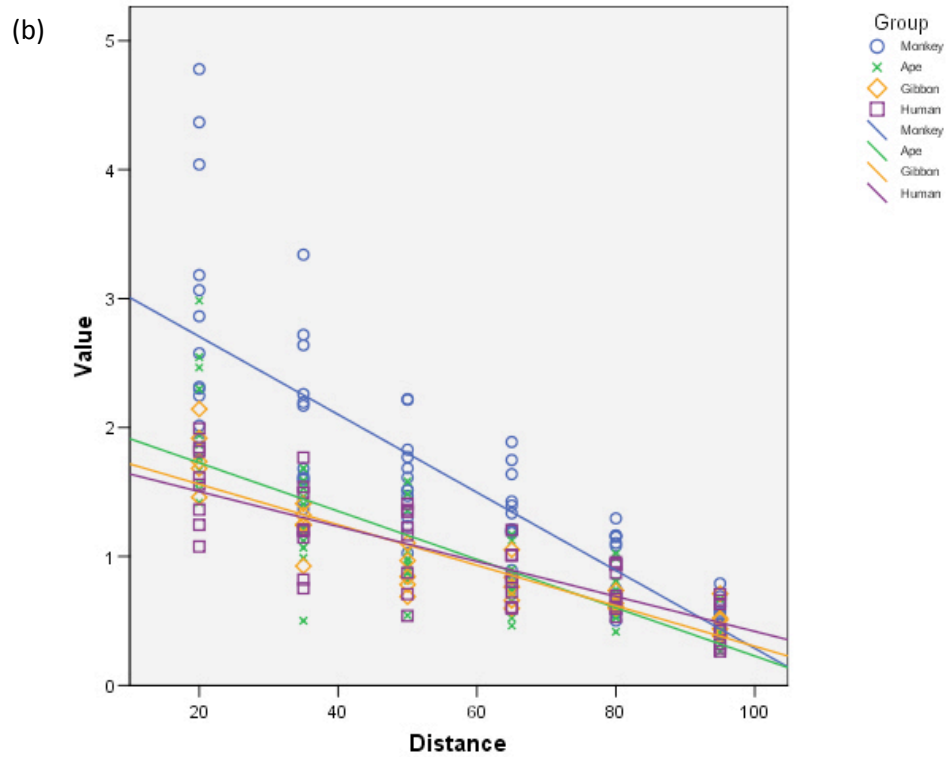
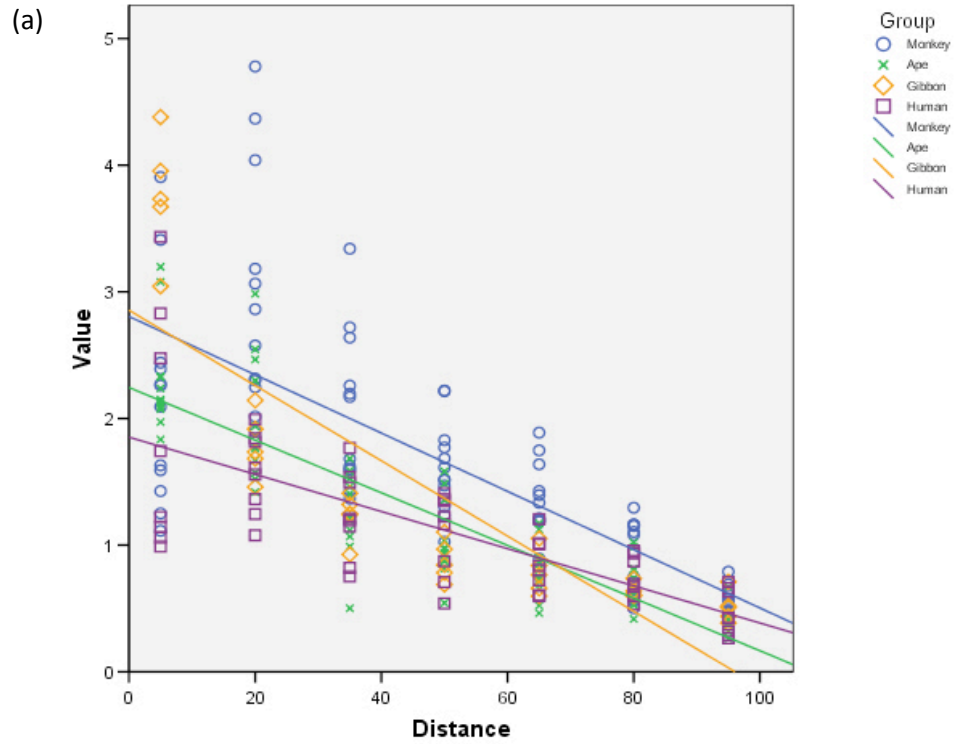


Figure 4. R/U values of all individuals plotted against distance. (a) All distances in the radius and ulna (b) 5% distance removed. A line of best fit has been added to the data for each group. R values for each line are listed for (a) in Table 3 and (b) in Table 4.

Table 4 Comparison of slopes across all distances

(a) Ordinary Least Squares (OLS) results

Group	R ²	Slope	Y-Intercept	p
Monkeys	0.542	-0.02302	2.805	0*
Gibbons	0.689	-0.02973	2.855	0*
Great Apes	0.768	-0.02079	2.245	0*
Humans	0.535	-0.01467	1.852	0*

(b) Test for common slope across groups: p=0.002*

(c) Post-hoc multiple comparison of slopes among groups – p-values

Group	Apes	Gibbons	Humans	Monkeys
Apes		0.022*	0.009*	0.393
Gibbons	0.022*		0.001*	0.103
Humans	0.009*	0.001*		0.009*
Monkeys	0.393	0.103	0.009*	

Table 3 (a) lists R² and Y-intercept values for all groups. All p values were significant indicating all regressions showed significant values. (b) The test for common slope across groups was significant, indicating heterogeneity among group slopes. (c) Comparison matrix comparing slopes of each group to the others. * marks a significant p-value indicating significant differences between group slopes.

Table 5 Comparison of slopes without 5% R/U values

(a) Ordinary Least Squares (OLS) results

Group	R ²	Slope	Y-Intercept	p
Monkeys	0.69	-0.03024	3.311	0*
Gibbons	0.784	-0.01572	1.875	0*
Great Apes	0.691	-0.01873	2.101	0*
Humans	0.644	-0.01356	1.775	0*

(b) Test for common slope across groups: $p = 0.001^*$

(c) Post-hoc multiple comparison of slopes among groups – p-values

Group	Apes	Gibbons	Humans	Monkeys
Apes		0.163	0.019*	0.001*
Gibbons	0.163		0.309	0.001*
Humans	0.019*	0.309		0.001*
Monkeys	0.001*	0.001*	0.001*	

Table 4 (a) lists R² and Y-intercept values for all groups. All p values were significant indicating all regressions showed significant values. (b) The test for common slope across groups was significant, indicating heterogeneity among group slopes. (c) Comparison matrix comparing slopes of each group to the others. * marks a significant p-value indicating significant differences between group slopes.

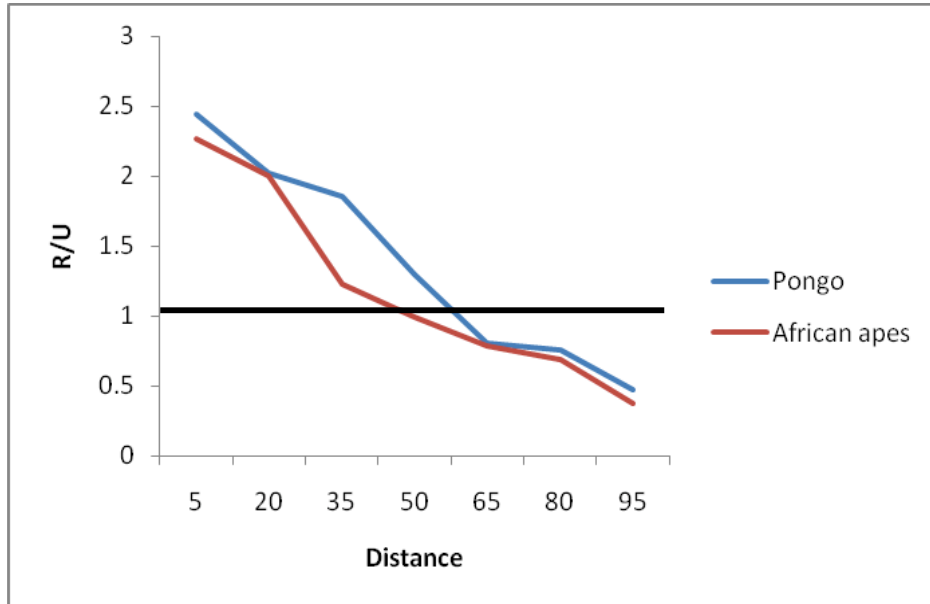


Figure 5. Line graph showing mean R/U values for *Pongo pygmaeus* (n=2) and African apes (n=10). Lower distances values indicate more distal positions in the bone. The horizontal black line represents a point at which R/U is equal to 1.0.

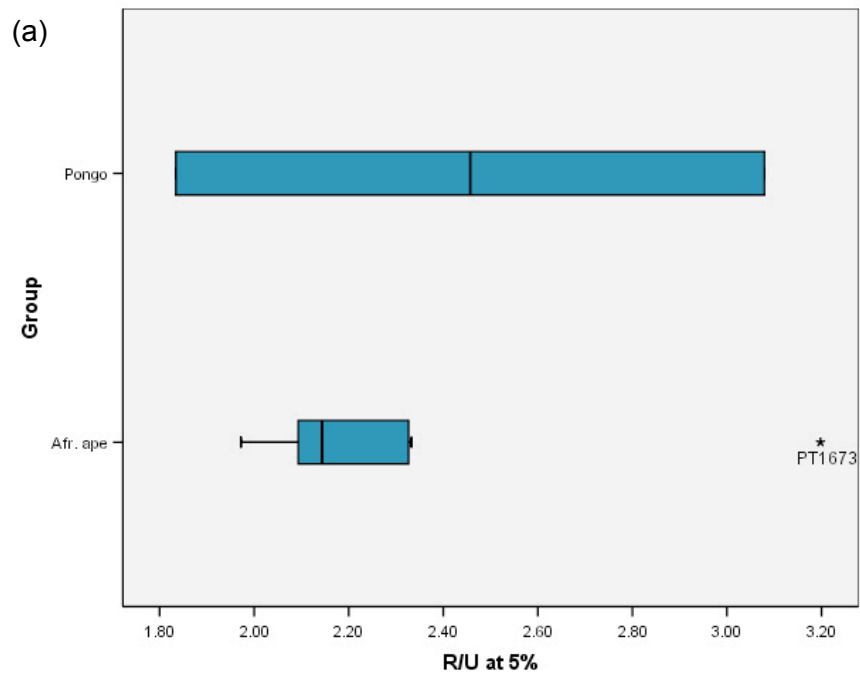


Figure 6. R/U values for *Pongo* (n=2) and African apes (n=10) displayed as Box-and-Whisker plots at (a) 5% of bone length. Black lines indicate the median value for each group.

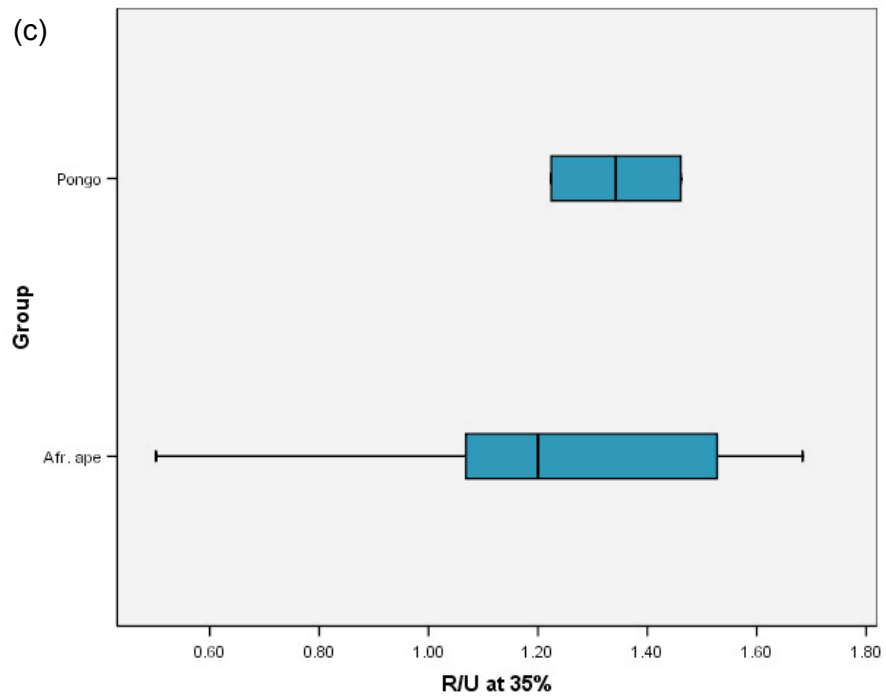
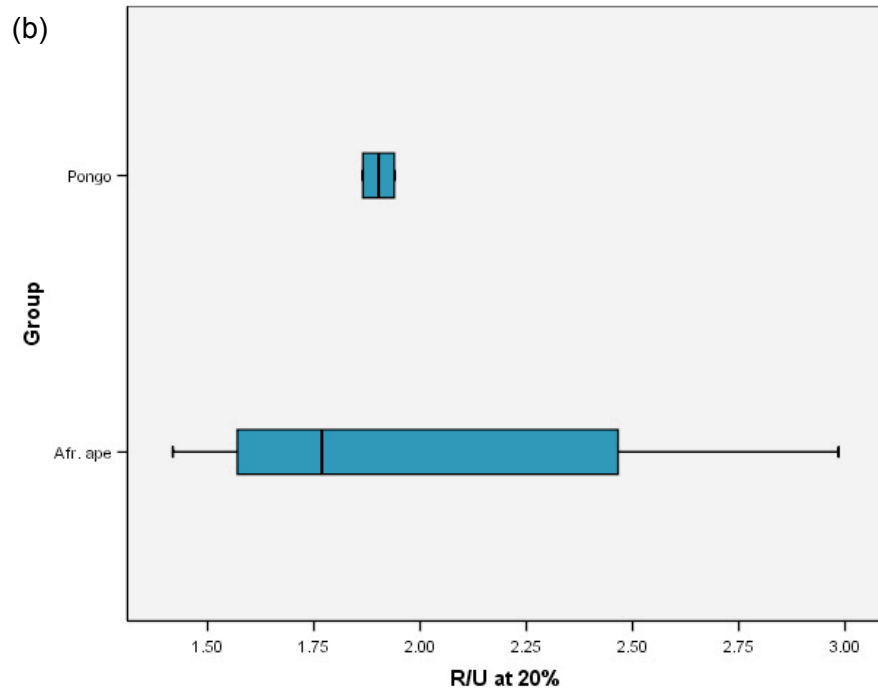


Figure 6. R/U values for *Pongo* (n=2) and African apes (n=10) displayed as Box-and-Whisker plots at (b) 20% and (c) 35% of bone length. Black lines indicate the median value for each group.

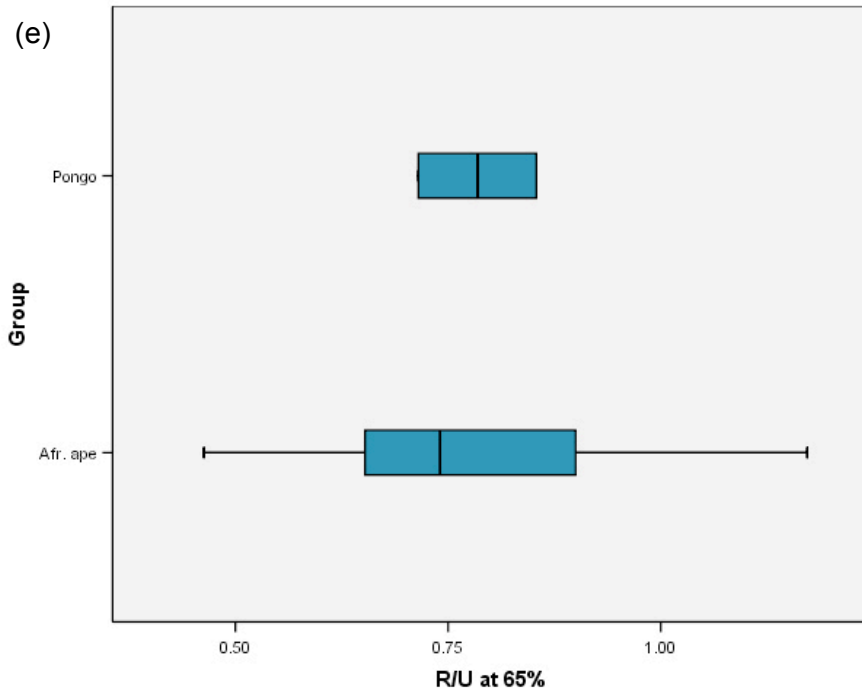
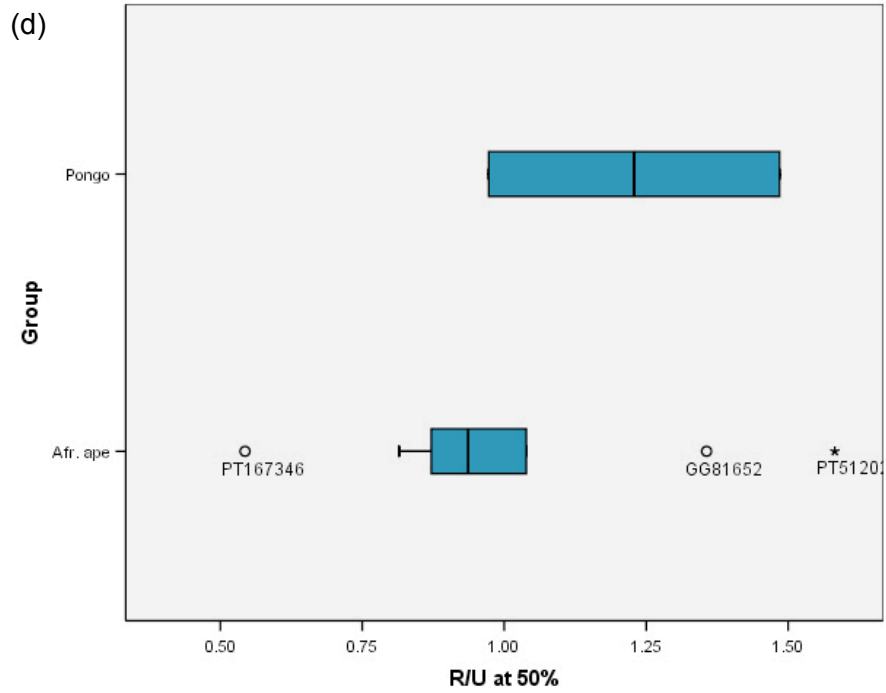


Figure 6. R/U values for *Pongo* (n=2) and African apes (n=10) displayed as Box-and-Whisker plots at (d) 50% and (e) 65% of bone length. Black lines indicate the median value for each group.

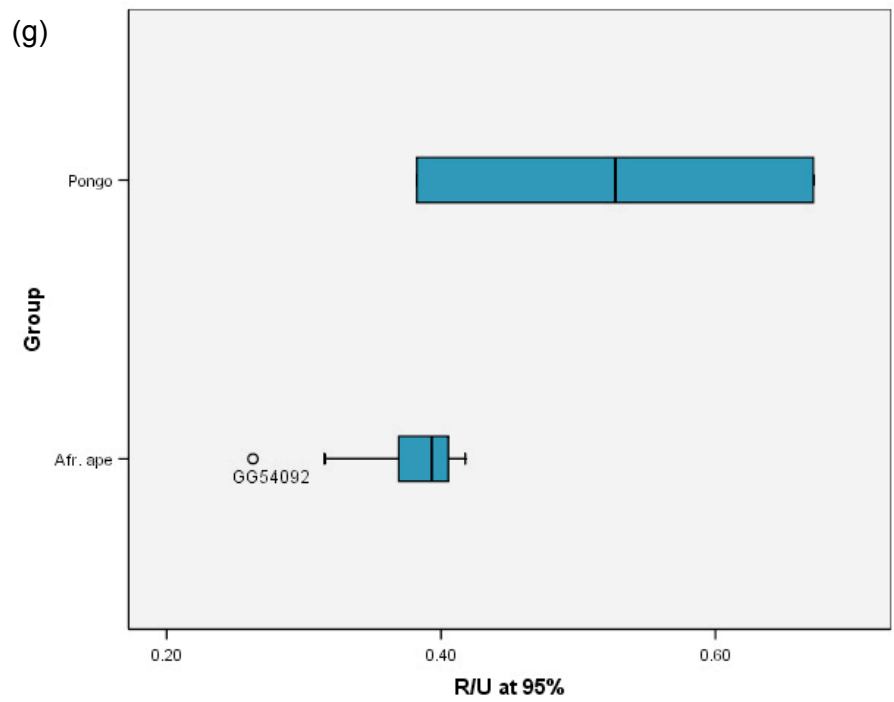
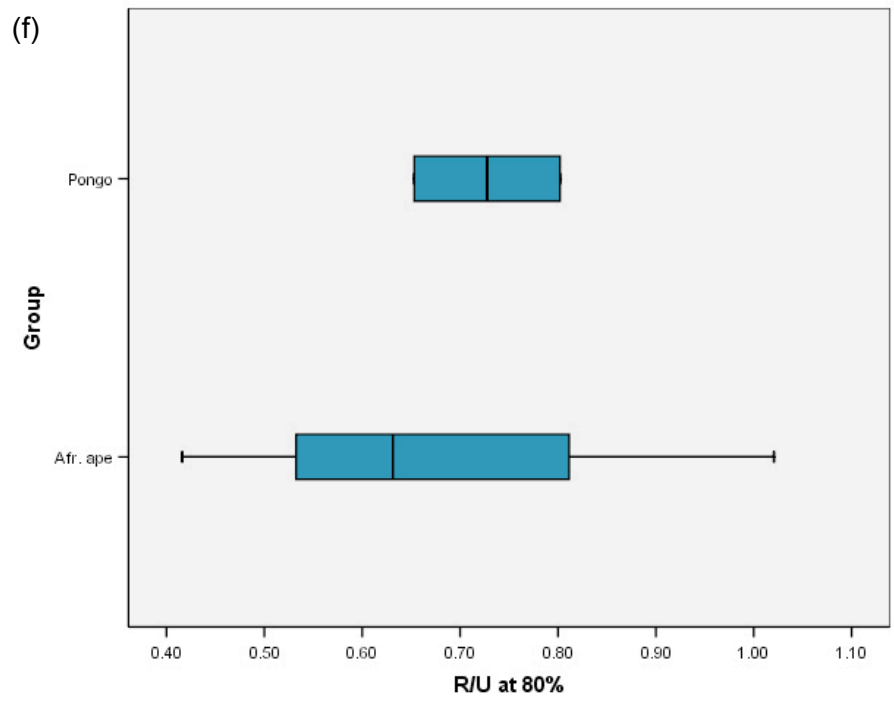


Figure 6. R/U values for *Pongo* (n=2) and African apes (n=10) displayed as Box-and-Whisker plots at (f) 80% and (g) 95% of bone length. Black lines indicate the median value for each group.