Functional morphology of the hominoid forelimb: Implications for knuckle-walking and the origin of hominid bipedalism

By

Myriam Zylstra

A thesis submitted in conformity with the requirements
for the degree of Doctor of Philosophy
Graduate Department of Anthropology
University of Toronto

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Abstract

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1999

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Modern African apes, *Pan* and *Gorilla*, engage in a unique form of terresrial quadrupedalism called knuckle-walking. They also share with humans a recent evolutionary heritage to the exclusion of Asian apes, and two competing hypotheses have been proposed to explain the origin of human bipedalism. One hypothesis views knuckle-walking as a synapomorphy of chimps and gorillas, having evolved after the divergence of humans from the last common ancestor with African apes. An alternate hypothesis proposes that knuckle-walking was present in the last common ancestor in the lineage leading to African apes and humans, implying that humans evolved from a knuckle-walker.

This project has two main objectives. The first is to analyze extant catarrhine forelimb skeletal elements in order to quantify characters that may be functionally linked to knuckle-walking in African apes. The second objective is to determine the presence or absence of these knuckle-walking traits in selected fossil taxa so that inferences regarding their locomotion can be made. Two-dimensional video image analysis is employed to gather data on joint surface areas, angular measures, and joint surface curvatures in three anatomical

The study demonstrates that extant knuckle-walkers are characterized by emphasis on loading across the radial aspect of the wrist, as indicated by larger scaphoid relative to lunate radial surfaces, differences in the pattern of scaling across the proximal carpal row compared to other taxa, and enlarged area of contact at the scaphoid-capitate joint. Profile analysis across metacarpal heads two through five shows that knuckle-walkers are distinguished in the degree of change in curvature from ventral to dorsal aspect of the head, indicating weight-bearing across these joints. In addition, significant weight-bearing is indicated only for metacarpals three and four, despite observed differences between Gorilla and Pan in preferential digit use during knuckle-walking. Finally, the proximal articular surface of the proximal phalanx is medio-laterally expanded in gorillas and chimps.

Comparison of a select number of Miocene and Pliocene fossil taxa does not reveal the presence of characters typically found in practicing extant knuckle-walkers.

Aknowledgments

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CHAPTER 1

INTRODUCTION

Background - Why Study Forelimbs?

Modern humans share a recent common evolutionary heritage exclusively with African apes. This is known from morphological comparisons of cranial and postcranial anatomy (for example Darwin, 1871; Huxley, 1863; and in more recent efforts Begun, 1992, 1994), as well molecular studies (Goodman *et* al, 1983,1989; Sibley and Alquist, 1984,1987; Miyamoto *et* al, 1987; Marks *et* al, 1988; Sarich *et* al, 1993; Rogers, 1993,1994; Ruvolo *et* al, 1991; Ruvolo, 1994). What is intriguing is that both modern humans and African apes engage in modes of terrestrial locomotion atypical of any other living species, primate or otherwise.

Indeed, Rose (1991) comments that modern humans are unique among higher primates in that we have a locomotor repertoire that is dominated by a *single* activity - namely bipedalism. African apes are more typical of all other primates in using varied positional behaviours, however they are also unique in their use of a stereotypic hand posture in terrestrial quadrupedal progression called knuckle-walking.

Given that African apes and humans share a common ancestor to the exclusion of Asian apes, they must also have shared a common mode of locomotion at one time. At present, it is unclear what the relationship is between knuckle-walking, as seen in *Pan* and *Gorilla*, and human erect bipedalism, or how these two diverse patterns of locomotor behaviour arose. Numerous hypotheses have been proposed attempting to explain the emergence of bipedal locomotion in modern humans.

Historically, there have been four significant schools of thought concerning the reconstruction of the first "protohominid" (the ancestor of modern great apes and humans) and the process of bipedalization in modern humans. The first of these is the *brachiating-troglodytian* model. Originally proposed by Keith (1903,1923,1927,1934) and Gregory (1927a,b, 1928a,b), it suggests that humans evolved from a large-bodied, orthograde arboreal ape ancestor. This stage was then followed by a phase of plantigrade (bipedal) progression on the ground. Many of the similarities of the upper limb and thorax shared between chimps and humans were thought to be explained by "brachiation" (meaning arm swinging similar to that of chimps, not true brachiation as seen in Hylobatids) and arm suspension. Orthograde postures that had evolved arboreally served as an effective pre-adaptation leading to the transformation to full blown bipedality once the large size of these "troglodytians" forced them to the ground.

Washburn championed the *knuckle-walking troglodytian* model (1963,1967,1968a,b, 1971,1973). This hypothesis was also based on structural similarities between chimps and humans, as well as their biochemical affinity. Washburn could not conceive of a fully arboreally adapted creature surviving on the ground and developing full blown bipedal behaviours without some intermediate step. He believed knuckle-walking solved the problem, since it is a semi-erect posture and would have allowed the proto-hominids to escape predators. Although falling out of favour for some time, support for this hypothesis has been resurrected largely due to advances in molecular research and more robust cladistic analyses of hominoid and hominid morphometric traits.

Morton (1924,1926,1927; Morton and Fuller,1952) was the chief proponent of the *hylobatian* model, which was later supported by Tuttle (1975). This hypothesis suggested that proto-hominids were gibbon-sized, and that they had fore and hindlimbs of roughly equal length, in addition to well developed grasping thumbs and big toes. They would have been excellent climbers and were capable of "brachiating" (arm swinging) like chimps. Morton suggested these early hominids engaged in gibbon-like aided bipedalism in the trees and on the ground. This model is very similar to the one proposed by Keith-Gregory, except in the hylobatian phase the proto-hominids were not forced to the ground as a result of increased bulk.

Finally, the *vertical climbing hypothesis* or *orangutanian* model was initially proposed by Stern (1971,1975). In this scenario, protohominids used their forelimbs much like orangs do today, and typical arboreal movements included climbing with high frequencies of fore/hindlimb suspension. Stern suggested that extreme elongation of the upper limb evolved in an arboreal setting, and that these animals were so adapted to antipronograde postures that the only way to manoeuvre on the ground was to completely free the forelimb from locomotor function. The latter scenario is highly unlikely, however more recent publications on the subject have argued that vertical climbing and hoisting behaviours have produced the adaptations seen in the hominoid forelimb, not brachiation (Fleagle *et* al, 1981). Furthermore, these authors state that vertical climbing is functionally pre-adaptive for hindlimb functions seen in human bipedalism. Since its proposal, this model has garnered considerable support (Aiello, 1981; Tuttle, 1981; Stern and Susman, 1983;

Jungers and Stern, 1983; Susman *et* al, 1984; McHenry, 1984,1991; Ishida *et* al, 1984,1985; Tuttle et al, 1991; Senut, 1991; Schmid, 1991; Duncan *et* al, 1994).

Despite its considerable backing, the vertical climbing hypothesis does not take into account the fact that terrestrial quadrupedalism is the preferred and habitual mode of locomotion among all African apes. The demonstrated close molecular affinity of African apes and humans, particularly the chimp-human relationship (for example, see Ruvolo, 1994), as well as shared derived morphological characters (Begun, 1992,1994) can not preclude some consideration of a terrestrial component in the locomotor repertoire of early hominid antecedents.

If one accepts the notion that the common ancestor of African apes and humans engaged in some form of terrestrial locomotor activity as part of its overall repertoire, there are two competing hypotheses within this premise. The first hypothesis is that knuckle-walking is either a shared derived character of African great apes (Keith, 1912; Tuttle, 1967,1969b, 1975, 1977, 1981; Lovejoy, Heiple, and Burstein, 1973; Stern and Susman, 1983; Susman and Stern,1991; Latimer and Ward, 1993; Filler, 1993; Hunt, 1994), or it is a convergent trait that arose independently in the separate lineages leading to *Gorilla* and *Pan* (for example, see Rose, 1991; Begun, 1994). In either case, knuckle-walking is thought to have evolved after the divergence of humans. This suggests humans evolved not from a knuckle-walker, but from some generalized arboreal quadruped (Straus, 1940,1942, 1949; Stern, 1975; Fleagle *et* al, 1981). The second hypothesis is that knuckle-walking was present in the last common ancestor of African apes and humans. This implies that knuckle-walking arose before humans diverged, and therefore that humans evolved from a knuckle-walker

(Washburn, 1963, 1967,1968a,b, 1971, 1973; Begun, 1992,1994; Pilbeam, 1989, 1996; Zihlman, 1990; Shea and Inouye, 1993).

Much of the morphological data from earlier research favoured a chimp-gorilla clade, based on proposed synapomorphies of the forelimb and hand considered as adaptations to knuckle-walking (Tuttle, 1969; Andrews and Martin, 1987), as well as patterns of enamel histology (Martin, 1985). Recent advances in molecular studies, however, have unequivocably determined the existence of an African ape-human clade. This clade represents either an unresolved trichotomy among *Gorilla-Pan-Homo* (for example, Marks, 1992; Rogers, 1993), or a *Pan-Homo* clade with *Gorilla* as the sister group (Ruvolo, 1994; Shoshani *et* al, 1996). In light of the shared genetic ancestry of gorillas, chimps and humans to the exclusion of *Pongo*, accepting the hypothesis that knuckle-walking is either a synapomorphy of African apes, or that it is an independent aquisition by chimpanzees and gorillas, would also require the acceptance of a number of other homoplasies of the forelimb considered to be a direct consequence of knuckle-walking, like the fusion of the *os centrale* for example. Thus, the second hypothesis wherein African apes and humans have evolved from a knuckle-walking or, at least, at "proto-knuckle-walking" (Begun, 1994) ancestor is most plausible.

There has been considerable speculation in the published literature as to the exact nature of early hominid postural and locomotor behaviour. The term hominid refers to great apes and humans, as well as human ancestors such as *Australopithecus* (see Tattersal *et al*, 1988). Many interpretations have been put forth, including suggestions that hominid ancestors and early australopithecines were highly arboreal (Morton, 1922,1924,1926, 1927, 1935; Keith, 1923,1927,1934; Gregory, 1927a,b,1928a,b, 1930; Tuttle, 1969a,b, 1974a,b, Leakey, 1971; Robinson, 1972; Kay, 1973; Day, 1978; McHenry and Temerin, 1979; Senut, 1981a,b; Stern and Susman, 1981,1983; Jungers, 1982; Jungers and Stern, 1983; Susman et al, 1984; McHenry, 1984; Susman and Stern, 1991; Senut and Tardieu, 1985; Clarke and Tobias, 1995; Berger and Tobias, 1996; McHenry and Berger, 1996). Other researchers suggest that our hominid ancestors engaged in terrestrial quadrupedalism (Hooten, 1946; Washburn, 1963, 1967,1968a,b, 1971, 1973; Marzke, 1971; Conroy and Fleagle, 1972; Pilbeam, 1972; Simons and Pilbeam, 1972; Sarmiento, 1988,1994; Zihlman, 1978, 1989; Jouffroy, 1991; Schmid, 1991; Begun, 1992,1994; Gebo,1992,1996; Marzke *et* al, 1994).

There is little arguement that early australopithecines such as *A.afarensis* were bipedal, however some dispute that any arboreal component characterized their locomotor repertoire, stating that early hominids were fully adapted and committed to bipedalism utilizing an upright gait that was kinematically indistinct from that of modern humans (Dart, 1958; Latimer *et al*, 1987, 1989,1990a,b; Latimer, 1991; Lovejoy *et al*, 1973; Lovejoy 1975, 1978,1979,1980,1981,1988; White, 1980, 1981). Finally, it has also been suggested that early australopithecine behaviour can best be described as a varied repertoire, consisting of a variety of terrestrial and arboreal activities (Rose, 1991, but see also 1983,1988; Stern and Susman, 1983; Susman *et* al, 1984; Senut and Tardieu, 1985).

Sarmiento (1988, 1994) has argued that a large number of similarities in the hands and feet of gorillas and humans can be interpreted as terrestrial features and that these structures evolved as a response to terrestrial quadrupedalism. However, features that typically occur together and are present in all knuckle-walkers are lacking in modern humans and early hominids such as *A.afarensis.* Irrespective of any potential arboreality in the locomotor activities of this taxon, it was undoubtedly bipedal in its terrestrial endeavours. Until recently, the Hadar hominids were the first to show evidence of directional selection towards bipedality (Latimer,1991). Stabilizing selection that had been acting on the lower limb to maintain arboreal competence was eliminated. This is clearly demonstrated in the dramatic changes that occurred in the lower limb that are directly functionally related to bipedalism (Lovejoy, 1975; Latimer *et* al, 1982, 1987; Latimer and Lovejoy, 1989, 1990a,b; Latimer, 1991; Gebo, 1992).

At the same time, the upper limb was not under the same immediate selection pressures as the lower limb (Latimer, 1991). Hence, the hand, wrist and forelimb of *A.afarensis* manifest a mosaic of primitive and derived characters. Primitive traits certainly relating to vertical climbing and suspension (ie: curved phalanges, reduced ulnar styloid process, elongated forelimb), as well as derived characters possibly associated with terrestrial quadrupedalism (ie: expanded capitate head, fused os centrale, elongated rod-like pisiform) are present. The retention of primitive ape-like climbing traits does not neccessarily mean that they were used for that purpose, but it is possible (but see Latimer 1991 and references above for alternate view). Radical changes in the pelvis and lower limb, in addition to evidence from the Laetoli footprints (for example, see Leakey and Hay, 1979; White and Suwa, 1987) are unquestionably indicative of an habitual bipedal gait, so it is unlikely that *A.afarensis* was engaging in any form of terrestrial quadrupedalism.

Another early hominid discovered in South Turkwel, Kenya, (dated to ~ 3.5 m.y.a.) is roughly contemporaneous with *A.afarensis* from Hadar and they share a number of morphological similarities of the hand. These features show clear affinities with modern human morphology and do not reflect terrestrial quadrupedal behaviours (Ward *et al.*, 1999). In addition, pedal morphology of the Turkwel fossil indicates bipedalism as the habitual mode of locomotion in this hominid (Ward *et al.*, 1999) and, if it is indeed conspecific with the fossils from Hadar, corroborates earlier interpretations of bipedalism in *A.afarensis*.

Finally, specimens recovered from Allia Bay and Kanapoi, Kenya, represent a new species of australopithecine, *Australopithecus anamensis* (Leakey *et al.*, 1995). These fossils are dated from 3.9 to 4.2 m.y.a. and are considerably older than *A.afarensis* from Hadar (Leakey *et al.*, 1995, 1998). *A.anamensis* also presents a mosaic of primitive and derived characters of the upper and lower limb. An almost complete tibia and distal humerus were recovered from the older stratigraphic levels at Kanapoi. The tibia possesses a number of features associated with habitual bipedalism (Leakey *et al.*, 1995), while the humeral fragment is considered by some to be most similar to modern humans (Aiello and Dean, 1990; Day, 1978; McHenry and Corruccini, 1975; McHenry, 1975,1976,1984; Senut, 1980,1981a,b; Senut and Tardieu, 1985) while others believe it to have closer affinities with

Australopithecus (Hill and Ward, 1988; Lague and Jungers, 1996; Patterson and Howells, 1967). A radius and a capitate recovered from the higher stratigraphic sequence at Allia Bay both possess a number of ape-like characteristics which may be associated with climbing behaviours (Heinrich *et al.*, 1993; Leakey and Ward, 1997; Leakey *et al.*, 1998; Ward *et al.*, 1999).

So, unanswered questions remain: when and how did bipedalism emerge? What form of locomotion preceded it? How will we identify it? According to Swartz (1989), species specific locomotor patterns may not differ significantly enough to result in dramatic modifications in joint surface design, and that only certain types of locomotor patterns may be reflected in joint morphology. Indeed, many knuckle-walking characters (for example, dorsal ridges on metacarpal heads) are variably expressed or size related (Susman, 1979; Inouye, 1992; Shea and Inouye, 1993; Begun, 1994). If many " typical" knuckle-walking characters are weakly expressed or absent altogether in typical knuckle-walkers, then clearly they are not essential for the task. This makes it extremely difficult to identify traits functionally associated with knuckle-walking in the fossil record based on characters that have been identified to date.

In order to address the issue of limb usage and locomotor patterns in the fossil record, a comprehensive analysis of joint surface size and shape is neccessary. Obviously, examining the total morphological pattern of any taxon, living or extinct, is preferable when making inferences about the relationship between morphology and function. Unfortunately, the fossil record is not complete and, in most cases, extremely limited with respect to the number of elements that are available for fossil species. In addition, such an analysis is beyond the scope of this research project. The study presented here focuses on joint surface aspects of the elbow, wrist and hand. Using video image analysis, skeletal elements from these anatomical regions are quantified in order to clarify characters known to differ among hominoids, as well as identify novel traits and patterns of variation that may be functionally linked to alternative loading regimes across the forelimb. Specifically, the goal is to tease out subtle differences in great ape forelimb morphology that reflect knuckle-walking as an habitual mode of locomotion in African apes. In turn, results from comparative analysis of extant catarrhines are then be applied to selected elements of fossil taxa, in an effort to clarify the relationship of fossil species to extant hominoids and their locomotor patterns.

If one assumes that a suite of knuckle-walking characters (subtle as they may be) are neccessary to engage in this activity, and that this suite is only present in practising knuckle-walkers, then it is neccessary to go back in the fossil record well beyond the emergence of *A.anamensis* to identify it. Discoveries at Aramis, Ethiopia, of a new genus identified as *Ardipithecus ramidus* and pre-dating *A.anamensis* (White et al, 1994,1995) indicate that this genus is even more primitive than the Kanapoi-Allia Bay and Hadar hominids. Hopefully, additional data on *A.ramidus* postcranial anatomy will soon be published, which may demonstrate that this taxon is morphologically very similar to the ancestral hominid morphotype, and will prove critical in the reconstruction of early hominid locomotor behaviour. At the same time, it is more likely that modifications to great ape forelimb morphology accompanying the transition to increased frequencies of terrestrial travel will be detected in Miocene fossil taxa. Available evidence of late Miocene hominoids is not exhaustive, and new interpretations of these skeletal elements would greatly enhance our understanding of forelimb usage and locomotor patterns preceding the emergence of fully bipedal early hominids in the Plio-Pleistocene.

Definitions of Locomotor Patterns

Many descriptions in the literature refer to the *positional behaviour* of primates. Originally proposed by Prost (1965), Rose (1973) resurrected this term and it is meant to include both locomotor behaviours (movements from place to place), as well as postural behaviours (wherein the subject and its surroundings remain relatively stable). Within this context, the locomotor repertoire of any primate usually consists of different types of activities, including a small number that are frequently used and others that are used less often. There is an optimum musculoskeletal design for the most efficient performance of a *particular* activity (Rose, 1991). Thus, in a primate possessing a varied locomotor repertoire, the postcranial morphology must represent a biomechanical compromise which is biased toward the *most important* activities (Rose, 1991).

In this context, the locomotor classifications used in the present study are based on preferential mode of travel, and will not describe in detail the complete list of positional behaviours that are possible and engaged in for any given primate. All primates, except humans, have grasping hands and feet and are adept climbers. Even the most terrestrially adapted cercopithecines climb trees regularly to obtain food items (for example, see Napier and Napier, 1970; Rose, 1977; Lahm, 1986), despite specializations of the upper limb that limit movements to primarily the parasagittal plane (Fleagle, 1988), as well as reduced phalangeal lengths that reflect a predominantly terrestrial habitus (Strasser, 1993). Similarly, all primates engage in varying frequencies of bipedal postures (see Schaller, 1963; Goodall, 1968; Fleagle, 1976; Cant, 1987; Doran, 1993), however these activities do not reflect adaptations or a biomechanical bias in the postcranial anatomy.

Knuckle-Walkers

Knuckle-walking is a unique form of locomotion used exclusively by African apes. In knuckle-walking stance, the forelimb acts as a supporting prop and the weight of the body is supported on the dorsum of the intermediate phalanx, while the metacarpophalangeal joint is hyperextended. Despite the fact that *Gorilla*, *Pan troglodytes* (chimps), and *Pan paniscus* (bonobos) all differ greatly in overall body size, they share this common mode of terrestrial locomotion. Body size has a major impact on primate ecology, and differences in frequency of arboreal activity and substrate use occur due to differences in body size even within species (Burns, 1979; Galdikas and Teleki, 1981; Tuttle and Watts, 1985; Sugardjito and van Hoof, 1986; Cant, 1987; Gautier-Hion,1988; Doran, 1993,1997). As a result, gorillas are more terrestrial than chimps (Schaller, 1963; Tuttle and Watts, 1985; Doran, 1996), and chimps are slightly less arboreal than bonobos (Badrian and Badrian, 1977; Doran, 1993).

Regardless of varying frequencies of arboreal activities and postures, the predominant mode of locomotion among all African apes is terrestrial knuckle-walking quadrupedalism (Schaller, 1963; Reynolds, 1967; Kano, 1979; Susman, 1984; Tuttle and Watts, 1985; Doran, 1993, 1997). Reports in the literature of subspecies differences in within *Gorilla* pertaining to frequencies of arborealism (Tutin and Fernandez, 1985; Kuroda, 1992; Remis, 1995; Doran, 1996), have little impact on gross overall forelimb morphology (Tuttle, 1967,1969a,b,1970; Inouye, 1992) since gorillas are exclusively terrestrial in their locomotor habits and possess no adaptations of the hand associated with high frequencies of suspensory activity (see Susman, 1979; Sarmiento, 1988,1994; Inouye, 1992,1994; Begun, 1993; Begun *et* al, 1994). As a result, for the purposes of this study, all subspecies of *Gorilla* are lumped together.

It has been suggested that chimps and gorillas may engage in kinematically distinct forms of knuckle-walking (Tuttle, 1967,1969a,b; Inouye, 1989,1992). While the basic hand posture is the same in these two taxa, there are some differences in the orientation of the elbow and hand, as well as preferred digit use. Gorillas tend to use highly pronated hand positions, with the dorsum of the hand held perpendicular to the forward line of progression and the elbow in hyperextension. Chimps, on the other hand, utilize more varied hand positions, often placing them obliquely to forward progression, and the elbow is not in a position of extreme hyperextension as in gorillas. (Tuttle, 1967,1969a ,b, 1970). Gorillas have absolutely and relatively the shortest metacarpals and phalanges of all great apes (Susman, 1979; Inouye, 1992,1994) and more evenly distribute body weight across the carpus while knuckle-walking. Inouye (1994) found that the second, third and fourth digits were used in knuckle-walking 89% of the time for all African apes, however significant differences in mean use of the fifth digit exist between *Pan* and *Gorilla*. Chimps and bonobos typically do not use the fifth digit for support in knuckle-walking, but gorillas do.

In her largest size category (85+ kg)[1], Inouye (1994) also found significant

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[1] This size is beyond the range reported by Jungers (1985) for male *P.troglodytes*, and may represent an obese, captive individual

differences between gorillas and chimps in mean use of the second digit. Chimps use the second digit less often for support than gorillas, even at this extreme size range for chimps. In addition, observations by Tuttle (1967,1969a,b) demonstrate that juvenile gorillas use knuckle-walking hand postures stereotypic of adults. Therefore, at common sizes, chimps and gorillas use slightly different postures. While there are no detailed descriptions in the literature regarding bonobo hand postures in knuckle-walking, comparisons with chimps in mean frequencies of use of any digit reveal no significant differences at any size category (Inouye, 1994).

Slow Climbers

Pongo (orangutan) is characterized as a slow, cautious climber utilizing all four limbs during climbing and scrambling activities (Davenport, 1967; MacKinnon, 1974; Galdikas, 1988). Quadrumanous climbing, forelimb suspension and "assisted brachiation" consisting of arm over arm movement accompanied by grasping of vegetation with the feet are common modes of progression in this taxon (Schaller, 1961; MacKinnon, 1974). Cant (1987) reports high frequecies of clambering, which is differentiated from climbing in the direction of movement. Clambering entails use of all four appendages and travel is in a horizontal direction. Orangs most often cross between trees by clambering (Cant, 1987). Only adult males are known to come to ground with any regularity and travel for short distances (MacKinnon, 1974; Cant, 1987; Galdikas, 1988), however terrestrial progression is achieved through "fist walking" or "crutch walking" as described by Tuttle (1967,1969a,b,1970) and is not considered to influence morphology significantly.

Brachiators

Brachiation, in the true sense, can be defined as slow to moderate pendular arm swinging where the trunk undergoes rotation under the supporting hand (Fleagle, 1974, 1976; Jungers and Stern, 1983; Larson and Stern, 1986). Only *Hylobates* (gibbons and siamangs) engage in this type of locomotion. Ricochetal brachiation, as described by Tuttle (1967,1969), incorporates greater speed and an aerial phase during progression through the canopy. The forelimb of brachiators serves as the prime propulsive organ during locomotion. During moderate speed arm swinging, both hands may momentarily contact the branch, but in rapid (ricochetal) swinging flexion at the elbow and shoulder joints may be so powerful that the animal is propelled forward and upward in free flight without hand contact (Carpenter, 1976).

Gibbons and siamangs are considered to be exclusively arboreal (Fleagle, 1980; Tuttle, 1990), engage in high frequencies of suspensory and climbing behaviours (Carpenter, 1976; Ellefson, 1974), and are highly adapted to an arboreal lifestyle in having proportionately the longest manual rays of all catarrhines (Schultz, 1973). Ricochetal brachiation in adult siamangs is less common than in gibbons, but juvenile siamangs engage in this type of locomotion more frequently (Fleagle, 1976). Climbing in siamangs is a forelimb dominated activity that involves more flexion than extension of the forelimb and hindlimb. Gibbons use less climbing, and more brachiation and leaping during travel, however brachiation comprises the highest percentage of locomotion in both gibbons and siamangs (Chivers, 1972; Fleagle, 1976).

Arboreal Quadrupeds

Arboreal quadrupedalism can be defined as above branch palmigrade progression. The sample of arboreal quadrupeds in this study consists primarily of *Colobus guezera* (black and white colobus), which incorporates a degree of leaping in its locomotor repertoire, but is predominantly quadrupedal in nature (Morbeck, 1977; Rose, 1978). In addition, one specimen of *Nasalis larvatus* (proboscis monkey) is included. This latter taxon is larger-bodied than colobus monkeys, but still restricts most activity to the trees and also incorporates some degree of leaping (Kern, 1964; Kawabe and Mano, 1972).

Terrestrial Quadrupeds

Terrestrial quadrupedalism in this sense refers to cercopithecine monkeys utilizing digitigrade postures (Napier and Napier, 1967). Digitigrady involves placing the ventral aspect of the proximal phalanx against the substrate with hyperextension at the metacarpophalangeal joint. Digitigrade monkeys such as *Papio anubis* will retreat to trees or cliffs at night to avoid predators, but in engage in very little climbing during the day (Rowell, 1966; Aldrich-Blake *et* al, 1971; Rose, 1977). Upon entering the trees, terrestrial quadrupeds will adopt digitigrade postures on branches during feeding (Rose, 1974,1977). Although essentially terrestrial, *Papio sphynx* (mandrill), a forest dweller from Gabon, engages in higher frequencies of branch walking and spends a greater amount of time foraging in the trees than other *Papio* species (Lahm, 1986).

Materials and Methods

Sample

This study is based on measurements of the forelimb taken from adult and sub-adult hominoids and Old World monkeys of differing sexes from wild-shot and captive populations. Appendix I (page 256) lists the specimens included in the study and the institutes in which they are housed.

Measurements

Osteological features under investigation were video taped and the images digitized to obtain linear, area and angular measures. Images were collected using a Canon A1 digital 8mm video camera mounted on a tripod and leveled to ensure that the lens was perpendicular to the surface being viewed. Images were recorded on 90 minute Hi-8 video tapes and measurements were obtained using *Mocha* 2-D video image analysis software from Jandel Scientific. The camera was placed within telephoto range (approximately 2 feet from the skeletal element) to maximize image size using the zoom control and reduce parallax error.

Specimens were mounted in plasticine to keep them stable with the surface being measured perpendicular to the lens. A 10x10 mm scale was placed beside and in the same plane as the articular surface in question for calibration purposes. Caliper measurements using Mitutoyo digital calipers were also taken for comparison to determine the degree of error in the digitized measures. Accuracy between the two methods was well within 0.5 mm for linear measures. Linear measurements obtained during the digitizing process were also compared to published data to ensure that results were comparable. For example, a measurement of 7.58 mm was obtained for the Rud 78 (*Dryopithecus brancoi*) proximal phalanx midshaft breadth. Begun's (1993) published result for this measure is 7.5 mm.

A set of variables was selected for each anatomical region of the forelimb where differences in gross morphology of the joint surface would be expected to reflect patterns of joint usage across taxa of differing locomotory styles. Specifically, this investigation includes the distal humerus and proximal ulna, the distal radius and proximal as well as distal carpal row, and the metacarpophalangeal joints. Table 1.1 (page 23) lists measurements taken on each element and figures 1.1-1.15 (pages 24-30) illustrates how measurements of articular surfaces were obtained during the digitizing process. Detailed descriptions of predictions tested and variables selected are outlined in each section.

One caveat regarding the measurements obtained is that video image analysis will *underestimate* the value of the true area of a highly curved surface, whether it is convex or concave. Measuring articular surface areas that are variable in 3 dimensions in a 2-dimensional plane cannot accurately account for changes in topography. Thus, the distal articular surface of the radius, for example, may appear to be similar between two taxa, however the *deeper* surface of the two will have a greater overall surface area. Having said that, the analysis presented here produces results that are comparable to previously published comparisons of taxa using linear measurements. For example, studies based on linear measurements by Harrison (1982, 1986) and Rose (1993) have shown that monkeys have smaller trochlear areas relative to capitulum areas on the distal humerus. Results from this study are in accordance with those findings. Hence, despite the limitations of 2 dimensional measurement of 3 dimensional objects, the technique is still valid and useful for making comparisons of area among various elements.

Statistics

All summary statistical analyses were performed on species means. Standard deviations (*s*) and coefficients of variation (cv) of variables are reported. Sample sizes for each group are unequal and relatively small. As a result, non-parametric statistical tests were used to investigate between-group differences in order to eliminate distributional and dispersional assumptions (Zar, 1984). Mann-Whitney U-tests were used on raw variables for pairwise between-group comparisons. Correlations between sets of variables and the relationship of variables to body size were investigated by generating Spearman Rank Order correlation coefficients.

Further bivariate comparisons of the relationship of variables to body size were accomplished using ordinary least squares (OLS) regression models. The preferred line fitting technique for most biological data is reduced major axis (RMA), which assumes error in both the x and y variables (Harvey and Pagel, 1991) and is the least biased estimate of a functional relationship (Kendall and Stuart,1979; Swartz,1989). The two methods derive different estimates of the slope of a line, unless the correlation coefficient is 1.0. Discrepancies between the two techniques are small when the coefficient of determination (r^2) is greater than 0.90, and increase as the coefficient of determination declines. However, residuals from OLS regression lines are uncorrelated with x, whereas those from RMA generally are correlated with x. Since the primary goal of this analysis is to control for the effects of size, ordinary least squares regression was used for all analyses (Harvey and Pagel, 1991; Jungers,1985) and RMA slopes and y-intercepts are merely reported where applicable. In those instances where differences in slopes and intercepts are investigated, only those differences that agree using both methods are reported.

Body weights for the specimens included in this analysis were unavailable, so a suitable size surrogate was substituted. Use of published mean body weights in the regression analyses was not desirable since intraspecific body mass is much more variable than skeletal or dental measures (Van Valkenburgh, 1990; see also Smith and Jungers, 1997). However, in order to select a size surrogate to be used in further investigations, published mean species body weights taken from Jungers (1988) and Rowe (1996) were regressed against a subset of variables. Selection was based on a high correlation coefficient (r) and low percentage prediction error (%PE).

Regressions based on the total sample, where the range of values for x is high, often produce correspondingly high values of the correlation coefficient. Similarly, when small size subsets are used, as in intraspecific regressions, resultant r values are typically quite low. However, this does not neccessarily reflect the predictability of the equation (Smith, 1980;1985). By calculating the residuals and comparing them to predicted values, a more accurate estimation of the predictive value of a regression or independent variable can be made. Thus, the percentage prediction error is calculated as:{ (observed-predicted value)}/predicted value) x 100. All regressions were performed on log transformed data, but simply adding up the residuals in log space and taking the antilog of the mean will result in a geometric mean prediction error (Smith, personal comm.). Consequently, the predicted value was detransformed back to linear scale to calculate the %PE.

In selecting a size surrogate, it is suggested that a measure that might be functionally related to the dependent variable be avoided, and instead a feature that is functionally and anatomically remote is preferred (Smith, 1993). However, one of the goals of this study is to examine the relationship of a small number of fossil species to extant taxa. It is extremely rare to find a complete skeleton or even a large portion of associated elements from the same individual in the fossil record. For this reason, only variables from the forelimb where used to determine a suitable body size surrogate. Measures that were selected were: the bi-epicondylar breadth of the humerus, the radio-ulnar breadth of the distal articular surface of the radius, and a composite of linear measures of all metacarpals (excluding the first metacarpal). This composite was calculated as the mean of the ventral head breadth, midshaft width, and midshaft breadth of metacarpals II-V. Regression values and %PE are listed in Table 1.2 (page 22)

Table 1.2: Size surrogate prediction variables regressed against body mass

Size variable	*r*	S.E.E.	%PE
metacarpal composite	0.97	0.01	18.4
epicondylar breadth	0.94	0.10	18.6
Radius distal articular breadth	0.97	0.11	20.5

As mentioned earlier, body mass is a highly variable characteristic of any species, so "we should not feel dismayed by the large prediction errors for estimates based on regressions of skeletal measures" (Van Valkenburgh, 1990,p.197). For the purposes of this study, values under 20% were deemed acceptable.

Discriminant function analysis is used to assess the reliability of variables used from each anatomical region of the forelimb for distinguishing among primates of differing locomotory styles. Predictive reliability of these variables is determined by reporting the number or percentage of missclassifications. Features of the elbow, the wrist, and the metacarpophalangeal joint are entered as variables and used to predict taxonomic group membership among extant species, followed by classification of extinct taxa where possible.

Table 1.1: List of Measurements Used in the Study

Element	Measurement
Humerus Figure 1.1, 1.2	Ventral trochlear area, distal trochlear area- area between the medial and lateral trochlear keels Ventral trochlear angle, distal trochlear angle - the angle formed from the most ventral and distal extensions of the medial keel to the base of the trochlea to the most ventral and distal extensions of the lateral keel. Ventral capitulum area - measured from line extending along zona conoidea and along ventral perimeter of capitular surface Distal capitulum area - measured along perimeter of capitulum surface
Ulna Figure 1.3	Trochlear notch angle - measure of degree of cranial orientation of the ulnar trochlear notch
Radius Figure 1.4	Distal articular surface - measured along perimeter of the facet Scaphoid area, lunate area - measured along radial and ulnar perimeters, and down along the articular demarcation between the scaphoid and lunate surfaces respectively
Lunate Figure 1.5	Proximal articular surface area- measured along the visible boundary of the proximal surface
Scaphoid Figure 1.6	Proximal articular surface area- same as above
Capitate Figures 1.7-1.10	Scaphoid facet area, hamate facet area, distal facet area - all measured along the perimeters of the facets
Hamate Figures 1.11-1.13	Capitate facet area, distal articular surface area - measured along perimeter of articular facets
Metacarpal Figure 1.14	Ventral and dorsal head arc lengths, and head curvatures (measured as included angle and normalized radius of curvature-see text).
Proximal Phalanx Figure 1.15	Proximal articular surface- measured along perimeter of facet

Figure 1.1

Ventral Humerus Measures

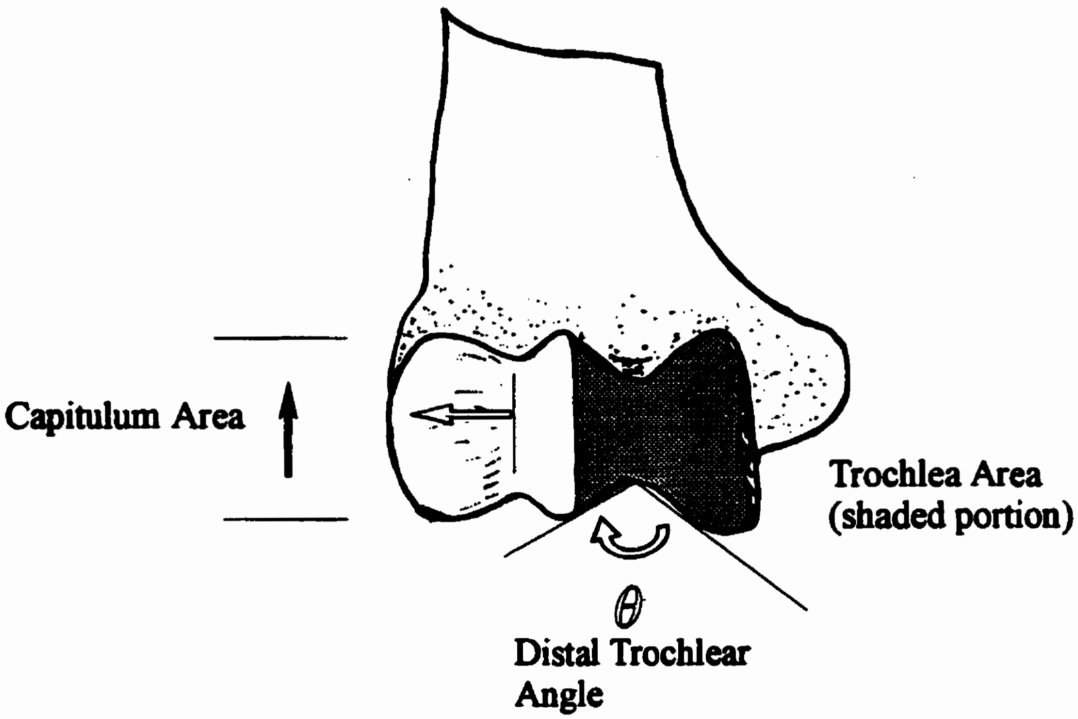
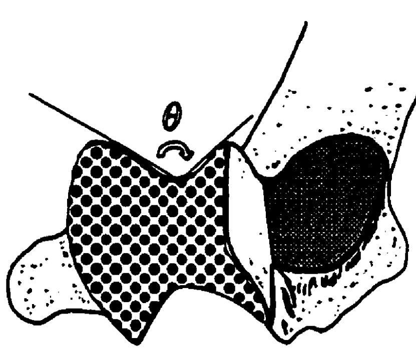


Figure 1.2
Distal Humerus Measures

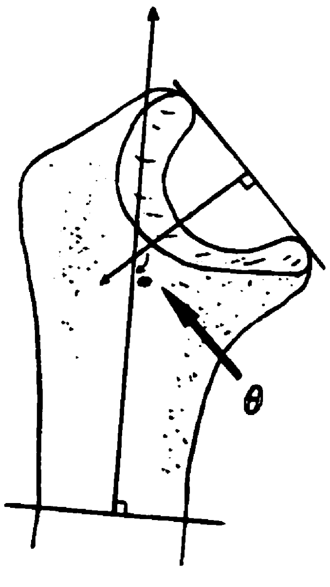


θ = trochlear angle

Shading = capitulum area

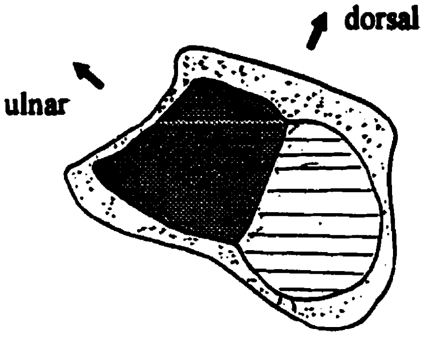
Dots = trochlea area

Figure 1.3: Ulna Trochlear Angle



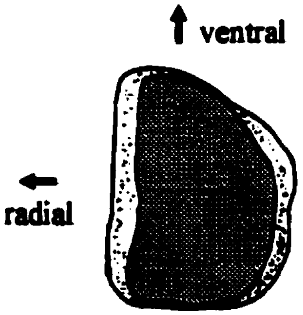
θ = angle in degrees
of trochlea orientation
relative to long axis of
shaft

Figure 1.4: Distal Radius Measures



Lines = scaphoid area
Shaded= lunate area
Total radius distal area measured along the facet perimeter

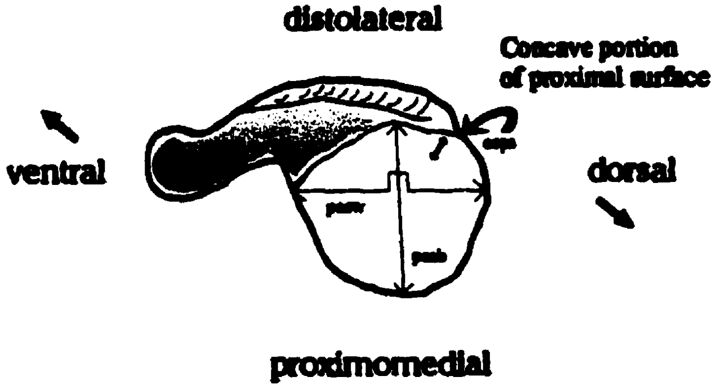
Figure 1.5: Lunate Proximal Surface Area



Shaded portion represents proximal articular surface

Figure 1.6 : Scaphoid Proximal Articular Surface Area

Proximolateral View



Proximal surface area measured along perimeter of radial facet

Capitate Measures

Figure 1.7: Lateral View

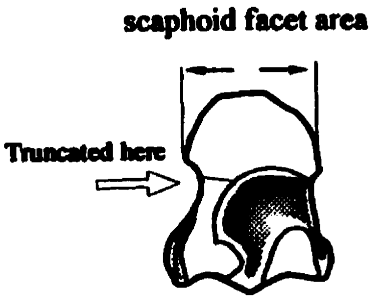


Figure 1.8: Proximal View

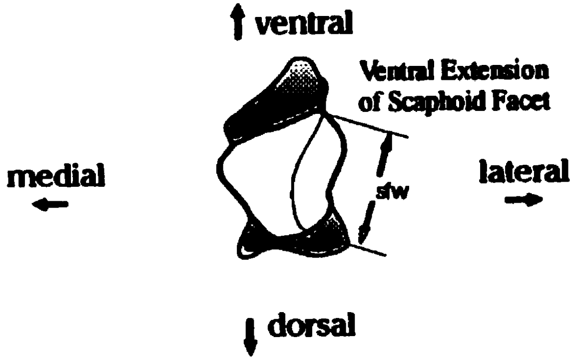


Figure 1.9: Distal View

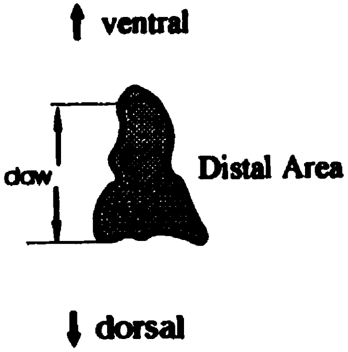
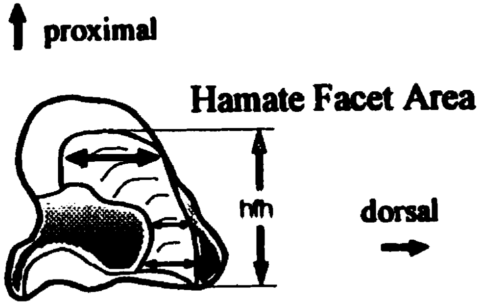


Figure 1.10: Medial View



Hamate Measures

Figure 1.11: Distal View

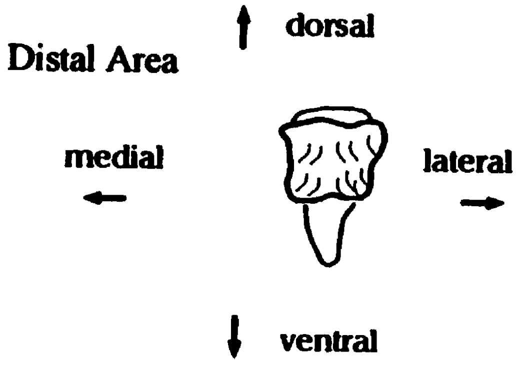


Figure 1.12: Dorsal View

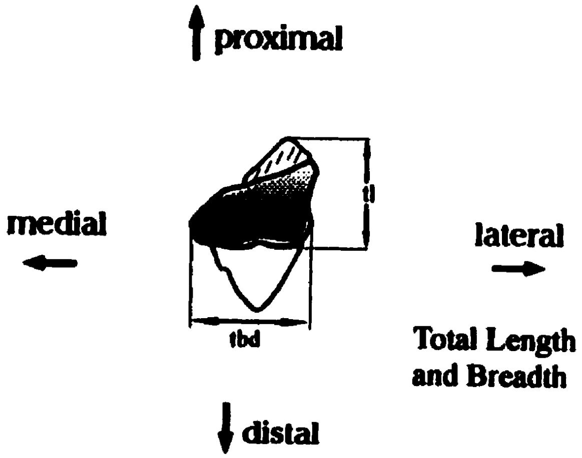


Figure 1.13: Lateral View

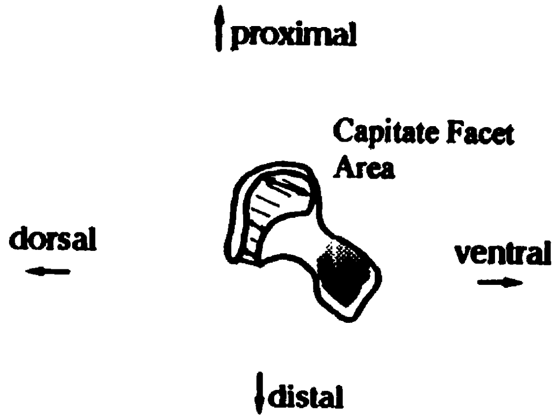
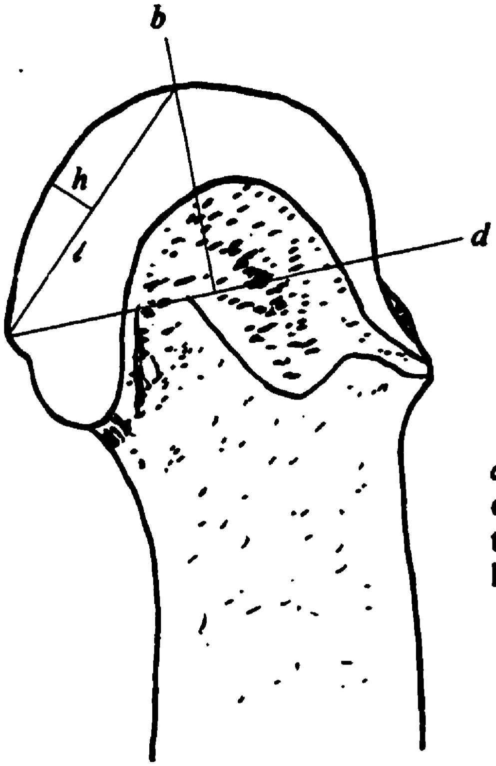


Figure 1.14: Metacarpal Head Curvature



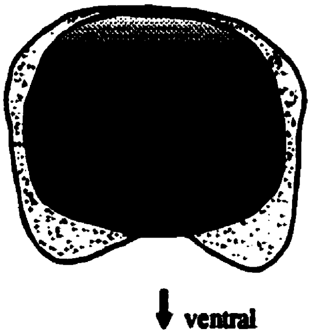
d delineates the ventral and dorsal boundaries of the articular surface of the head

b divides the surface of the head into ventral and dorsal halves

l is the chord length

h = the height of the arc

Figure 1.15: Proximal Phalanx Proximal Articular Surface Area



Shaded Area = proximal facet - area measured from perimeter of facet

CHAPTER 2

The Elbow

Background

The primate elbow exhibits a number of morphological patterns, since it is comprised of several different joints, each with functionally distinct components (Rose 1988,1993). Characteristic features of these elements in extant species provide insight into the influence of different locomotor styles and postural activities on excursion ranges and joint loading across the elbow. The use of the forelimb in locomotion is universal in all anthropoids except humans. As discussed in chapter 1, monkeys are typically quadrupeds and as such, use the forelimb as a prop for support and propulsion during forward progression. Hominoids, on the other hand, possess a unique suite of characters enabling them to hang or swing below branches, and engage in vertical climbing and hoisting behaviours. African apes are proficient at these activities, however they prefer terrestrial pathways for habitual locomotion and utilize knuckle-walking quadrupedalism. As a result, the articulations between the distal humerus and proximal ulna and radius are regularly subject to either compressive, tensile or shear stresses, or any combination of these.

It has been well documented that hominoids posses several features of the elbow that emphasize universal stability throughout the full range of flexion-extension and pronation-supination of the forelimb (Harrison 1986,1987,1991; Rose 1988,1993; Sarmiento 1985,1988). In contrast, monkeys have a particular stable position, resulting from close-packing in full pronation (Rose,1988). The trochlea of the distal humerus, so named because of its spool-like or trochleiform shape, fits into the trochlear notch of the proximal ulna. This joint is essentially uniaxial and permits flexion and extension of the forelimb. In hominoids, the medial boundary of the trochlea, or medial keel, is well developed all the way around its margin from ventral to dorsal aspect. In monkeys, this keel is most prominent ventrally and distally (Rose, 1988). The lateral border or keel is robustly developed in apes, although somewhat less pronounced in gibbons (Harrison,1986). It continues posteriorly and extends proximally onto the lateral wall of the olecranon fossa, forming an articular surface for the proximal portion of the trochlear notch of the ulna. According to Harrison (1987), presence of a lateral keel in non-cercopithecine monkeys is determined by body size, but although large arboreal colobines such as *Nasalis* have minimally developed lateral keels, in most non-hominoids this feature is very reduced or absent (Rose,1988,1993). As a result, the trochlea in monkeys is more cylindrical in shape and best suited to resist medially directed forces such as those incurred during use of the limb in quadrupedal stance, as well as forces exerted by muscle contraction. Component forces of muscles such as *flexor digitorum superficialis*, *flexor carpi ulnaris*, *flexor carpi radialis*, and *pronator teres* act perpendicular to the long axis of the ulna and exert considerable force. Consequently, a large area of the humeral joint surface must be placed perpendicular to these component forces to prevent compressive stresses from becoming too great (Preuschoft,1973).

The morphology in hominoids is quite different. In addition to prominent medial and lateral keels, the trochlear surface is concave, thus truly *trochleiform* and is described as being strongly "waisted" (Harrison 1986,1987,1991; Rose 1988,1993). Thus, the deeply excavated articular surface of the trochlea, the robustly developed medial and lateral keels, and the humero-ulnar contact on the lateral aspect of the olecranon fossa with the forearm in full extension are all traits associated with load transfer and stabilization of the elbow under compressive or tensile stress (Jenkins,1973; Harrison,1986,1987; Rose,1988,1993; Sarmiento, 1985,1988). According to Sarmiento, stabilization of the humero-ulnar joint is particularly important in suspensory activities, as the trochleiform shape of the trochlea prevents displacement of the ulna during pronation/supination of the forearm or rotation at the shoulder. He notes that of all hominoids, excavation of the trochlea and development of the medial keel is most pronounced in orangutans. In contrast, gorillas possess a medial keel that is relatively small and a much less trochleiform anterior trochlea (Rose,1993).

The expression of these characters relating to humero-ulnar joint stability in apes is considerably less remarkable in modern humans. Hence, the lateral keel is poorly developed, the trochlea is less spool-shaped, and lack of dorsal extension of the trochlea into the olecranon fossa limits hyperextension capabilities of the elbow (Rose,1993; Carlsoo and Johansson,1962). In humans, adduction of the ulna accompanies supination of the forearm, and abduction accompanies pronation (Palmer *et* al, 1982; Pirela-Cruz *et* al, 1991, cited in Rose, 1993a), suggesting that there is a lack of complete congruency at the humero-ulnar joint (Rose,1993a).

The morphology of the proximal ulna also differs among extant taxa. Among hominoids, the olecranon fossa is greatly reduced in height, the coronoid process projects ventrally, and the trochlear notch has a cranial orientation. The extreme reduction of the olecranon process permits an increased range of motion, since the proximal portion of the trochlear notch does not fully engage the olecranon fossa of the humerus until a position of extreme extension or hyperextension is reached (Fischer,1906; Harrison, 1986,1991; Martin,1934; Rose,1988,1993a). Gorillas exhibit the greatest reduction in olecranon height, followed by gibbons, orangutans and then chimps (Martin,1934). However, in order to maintain a full range of motion at the elbow (the forearm encompassing an arc of approximately 180°), there is a comcommitant ventral projection of the coronoid process, resulting in a cranially oriented tilt of the articular surface (Harrison,1986; Rose,1993a). This tilt is characteristic of all apes, but according to Harrison (1986) its expression is somewhat reduced in gibbons. The projection of the coronoid process is accommodated by a deep coronoid fossa above the trochlea of the humerus. As a consequence of having deep olecranon and coronoid fossae, the bone between these two structures becomes quite thin, and large hominoids especially have a high incidence of fenestration above the trochlea (Harrison,1991; Rose,1993).

Hominoids also share a high degree of stability at the humeroradial joint at all positions of supination-pronation. The capitulum is large and globular, equally curved in all directions, and extends farther posteriorly than in any other primates, allowing the radius to move with the ulna into a position of hyperextension. This is particularly advantageous in compressive load transfer by providing a large surface area of contact, and resists dislocation of the radial head when the elbow is subjected to compression, tension, or shear (Rose,1988,1993). According to Sarmiento (1985), the relative size of the capitulum is greatest in gibbons. Thus, great apes tend to have relatively large humero-ulnar joints, while gibbons have large humeroradial joints. Both Harrison (1982,1986) and Rose (1993) argue that the relative size of the trochlea with respect to the capitulum is not directly associated with body size, and among anthropoids there is an allometric tendency for the width of the trochlea to increase at a faster rate than the width of the capitulum. It would seem, then, that gibbons depart from this pattern.

It has been demonstrated that structural modifications of the distal humerus and proximal ulna in extant hominoids are directly linked to maximally stabilizing the elbow during all positions of flexion-extension and/or pronation-supination. These varied forearm positions are typical components of daily activity of large hominoids in an arboreal milieu. Indeed, in their EMG study of muscles acting on the forelimb, Tuttle and Basmajian (1974) have shown that osseo-ligamentous structures are primarily responsible for stability across the elbow during suspensory postures. This is illustrated by the complete lack of activity of all brachial muscles, triceps and anconeus during hanging and rotary movements with the arm fully extended. In contrast, knuckle-walking posture in African apes is not maintained by close-packed positioning of osseous and ligamentous structures (Tuttle and Basmajian,1974).

In knuckle-walking stance, the forearm forms a relatively straight supporting prop. Continuous activity of the triceps muscles, as well as anconeus which acts as an auxillary extensor in gorillas, confirms that considerable muscular force is necessary to maintain the extended elbow position. Anconeus may function in a manner analogous to that of the popliteus in the human knee. It is particularly active when the forearm is fixed and shows bursts of activity, "snapping" the elbow into close-packed extended position, as the load passes over the joint. In comparing the elbow of knuckle-walkers to the knee of bipeds, Tuttle and Basmajian (1974) state that much of the weight of the body falls on the hindlimbs in gorillas, such that the forearm is proportionately less loaded than the hindlimb of humans.

However, the extensors of the elbow are continuously active during knuckle-walking stance, whereas extensors of the knee are inactive in bipedal stance in humans. The implication, according to these authors, is that the elbow in African apes is not especially adapted for knuckle-walking as the human knee is for bipedalism. I would argue that the extensor muscles of knuckle-walking apes are more likely functioning in a manner similar to the gluteus medius muscles in the human hindlimb. Insofar as the gluteals prevent the hip from adducting when the line of center of mass passes medial to the joint, the extensors act in a similar fashion preventing the forearm from flexing. Indeed, the shoulders of African apes are proportionately much broader than the hips of humans, and the line of center of mass passes farther away from the elbow joint than it does from the human knee joint.

Finally, in studies of humans Carlsoo and Johansson (1962) have shown that more stable support in a falling body is provided when the forearm is over-extended rather than slightly flexed. The reduced olecranon process in all hominoids permits hyperextension of the forearm, but may be particularly advantageous to knuckle-walkers by maximizing stability when the joint is under compressive stress (Tuttle and Basmajian,1974).

Much of the interpretation in the previous work briefly outlined here is based on linear measurements and qualitative description. The purpose of this chapter is to examine features of the distal humerus and proximal ulna discussed above in a more accurate and quantitative manner.

It has been well established that joint surface area scales positively with body size (Jungers,1988; Kappelman,1995; Swartz,1989). It may be predicted that animals engaging in specialized locomotor behaviours involving distinctive loading patterns will show unique joint design characteristics departing from allometric trends. Harrison (1982,1986) has stated that in large primates, the increased relative surface area of the trochlea for articulation with the ulna is directly responsible for the development of structural modifications that are associated with humero-ulnar joint stability. Since joint surface geometry differs among anthropoid taxa (Swartz,1989), linear measures may not accurately reflect surface areas. For this reason, digitized video images are used to calculate joint surface areas of the trochlea and capitulum. In addition, rather than describing the "trochleiform" nature of the trochlea or the "tilt" of the trochlear notch of the ulna, these features are quantified by measuring the angles between the medial and lateral keels on the trochlea, and the angle of the trochlear notch relative to the long axis of the shaft of the ulna. Figures 1.1 - 1.3 (pages 24-25) graphically illustrates how these measurements were obtained.

Results from this analysis are then used to either corroborate previous findings or demonstrate novel structural modifications in the elbow region among hominoids. Of particular interest is whether these measurements can tease out unique morphological traits in knuckle-walking African apes. More specifically, the questions to be addressed include:

1. What is the pattern of scaling of trochlea and capitulum area relative to body size?
2. Do capitulum and trochlea area scale differently from each other?
3. Is the shape of the trochlea (ie: the size of the angle between the medial and lateral keels) merely a function of body size, or can it be associated with limb usage and locomotor repertoires?
4. Is the orientation of the trochlear notch of the ulna linked with humeral trochlear

shape?

Results

Descriptive statistics for all humeral and ulnar dimensions are given in Table 2.1 (page 50), and summaries of Mann-Whitney U-test comparisons for selected variables are found in table 2.2 (page 52). The square roots of trochlear and capitular areas were taken for ease of comparison to linear measures of body size surrogate in regression analyses. Mann-Whitney U-tests of pairwise comparisons on trochlea and capitulum articular areas reveal expected significant differences among taxa due to gross body size differences (Figure 2.1-2.2). Looking at the *ratio* of trochlea to capitulum area ventrally chimps, bonobos, orangs and humans are all similar, and gorillas have slightly larger relative trochlear areas (figure 2.3).The pattern distally is slightly different. Here we see that humans are significantly different from all other taxa in having the highest trochlea to capitulum ratio (figure 2.4). The reason for this high ratio is a slightly smaller capitulum area distally (as indicated by z-scores for this variable) as opposed to a greatly enlarged trochlea relative to other large hominoids.

Group means for trochlear angles and ulnar notch angle are depicted in figures 2.5-2.7. The error plot of ventral trochlea angle clearly illustrates that all hominoids have small angles, or highly constrained elbow joints. This is especially true of orangutans, which supports Sarmiento's (1985) earlier conclusions. Results from pairwise comparisons corroborates this finding, in that humans are significantly different from all large hominoids and siamangs in the degree of humero-ulnar constraint ventrally. Interestingly, siamangs are significantly different from gibbons and most similar to orangs in ventral trochlear angle. Arboreal monkeys have the least constrained elbow joint, suggesting a more generalized pattern of limb loading.

Measurements of trochlea angle along the distal aspect of the humerus shows a very similar pattern among large hominoids (figure 2.6). Brachiators, however, appear to have *less* constrained joints distally than ventrally. This is particularly true of siamangs. Both gibbons and siamangs are not significantly different from humans in this dimension.

Figure 2.7 shows the relationships among taxa based on ulnar notch angle. As mentioned earlier, a high trochlear angle is characteristic of all large hominoids, and pairwise comparisions demonstrate that knuckle-walkers, orangs and modern humans have much more cranially oriented trochlear notches compared to brachiators and monkeys. Harrison's (1986) claim that cranial orientation of the ulnar notch is present but somewhat reduced in gibbons is challenged by the results presented here. Indeed, there is a complete overlap in ranges among brachiators, arboreal and terrestrial monkeys and no statistically significant differences exist among them. Chimps, bonobos and humans are most similar in the degree of cranial orientation of the trochlear notch, while orangs and gorillas respectively have somewhat higher values.

In order to determine the effects of body size on structural features of the elbow, further bivariate comparisons are neccessary. Results from regression analyses are found in Table 2.3 (page 53). Values for OLS and RMA are reported. Humeral and ulnar variables were regressed against both the metacarpal composite and radius distal articular surface body size surrogates. Neither of these surrogates is from a region anatomically remote from the elbow, therefore it is quite likely that they are functionally related to features of the distal humerus and proximal ulna. Hence, interpretation of regression results must be made with caution. For this reason, both surrogates are used for comparison. Results from both are very similar, and the following discussion will be based on variables regressed against radius distal articular surface breadth. Any discrepancies between the two methods will be noted.

It is clearly demonstrated that trochlear area both ventrally and distally is highly correlated with body size, and increases at a rate close to isometry. Gorillas show the greatest amount of dispersion about the regression line (see figures 2.8-2.9), indicating a wide range of variability in both trochlear area and body size (whether radius articular breadth or metacarpal size). The same pattern is true for capitulum area, although the slopes for this measure are much lower both ventrally and distally compared to those for the trochlea (figures 2.10-2.11). Examining the scaling pattern of trochlea verses capitulum areas more carefully (figures 2.12-2.13), using Clarke's (1980) test for RMA slope differences reveals that, although the rate of increase of trochlea area is higher than that of capitulum area, no significant differences exist in slopes for ventral measures. Distally however, capitulum area increases at a significantly lower rate than trochlea area with respect to body size, confirming Harrison's (1982) earlier findings. Thus, as body size increases, it seems there must be a greater need for structural modification in the trochlea rather than the capitulum.

In order to assess the possible contribution of trochlear angle to trochlear *size*, these two variables were regressed against each other. The question is, does the degree of elbow joint constraint have some bearing on joint size? Those taxa having highly constrained humero-ulnar joints are expected to have large negative residuals, while those with broader trochleas should have more positive residuals. Figures 2.14-2.15 illustrate that the actual correlation between these variables is very low for the ventral aspect, and somewhat higher distally. There is, however, a pattern in the distribution about the line that is consistant in both plots. Gorillas all tend to have much larger trochlear areas than would be expected given their trochlear angles. Conversely, gibbons and siamangs all fall well below the line, indicating that they have much smaller trochlear areas than would be expected given their trochlea angles.

Values for angular measures in a regression do not readily convey information regarding the relationship to body size. Thus, following the methodology described by Swartz (1989), the residuals from the previous regression were in turn regressed against body size surrogates to determine if the distribution of positive and negative residuals about the regression line is related to body size. These plots are shown in figures 2.15-2.17. The results indicate that the contribution ventrally of trochlear angle to trochlear size is more closely associated with body size, having a slope nearer isometry, than measures distally. Nonetheless, both regressions show a similar pattern of distribution about the line. A Chi-square comparison of the distribution of positive and negative residuals by taxon (table 2.4, page 54) illustrates that, among large hominoids, gorillas and humans have the highest percentage of positive residuals with respect to body size. This means that trochlear angle is, in fact, broader than would be expected given their body size. Conversely, chimps, bonobos, orangutans, gibbons and siamangs all have higher percentages of negative residuals. Hence, their trochlear angles are narrower, more constrained than would be expected for their body sizes. Gorillas are significantly different from chimps, bonobos and orangs in the distribution of their residuals.

The same tests were run against the metacarpal composite as a size surrogate. Although the pattern was similar for all great apes, the residual distributions were different for humans and brachiators. The reason for this is likely that these taxa possess unique morphologies of their metacarpal dimensions. Humans have particularly stout, robust metacarpals, whereas those of brachiators are extremely slender and gracile.

Examination of ulnar trochlear notch orientation verses radius articular breadth (figure 2.17) indicates a pattern of increasing ulnar notch angle as body size increases, however the correlation is not particularly high (*r*=.84) and there is a fairly wide range of variation. Indeed, values for ulnar notch angle are similar for small gibbons and larger terrestrial monkeys, as noted previously in tests of pair wise comparisons, despite the fact that these taxa engage in vastly different modes of locomotion. Regardless of the trend for increasing cranial orientation of the ulnar notch in large hominoids , this trait *has* been functionally linked to greater extension capabilities of the forelimb, a characteristic neccessary for large apes engaging in suspensory activities. If comparably sized terrestrial anthropoids were available for comparision, perhaps the results would show a noticeably different pattern. Gibbons are second only to gorillas in reduction of the olecranon process (Tuttle and Basmajian, 1974), allowing them a greater range of extension than is possible in monkeys. This would suggest that reorientation of the trochlear notch of the ulna in more cranial direction is a derived trait arising out of need for high ranges of flexion and extension neccessary in large arboreal species engaging in climbing and suspensory activities.

To summarize the findings thus far, it has been demonstrated that:

1. Increase in trochea and capitulum areas is correlated with increasing body size, but trochlea area increases at a faster rate than does capitulum area.
2. The "trochleiform" nature of the the trochlea, represented as the angle between the medial and lateral keels, is not strictly a function of increasing body size. It is best expressed in those species engaging in climbing and suspensory behaviours, suggesting a greater need for stability at the humeroulnar joint.
3. Reorientation of the trochlear notch of the ulna in a more cranial direction is functionally related to the need for increased flexion-extension capabilities in large arboreal species engaging in vertical climbing and suspensory activities, rather than strictly a function of increasing body size.

In order to assess the reliability of these features in predicting taxonomic group membership and associated locomotor proclivities, discriminant function analysis was performed. All features of the distal humerus and proximal ulna that have been discussed so far were entered as variables into the discriminant analysis. Results are found in table 2.5. One of the assumptions of discriminant function analysis is that predictor variables should have normal distributions and within group variance-covariance matrices should be equal across all groups. Visual inspection of histogram plots reveal that area measures of the distal humerus are not distributed normally across all taxa. This is likely a function of sampling error (small sample size), differing levels of sexual dimorphism within each taxon, and/or unequal representation of males and females. Homogeneity of variance tests indicate that equal variance can be assumed for trochlear angle ventrally, the ratio of trochlea to capitulum area ventrally, and ulnar notch angle. All other variables considered have significantly different variances, however. Again, this is likely a consequence of groups represented by pooled sexes and differing levels of sexual dimorphism among the taxa under investigation. Furthermore, variables that are correlated will tend to share discriminant weights. Ventral area measures of the trochlea are correlated with distal areas, however ratios of area measures and angular measures (ventral and distal trochlea, ulnar notch angle) are not correlated with area measures or each other. Since certain variables do violate some of the assumptions of discriminant function analysis, the results should be interpreted with caution.

As seen in Figure 2.18, all large hominoids are grouped together on the basis of their elbow morphology. Function 1 along the *x* axis discriminates species on the basis of trochlea area ventrally and distally, and ulnar notch angle. Function 2 separates groups according to distal and ventral trochlear angle. The centroids for chimps, bonobos and orangutans are tightly arranged, while gorillas are slightly separate based on size and somewhat larger trochlear angles. Brachiators group with monkeys based on trochlear size and ulnar notch angle, but are clearly distinct from them with respect to humeral trochlea morphology. Humans are of similar size to large apes, but are also clearly distinct from them based on trochlea morphology. There is a slight overlap in ranges, however the centroids are quite separate.

Classification results of predicted group membership are found in Table 2.6 (page 56). Eighty-four percent of cases are correctly classified into taxonomic group membership. Orangutans were correctly classified 100 percent of the time, and 11 percent of gorillas were mistaken for orangs. Chimps and bonobos were classified correctly most of the time, and the majority of errors occurred in missclassification as eachother. For modern humans, 10 percent were mistaken for chimps. Although sample sizes in some cases are very small, the results do demonstrate that the traits used in this analysis are useful and functionally significant in discrimating among taxa according to locomotor repertoire.

Discussion

This analysis of the elbow region does corroborate certain findings of previous research. Surface area measurements show that the humeral trochlea area scales very close to isometry, and is only slightly positively allometric (RMA results). This indicates there is but a very small size-dependent increase in relative surface area in this structure. The relationship of trochlea area to that of the capitulum paints a somewhat different picture. The latter increases at a rate below isometry and slopes for the two measures are significantly ($p<.05$) different along the distal aspect. Slope values for capitulum area are virtually identical both ventrally and distally, however it is the trochlea area that is more positively allometric distally. This supports Harrison's (1982) conclusions, as well as Rose (1993) who states that "The size of the anterior part of the trochlea - relative to the area for articulation with the radius- is not linked to absolute size" (p.75). Among hominoids, there is a tendency towards a medial shift in the transmission of force through the elbow (Godfrey *et* al, 1991). As demonstrated, hominoids have larger humeral trochlear surfaces relative to capitulum surfaces, such that much of the load is borne through the humero-ulnar joint. The opposite is true of cercopithecine monkeys, wherein the capitulum area is enlarged and load bearing is shared more evenly between the humero-ulnar and humero-radial joints.

Results from this analysis would seem to indicate that, albeit small, there is a slightly more size-dependent increase in trochlea surface area distally than ventrally, implying that habitual limb loading with a fully extended forearm has a significant functional impact on the structural morphology of the distal humerus. Change in size of the capitulum is much more conservative, however overall geometry (ie: rounded globular shape in hominoids verses flattened shape anterodistally in monkeys) reflects the dependence in hominoids on rotational capabilities rather than transmission of compressive joint stress at the humeroradial joint.

Examining the angles between the medial and lateral trochlear keels, it has been demonstrated that all hominoids share highly constrained joint surfaces. Rose (1993) has stated that orangutans have the "most trochleiform anterior trochlea"(p.89) and gorillas have an anterior trochlea that is "less trochleiform than in other apes" (p.90). Mean values for this measure reveal that *Pongo* does indeed have the smallest trochlear angle both ventrally and distally of all hominoids. However, it is gibbons and siamangs that have the largest trochlear angles among hominoids, while gorillas have the broadest measure among large apes.

That gibbons and siamangs have much less constrained humero-ulnar joints distally is interesting. Brachiators posses an extremely powerful flexor apparatus, aided by the long digital flexors. In particular, development of *fl.digitorum superficialis* is most pronounced in gibbons (Tuttle,1969). Presumably, the same is true for siamangs. In all other hominoids, the *fl.digitorum profundus* is the predominant long digital flexor. Many gibbons, however, possess superficial digital flexors that are *more* developed than the profundus muscles, a condition never seen in great apes. If the chief function of the superficial flexors were for powerful flexion during suspensory activities, one would expect that orangutans would have the largest superficial flexors (Tuttle,1969). Gibbons also have a prominant head of *fl.digitorum profundus* that originates as a deep portion of the common flexor mass from the medial epicondyle of the humerus, a condition not typically found in other hominoids (Tuttle,1969). These muscles not only exert powerful forces across the ventomedial aspect of the elbow in flexion, neccessary for the propulsive phase in ricochetal brachiation, but they likely help to stabilize the humeroulnar joint as well. Movements are very rapid during locomotion, and the arm is placed in a position of extreme lateral rotation at the end of support phase (Larson,1988). It may be possible that a highly constrained humeroulnar joint distally is mechanically disadvantageous when engaging in ricochetal brachiation. Furthermore, observations of siamang locomotor activity indicate that they engage in higher frequencies of vertical climbing and scrambling than gibbons, hence the smaller ventral trochlear angles of siamangs are likely a reflection of this.

Analysis of trochlea angle does demonstrate that all hominoids have relatively small angles, and that stability at the humero-ulnar joint is paramount in large bodied animals engaging in suspensory activities. Harrison (1986) has stated that "with increased relative surface area of the trochlea for articulation with the ulna in large primates, there is a greater need for structural modifications, such as medial and lateral trochlear keels, and a waisted trochlea to stabilize the humeroulnar joint during flexion and extension of the elbow." (p.548). This is true to an extent. On examining the contribution of trochlea angle to trochlea area, it is shown that, although gibbons are of similar size to monkeys, brachiators have much smaller trochlea angles than would be expected. Similarly, chimps, bonobos and orangutans all have smaller angles than would be expected for their body size. This suggests that the need for stability at the humeroulnar joint supercedes that for increased joint surface area, supporting Sarmiento's (1985,1988) conclusions. Gorillas and humans, on the other hand, tend to have broader trochlear angles than would be expected for their body size. Thus, they have compromised stability somewhat in favour of increased surface area. This situation is advantageous for a large animal habitually subjecting the elbow to a compressive loading regime in knuckle-walking. For humans, the forelimb is not used in locomotion, therefore structural modifications emphasizing humero-ulnar joint stability are not neccessary.

All large hominoids share a cranial orientation of the ulnar trochlear notch. Whether this character is merely a function of large body size is difficult to assess here. Futher analysis with much larger sample sizes will enable testing of independent slopes for taxa of differing body size and locomotor patterns. Insofar as gibbons and siamangs have ulnar notch angles not significantly different from that of monkeys, it would appear that cranial orientation of the ulnar notch is associated with extreme ranges of flexion-extension capabilities, neccessary for large apes moving about in an arboreal milieu. It is also advantageous in knuckle-walking behaviour, in that the forward projecting coronoid process forms a larger support platform through which compressive forces can be transmitted. That humans share with apes a cranial orientation of the ulnar notch likely reflects phylogenetic history retained from a common ancestor. Retention of this trait, however, is equally valuable to humans with respect to manipulatory behaviours and activities such as tool-making.

Finally, discriminant function analysis of the distal humerus and proximal ulna has shown that structural features of the elbow are functionally significant and effective indicators of locomotor behaviour. This will be particularly usefull in making inferences about locomotor patterns and limb usage in fossil taxa.

TABLE 2.1: Summary Statistics For Humeral and Ulnar Measures

Taxon	Vent troch Area *	Dist troch area	Vent cap area	Dist cap area	Vent tro/cap	Dist tro/cap	Vent troch angle	Dist troch angle	Ulnar notch angle
Gorilla n	23	23	23	23	23	23	23	23	18
X	739.02	908.96	500.85	451.05	1.49	2.02	131.53	131.49	131.70
s	233.88	266.30	149.65	119.98	.32	.27	6.80	6.39	9.06
cv	31.65	29.30	29.88	26.60	21.48	13.37	5.17	4.86	6.88
Chimp n	22	22	22	22	22	22	22	22	16
X	369.83	452.02	284.70	246.72	1.31	1.84	130.00	128.59	120.72
s	60.17	65.96	47.60	31.53	.18	.23	5.95	5.89	4.61
cv	15.16	14.59	16.72	12.78	13.74	12.5	4.58	4.58	3.82
Bonobo n	13	13	13	13	13	13	12	13	13
X	313.39	380.57	237.92	214.25	1.33	1.80	126.93	128.83	121.11
s	44.27	46.19	39.40	37.81	.15	.23	7.20	8.03	3.92
cv	14.13	12.14	16.56	17.64	11.29	12.5	5.67	6.23	3.24
Pongo n	5	5	5	5	5	5	5	5	5
X	456.61	496.30	332.45	251.44	1.39	2.00	123.67	126.94	124.30
s	74.75	80.46	64.47	60.67	.14	.22	9.60	14.56	8.44
cv	15.48	15.28	18.42	22.26	10.07	11.22	7.87	11.69	6.59
Human n	10	10	10	10	10	10	10	10	10
X	393.26	469.09	282.76	201.67	1.40	2.38	142.77	138.02	122.19
s	79.34	85.99	59.96	51.17	.12	.35	7.43	7.65	5.47
cv	20.17	18.33	21.20	25.37	8.57	14.70	5.20	5.54	4.48
Gibbon n	11	11	11	11	11	11	11	9	9
X	77.79	89.36	81.51	73.43	.96	1.23	135.40	145.1	100.24
s	14.89	18.33	15.80	14.84	.14	.18	8.43	11.46	6.39
cv	19.14	20.51	19.38	20.21	14.43	14.63	6.23	7.90	6.37
Siamang n	2	3	3	3	2	3	3	3	2
X	109.95	139.72	96.09	89.65	1.01	1.58	122.40	141.74	109.96
s	12.04	18.50	28.53	20.74	.11	.18	.96	4.05	12.26
cv	10.95	13.24	29.69	23.13	10.78	11.39	.78	2.86	11.15

Taxon		Vent troch Area *	Dist troch area	Vent cap area	Dist cap area	Vent tro/cap	Dist tro/cap	Vent troch angle	Dist troch angle	Ulnar notch angle
AQ	n	7	4	7	4	7	4	4	7	6
	X	90.05	127.65	94.60	75.87	.97	1.72	157.04	158.40	96.32
	s	28.81	63.14	26.42	33.40	.21	.56	4.35	7.46	7.37
	cv	40.00	49.46	27.93	44.02	21.65	32.56	2.77	4.71	7.66
TQ	n	10	9	10	9	10	9	7	10	9
	X	143.15	148.79	143.55	127.31	1.00	1.24	148.41	152.76	102.48
	s	37.62	40.76	34.95	34.57	.15	.38	12.50	10.57	7.51
	cv	35.97	33.59	37.00	36.94	15.31	28.35	8.87	7.03	7.42

* Area measurements in mm^2: AQ=arboreal quadruped, TQ=terrestrial quadruped,

Table 2.2: Summary of Mann-Whitney U-test Pairwise Comparisons For Elbow Variables

Taxa	Troc-Cap Area Ventrally	Troc-Cap Area Distally	Troc Angle Ventrally	Troc Angle Distally	Ulnar Notch Angle
Gor-Chimp	ns	ns	ns	ns	***
Gor-Bonobo	*	*	ns	ns	***
Gor-Pongo	ns	ns	*	ns	ns
Gor-Human	ns	***	***	*	**
Gor-Gib	***	***	ns	***	***
Gor-Siam	*	*	*	*	*
Gor-AQ	***	*	**	***	***
Gor-TQ	***	***	***	***	***
Chimp-Bonobo	ns	ns	ns	ns	ns
Chimp-Pongo	ns	ns	ns	ns	*
Chimp-Human	ns	***	***	**	ns
Chimp-Gib	***	***	*	***	***
Chimp-Siam	*	*	*	**	ns
Chimp-AQ	***	ns	**	***	***
Chimp-TQ	***	**	***	***	***
Bonobo-Pongo	ns	ns	ns	ns	*
Bonobo-Human	ns	***	***	**	ns
Bonobo-Gib	***	***	*	**	***
Bonobo-Siam	*	ns	ns	*	ns
Bonobo-AQ	*	ns	**	***	***
Bonobo-TQ	***	*	***	***	***
Pongo-Human	ns	*	**	*	ns
Pongo-Gib	**	**	*	*	**
Pongo-Siam	*	*	ns	ns	*
Pongo-AQ	**	ns	*	**	**
Pongo-TQ	**	*	**	**	**
Human-Gib	***	***	ns	*	***
Human-Siam	*	**	**	ns	ns
Human-AQ	**	**	**	***	**
Human-TQ	***	***	*	**	***
Gib-Siam	ns	*	*	ns	ns
Gib-AQ	ns	ns	**	**	ns
Gib-TQ	ns	ns	***	ns	ns
Siam-AQ	ns	ns	*	*	ns
Siam-TQ	ns	ns	*	*	ns
AQ-TQ	ns	ns	*	*	*

* $p <= 0.05$; ** $p <= 0.01$; *** $p <= 0.001$; Troc = trochlea of humerus; Cap= capitulum of humerus; Troc-Cap = ratio of trochlea to capitulum area

TABLE 2.3: Regression Analysis of Humeral Measures and Ulnar Notch Angle

Variable*	*r*	Slope	95% conf.	S.E.E.	y-intercept	95% conf.
vent troch area	.934	.963 (1.027)	.889 - 1.036 (.953 - 1.102)	.061	-.109 (-.199)	-.212 - -.006 (-.303 - -.094)
dist troch area	.929	.982 (1.058)	.903 - 1.062 (.977 - 1.138)	.127	-.097 (-.202)	-.209 - .016 (-.316 - .088)
vent cap area	.925	.775 (.837)	.712 -.838 (.722 -.901)	.052	.104 (.018)	.015 - .193 (-.073 -.108)
dist cap area	.903	.757 (.838)	.683-.831 (.673-.914)	.059	.097 (-.017)	-.008 - .201 (-.123 - .090)
vent troch area-angle	.343	-1.688	-2.636 - -.740	.158	4.831	2.817 - 6.846
vent resid-radius breadth	.870	.868	.766 - .970	.078	-1.221	-1.366 - -1.077
dist troch area-angle	.655	-2.851	-3.520 - -2.181	.127	7.358	5.931 - 8.785
dist resid-radius breadth	.681	.555	.432 - .678	.094	-.782	-.956 - -.608
Ulnar notch angle	.839	.261	.224 - .297	.027	1.706	1.656 - 1.757

All variables are regressed against log radius distal articular surface breadth
RMA values are reported in parentheses below OLS values
* Areas are transformed to square root values

TABLE 2.4: Chi-Square Results of Residual Distribution for Trochlea Angle Regressed Against Radius Distal Articular Surface Breadth

	Ventral		Distal	
Taxon	% positive residuals	% negative residuals	% positive residuals	% negative residuals
Gorilla	34.78	65.22	21.74	78.26
Chimp	72.73	27.27	77.27	22.73
Bonobo	83.33	16.67	91.67	8.33
Pongo	60.00	40.00	80.00	20.00
Human	10.00	90.00	20.00	80.00
Gibbon	54.55	45.45	66.67	33.33
Siamang	100.00	0	66.67	33.33
Arboreal monkey	0	100.00	50.00	50.00
Terrestrial monkey	0	100.00	22.22	77.78

TABLE 2.5: Summary of Discriminant Function Analysis For First 3 Functions

	FUNCTION		
Variable	1	2	3
Dist troch area	.675*	-.080	-.561
vent troch area	.627*	-.069	-.532
vent cap area	.561*	-.033	-.526
ulnar notch ang	.428*	-.169	-.089
dist troch angle	-.130	.757*	-.225
vent troch angle	-.226	.455*	-.420
dist cap area	.542	-.209	-.606*
dist tro/cap	.263	.295	.213
vent tro/cap	.296	-.078	.080
% variance	78.9	11.0	6.2
cum.% variance	78.9	89.9	96.0

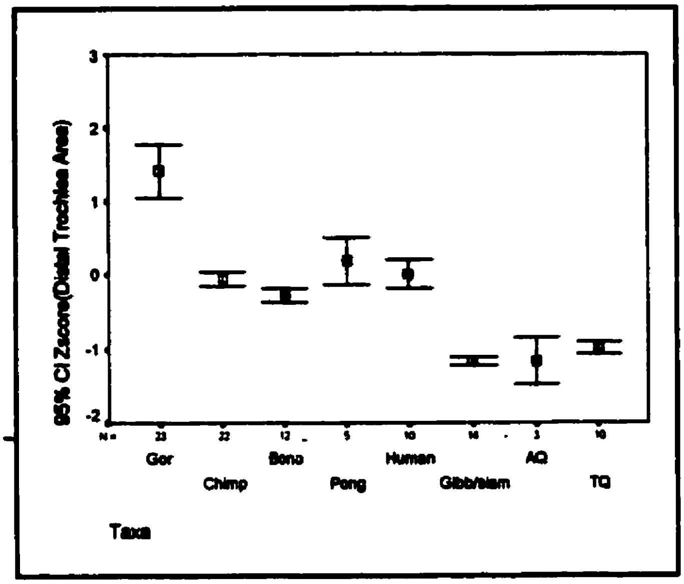
Pooled within groups correlations between discriminating variables and standardized canonical discriminant functions. Variables ordered by absolute size of correlation within function.

* denotes largest absolute correlation between each variable and any discriminant function.

TABLE 2.6: Classification Results of Predicted Group Membership Expressed as Percentage

Taxon	Gorilla	Chimp	Bonobo	Pongo	Human	Gibbon	Siamang	AQ	TQ
Gorilla	88.9			11.1					
Chimp		68.8	25.0	6.3					
Bonobo		33.3	66.7						
Pongo				100.0					
Human		10.0			90.0				
Gibbon						100.00			
Siamang							100.00		
AQ								100.00	
TQ								16.7	83.3

Figure 2.1: 95% CI Error Plot of Distal Trochlea Area Z-scores



* Center = mean, bars represent 95% confidence interval (a range of values based on the mean that, with a 95% liklihood, include the population mean)

Figure 2.2: 95% CI Error Plot of Distal Capitulum Area Z-scores

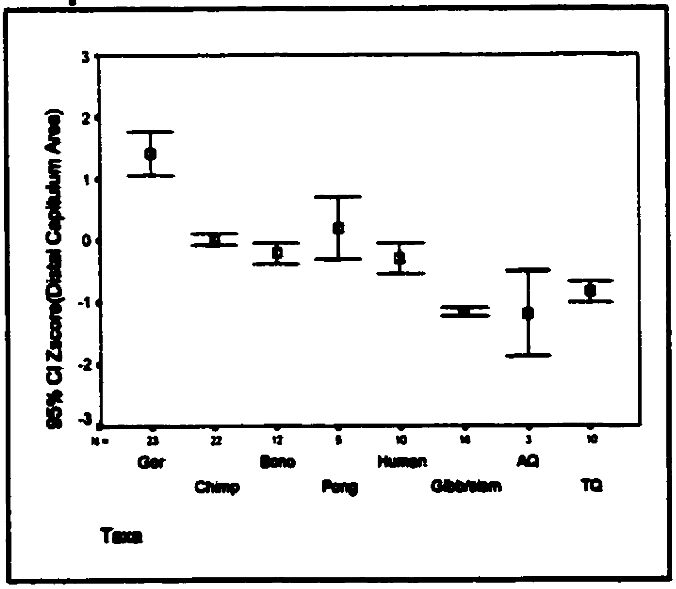


Figure 2.3: Ratio of Ventral Trochlea to Capitulum Area

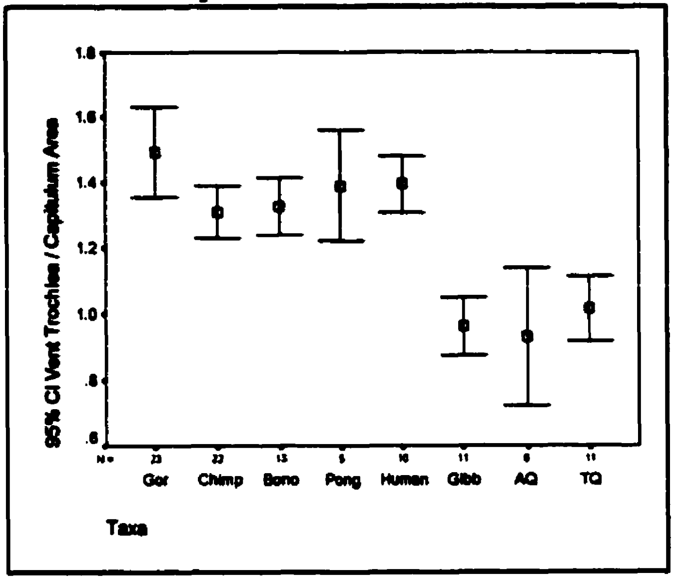


Figure 2.4: Ratio of Distal Trochlea to Capitulum Area

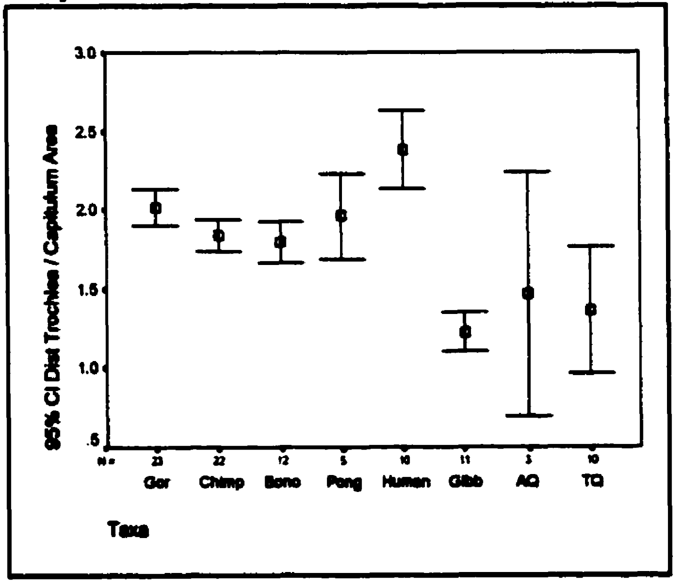


Figure 2.5: Humerus Ventral Trochlear Angle

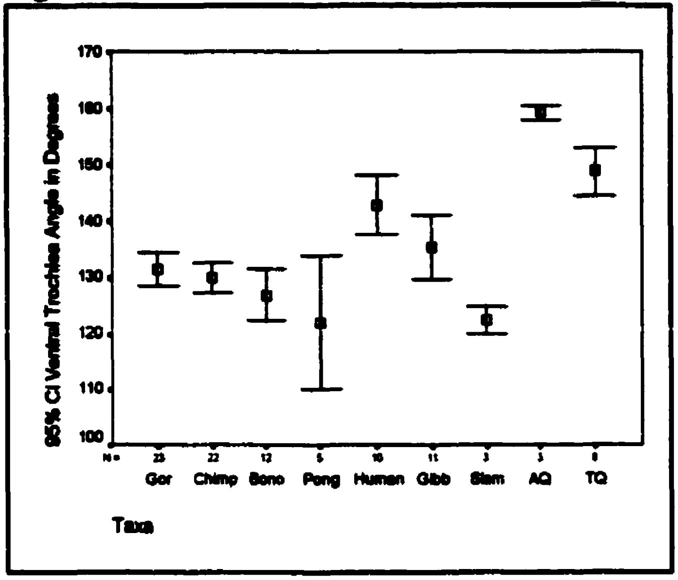


Figure 2.6: Humerus Distal Trochlea Angle

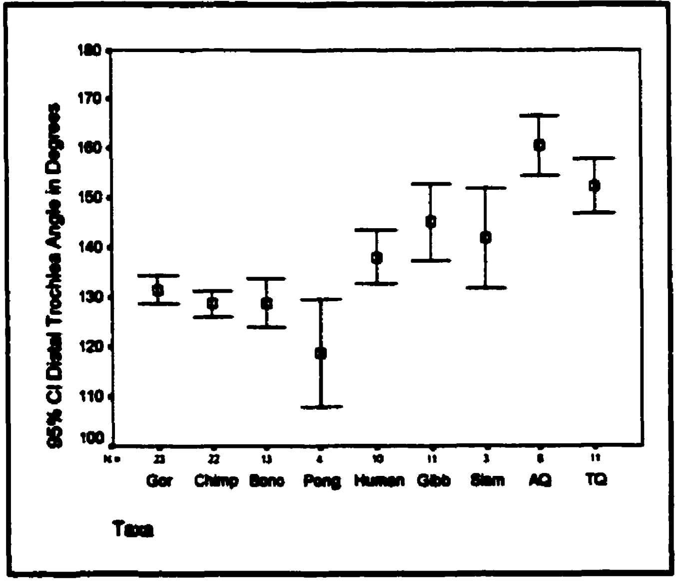


Figure 2.7: Ulnar Trochlear Notch Angle

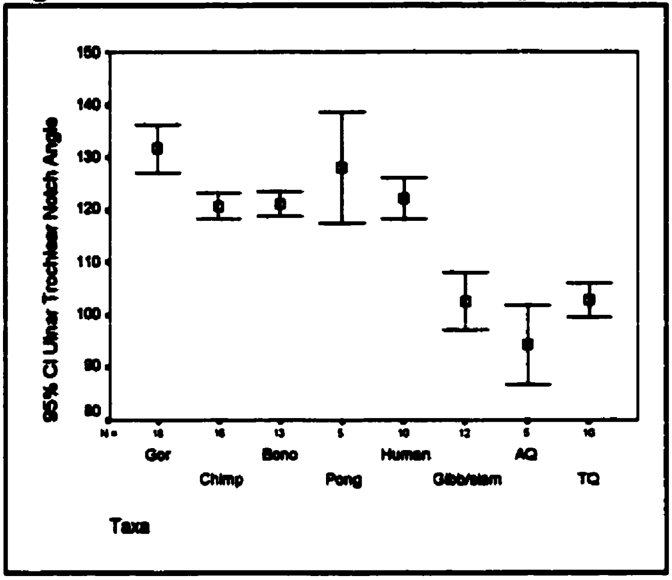


Figure 2.8: Regression Plot of Ventral Trochlea Area verses Radius Distal Articular Breadth

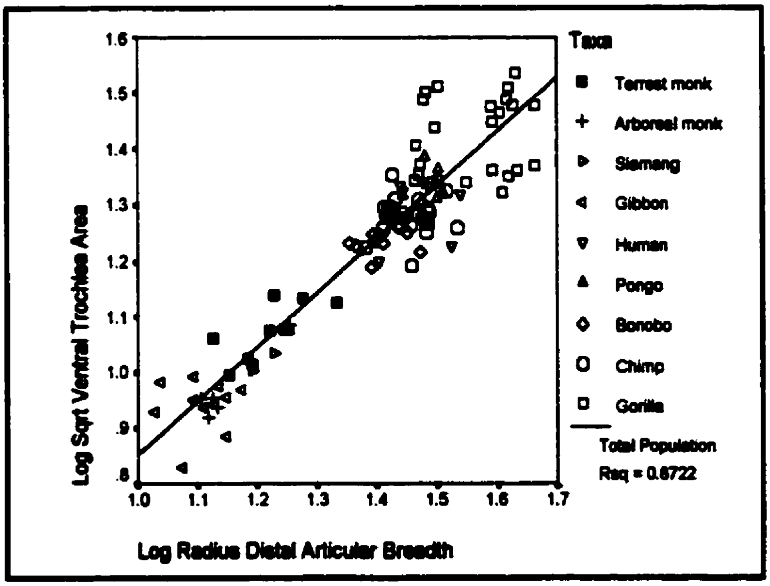


Figure 2.9: Regression Plot of Distal Trochlea Area verses Radius Distal Articular Breadth

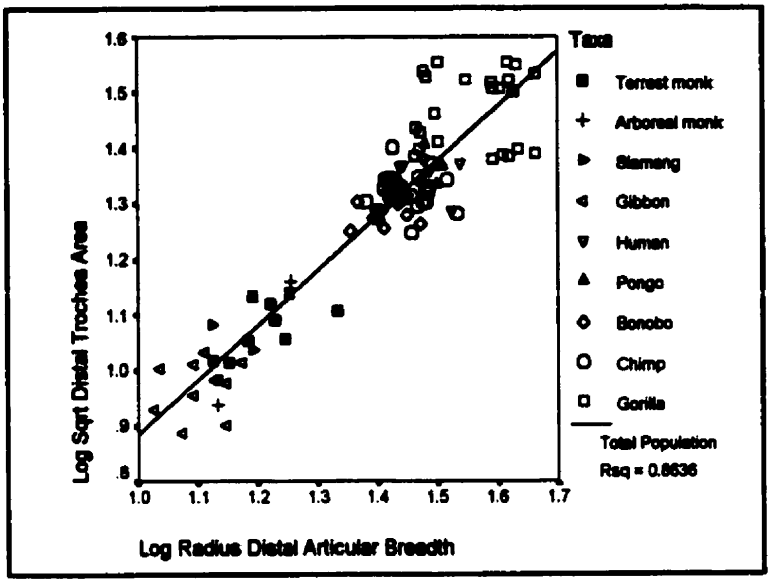


Figure 2.10: Regression Plot of Ventral Capitulum Area Verses Radius Distal Articular Breadth

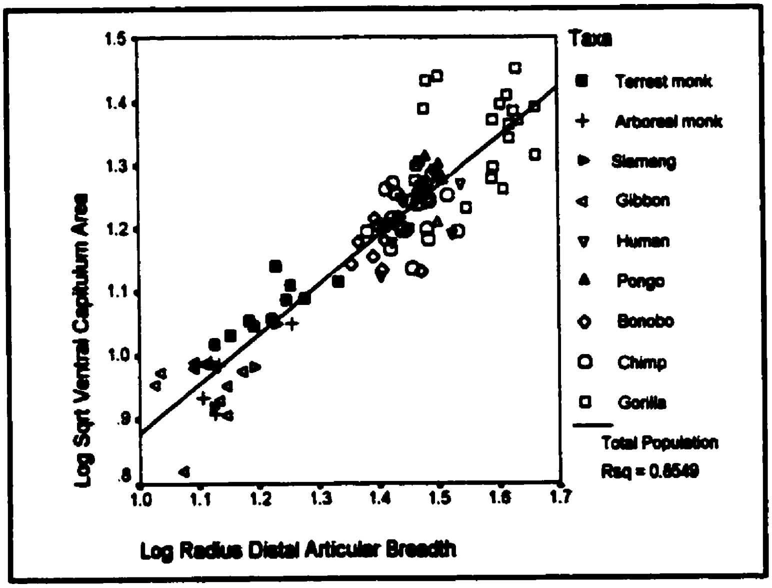


Figure 2.11: Regression Plot of Distal Capitulum Area Verses Radius Distal Articular Breadth

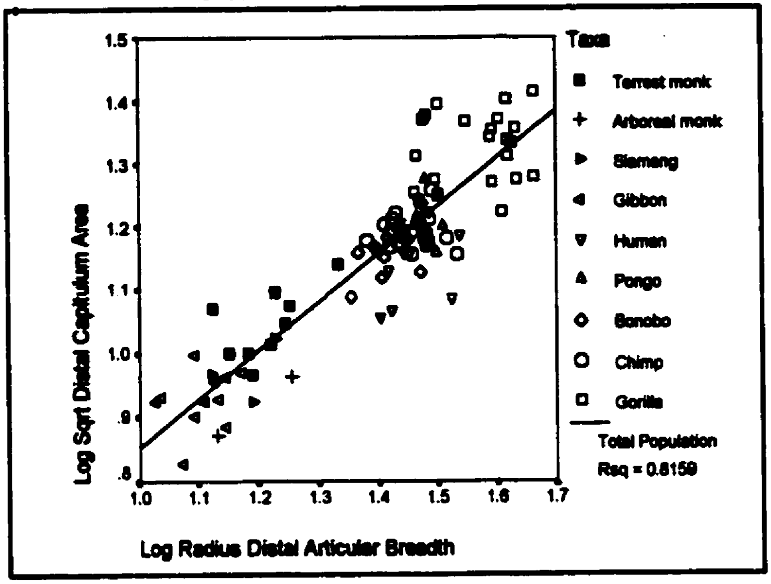
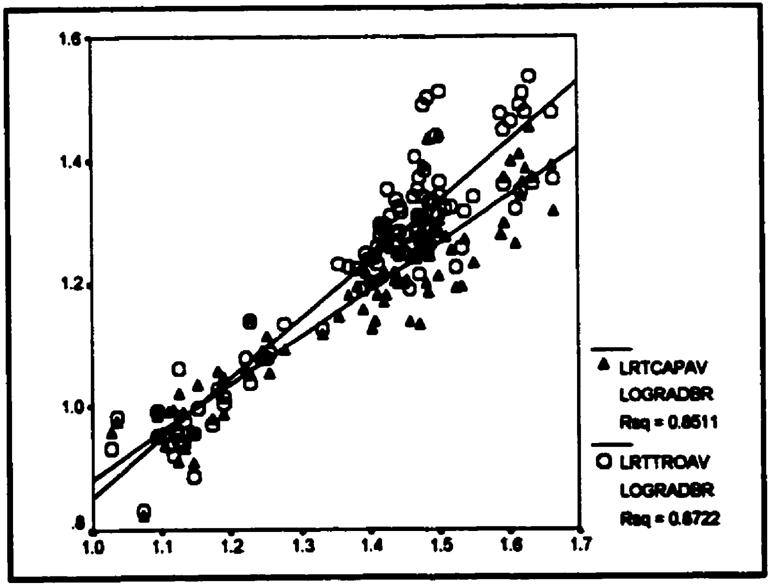
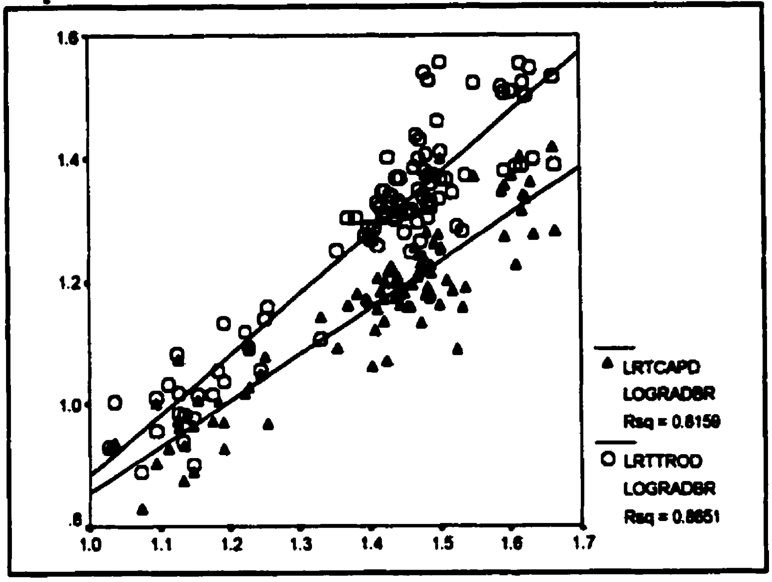


Figure 2.12: Regression of Ventral Trochlea and Capitulum Areas verses Radius Distal Articular Breadth



O = log square root ventral trochlea area vs log radius articular breadth. Slope (RMA) = 1.02
= log square root ventral capitulum area vs log radius articular breadth. Slope (RMA)=.84

Figure 2.13: Regression of Distal Trochlea and Capitulum Area verses Radius Distal Articular Breadth



O = Log square root trochlea area vs log radius articular breadth. Slope(RMA) = 1.06
▲ = Log square root capitulum area vs radius articular breadth. Slope(RMA) = .836
* Slopes are significantly different for p<=.05

Figure 2.14: Regression of Ventral Trochlea Area verses Ventral Trochlea Angle

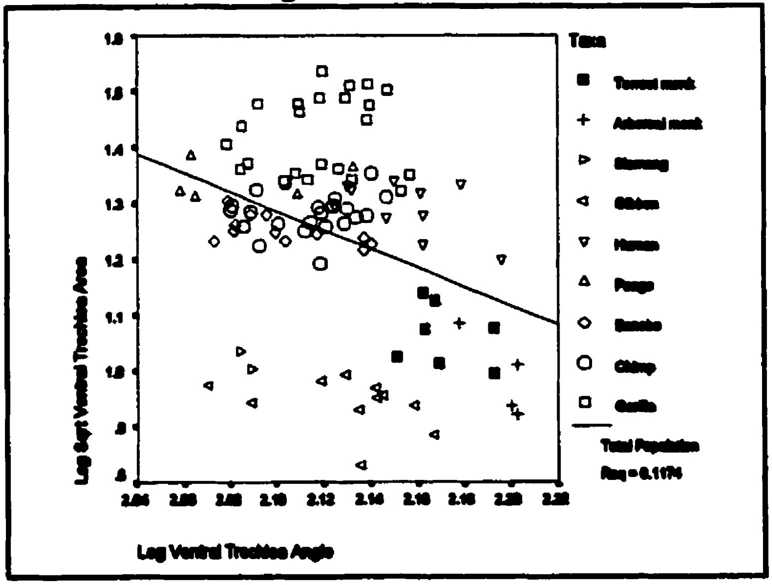


Figure 2.15: Regression of Distal Trochlea Area verses Distal Trochlea Angle

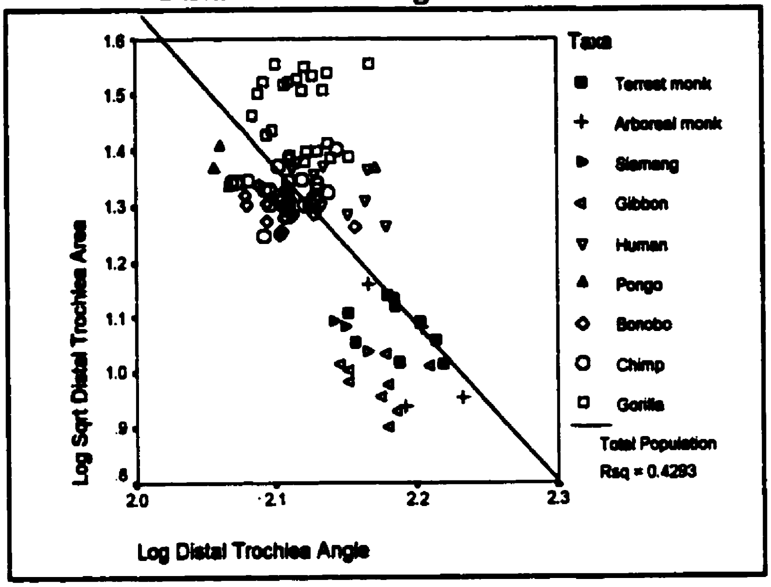


Figure 2.16: Regression Plot of Residuals for Ventral Trochlea Area - Ventral Trochlea Angle vs Radius Distal Articular Breadth

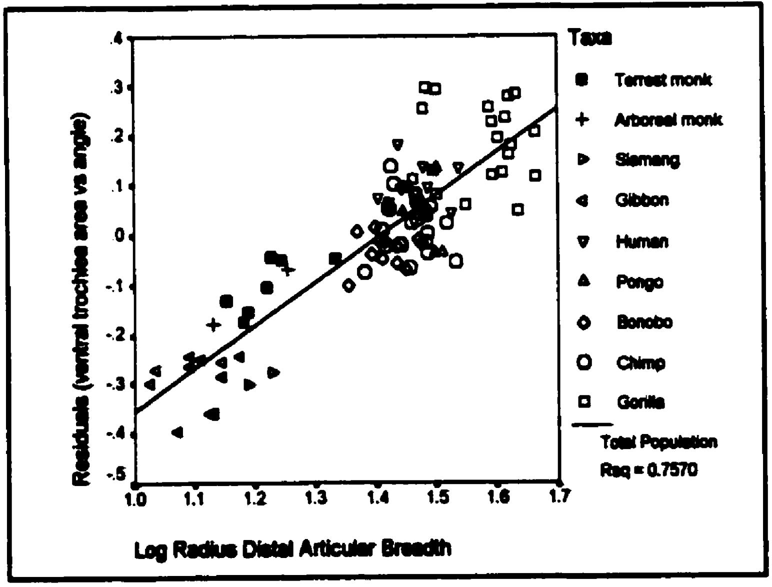


Figure 2.17: Regression Plot of Residuals for Distal Trochlea Area-Distal Trochlea Angle vs Radius Distal Articular Breadth

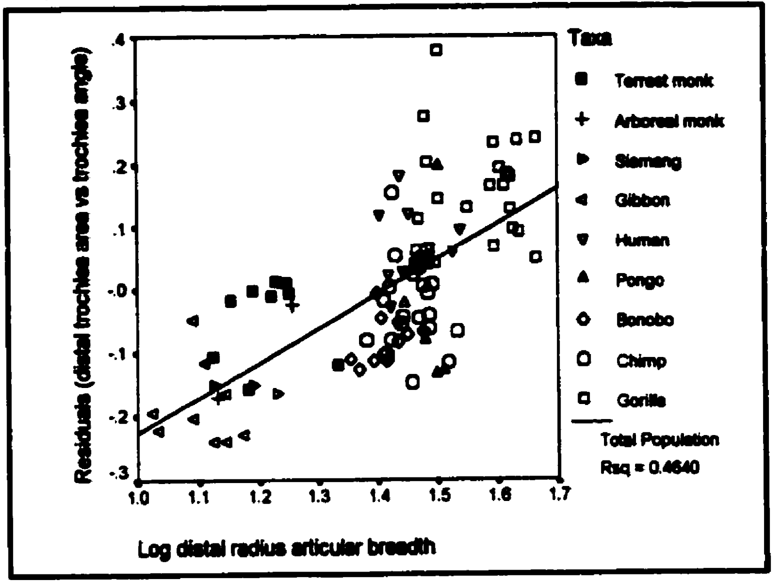


Figure 2.18: Regression Plot of Ulnar Trochlear Notch Angle verses Radius Distal Articular Breadth

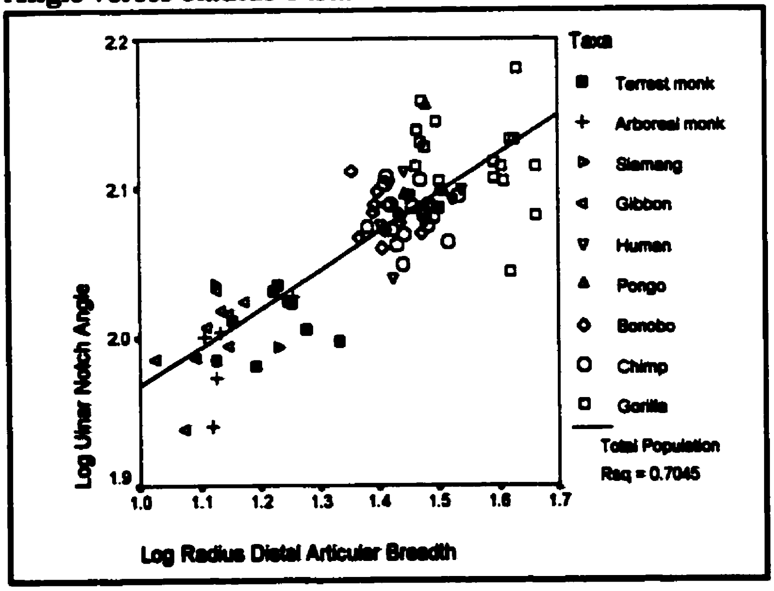
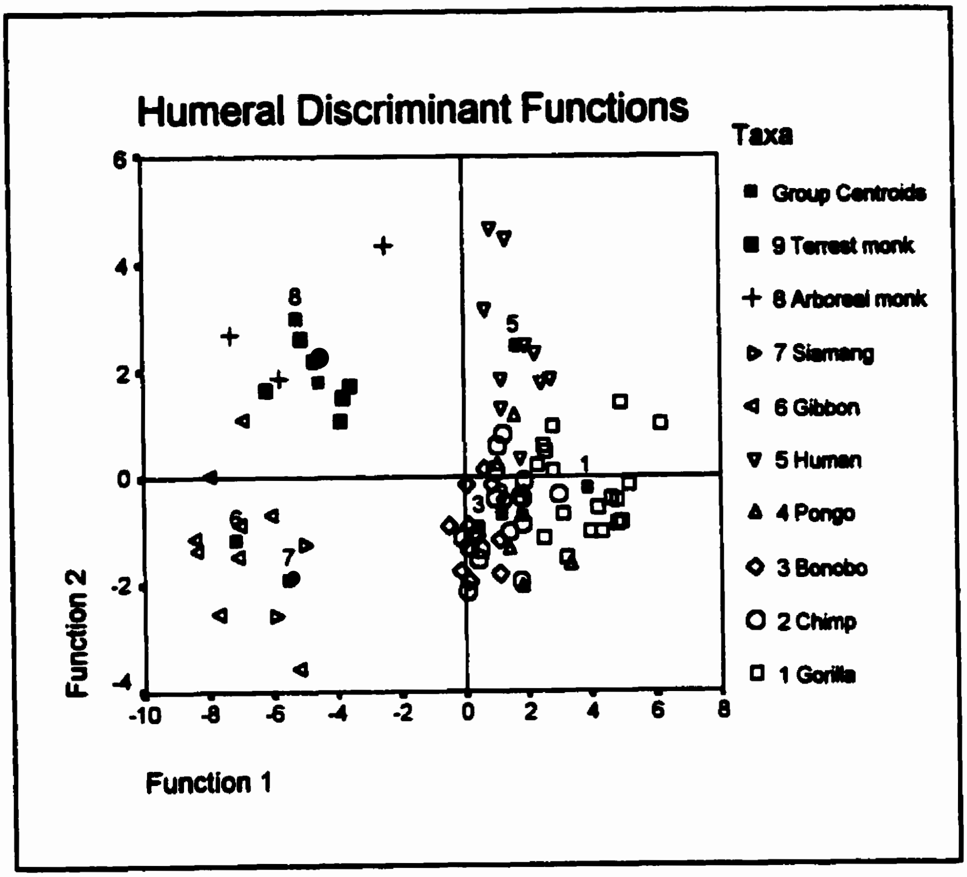


Figure 2.19: Canonical Discriminant Function Results for Elbow Variables



CHAPTER 3

The Wrist

Background

All hominoids share uniquely derived characters of the antibrachial joint and carpus that distinguish them from other anthropoids (Corruccini 1978; Corruccini *et al* 1975; Harrison 1986, 1987; Jenkins and Fleagle 1975; Lewis 1965, 1969, 1971, 1972, 1974, 1985, 1989; Morbeck 1975; O'Connor 1975; Sarmiento 1985, 1988, 1994; Tuttle 1967, 1969, 1970, 1975; Tuttle and Basmajian 1974; Washburn 1963, 1968b). These traits pertain primarily to wrist mobility and pronation - supination capabilities, reflecting an adaptation to suspensory and slow climbing in an arboreal milieu. African ape wrist morphology differs from that of Asian apes in structural features that are functionally related to greater stability. The need for increased stability is suggested to be correlated with use of the forelimb in compression during knuckle-walking.

The following brief summary of hominoid wrist anatomy and function is based largely on the work of Lewis (1965 and *seq.*) and Sarmiento (1985,1988,1994), unless otherwise cited. Elements under discussion are restricted to the distal radius and ulna, the scaphoid and lunate, and the capitate and hamate. These structures are integral components of wrist stabability and/or mobility and are deemed to be most functionally relevant to the question of knuckle-walking traits in African apes.

In the antibrachial compartment, reduction in the length of the styloid process of the ulna is unique to hominoids. In monkeys, the styloid process fits into a cup formed by the pisiform and triquetral, providing a stable platform through which compressive forces can be transmitted in quadrupedal locomotion. Reduction in the size of the styloid has led to its partial or complete exclusion from participation with the proximal carpal row, and permits a wider range of excursion in ulnar deviation of the wrist (see Tuttle 1969,1970).

Gibbons are intermediate between monkeys and great apes in development of the styloid process. In some cases, it is quite long and may contact the surface of the triquetral in maximum adduction of the wrist (Jenkins, 1981). Hylobatids differ from great apes in having an extra carpal bone - the os daubentonii - which exhibits varying degrees of development. It is suggested (Sarmiento 1988) that this bone may represent a second centre of ossification of the triquetral, which is present in monkeys. Typically, the os daubentonii is semilunar in shape and articulates with the ulnar styloid process proximoradially, and with the triquetral distally. When it is poorly developed, two continuous fibrocartilaginous ligaments bind the os daubentonii to the radius and completely encircle the ulnar styloid process. This structure, referred to by Lewis (1965,1969,1988) as the semilunar meniscus, has the same shape and function as a well developed os daubentonii, which serves to prevent the radius and ulna from separating while allowing free rotation of these two bones about each other. Gibbons also have a triangular ligament that connects the distal radius and ulna, but is separate from the semilunar meniscus. The ulnar styloid process passes through the opening between the meniscus and triangular ligament to achieve contact with the triquetral.

In great apes and humans, the os daubenonii is not present and the triangular ligament becomes a true fibrocartilaginous articular disc, contacting the ulnar head and styloid proximally and the triquetral and lunate distally. In common chimps, the semilunar meniscus and triangular disc usually are distinct structures, allowing passage of the ulnar styloid process which may then contact the triquetral. However, occasionally the two structures may merge forming a partially closed cavity for the ulnar styloid process. The styloid bears articular facets for both the meniscus and the triquetral.

In gorillas, the meniscus is completely incorporated into the proximal articular surface of the wrist, fusing with the smooth, stiff triangular articular disc such that only one structure is discernable. The homologue of the semilunar meniscus consists of a somewhat more pliable ligamentous portion that is continuous with the triangular disc, and connects it to the radius, ulna and proximal carpals. The ulnar styloid process, reduced in size relative to chimps and situated proximal to the meniscus homologue, is enclosed in its own synovial compartment. This cavity contains numerous yellow, fat-filled villi. The styloid itself is covered in cartilage and contacts the upper surface of the meniscus homologue. Lewis (1965,1969,1974,1988) states that the gorilla morphology represents a condition derived from that of chimps, whereby the semilinar meniscus and triangular disc have fused to form the larger triangular disc in gorillas. According to Sarmiento (1985,1988), increasing the surface area along the ulnar aspect of the wrist by means of the triangular disc implies greater emphasis on weight support functions than in chimps, thus less commitment to terrestriality in the latter.

Orangutans also have a fibrocartilaginous triangular articular disc with its incorporated semilunar meniscus homologue. The ulnar styloid is even more reduced and enclosed in its own synovial cavity, however it is not covered in cartilage and is completely non-articular.

The condition in humans is most similar to chimps (*contra* Sarmiento 1988). The triangular disc is sometimes fused with the meniscus, sometimes not. The ulnar styloid process is variable in length. When the styloid is long, it protrudes into a "pre-styloid recess" (similar to the synovial cavity found in great apes), it is covered in cartilage and it may contact the upper surface of the triquetral.

The radiocarpal joint in lesser apes is designed for maximum mobility. Abduction and adduction occur at the radiocarpal and midcarpal joints. At the midcarpal joint, the articulation between the capitate and hamate forms a hemispherical ball contacting the lunate surface, and the proximal carpal surface has a relatively small mediolateral radius of curvature, indicating wide possible excursions of the wrist in a mediolateral direction. Gibbons are second only to orangs in adduction capabilities (Tuttle 1967,1969a,b,1970,1974) despite having a much longer ulnar styloid process. According to Jenkins (1981), there is considerable adduction and abduction at the end and begining of support phase during brachiation. In dorsoventral curvature, the proximal carpal surface is more highly curved than the distal radius articularl surface, indicative of wide ranges of possible flexion and extension of the wrist. Indeed, gibbons have the greatest degree of volar flexion capabilities of all hominoids, insofar as the palmar surface of the hand is able to contact the ventral aspect of the forearm (Tuttle 1967, 1969a,b, 1970, 1974).

In orangs, the articular surface of the proximal carpal row is more curved in a mediolateral plane than is the distal radius surface (Sarmiento, 1988). This disparity in joint surface curvatures results in greater radioulnar deviation capabilities of the wrist. This, coupled with an expanded lunate surface which extends ulnarly forming a "radial shelf" (entirely excluding the ulnar styloid from the carpus), provides orangs with the highest range of adduction of all hominoids. *Pongo* is also characterized by having equal development of flexor and extensor muscles of the wrist, associated with relatively free mobility at this joint (Tuttle 1967, 1969a,b, 1970, 1974). In contrast, African apes have much larger wrist flexors than extensors.

African apes have a distal radial surface that is more deeply concave than that of orangs, and which is angled ventrally and medially (Jenkins and Fleagle, 1975). The surface is broader mediolaterally than dorsoventrally (Corruccini, 1978), affording greater stability and less radioulnar deviation in African apes than in orangs (Tuttle 1967, 1969a,b, 1970, 1974). This condition is exaggerated in gorillas, which have a flange of bone that projects distally on the ventromedial aspect of the distal radius.

The conformation of the distal half of the radiocarpal joint, consisting of the scaphoid and lunate, distinguishes African from Asian apes. On the basis of linear measures, the lunate is much larger, having a greater relative contribution to the antebrachial joint, in *Pongo* than in gorillas or chimps. Knuckle-walkers have scaphoids and lunates of almost equal size, with the scaphoid being somewhat larger (Corruccini, 1978; Jenkins and Fleagle,1975; Sarmiento, 1988,1994). Mirroring the morphology of the distal radius, together these two bones form a surface that is narrower dorsoventrally than mediolaterally. The radius of curvature of the proximal surface of the proximal carpal row is much greater (ie: less curved) in African apes than in Asian apes (Sarmiento, 1985,1988,1994), resulting in a joint that is very stable and less mobile, particularly in radioulnar deviation.

The lunate proximal surface in gorillas and chimps is convex, narrow ventrally and broader dorsally, such that much of the articular surface faces dorsally. The scaphoid proximal facet is concavo-convex, with the convex portion oriented proximally, and the concave portion facing proximo-dorsally. In flexion, the convex portions of the scaphoid and lunate articulate with the distal radius. In extension, the concave part of the scaphoid comes in contact with the distal radius, limiting any futher extension (Jenkins and Fleagle, 1975), contra Tuttle (1967,1969a,b) who claimed that the dorsal ridge separating the adjoining surfaces represented an extension-limiting trait.

During the middle and late propulsive phases of knuckle-walking, the somewhat dorsally facing proximal facets of the scaphoid and lunate are brought into maximum contact with the distal radius (Jenkins and Fleagle,1975). The proximal carpal row remains essentially static during knuckle-walking, with the forearm, carpals and metacarpals rotating forward on the digits around a center of rotation located approximately at the level of the metacarpophalangeal joints. The axis of rotation initially lies between digits 3 and 4, then shifts toward the radial side as body weight passes over the limb (Jenkins and Fleagle,1975).

Habitually loading the carpals in compression, with emphasis on the radial side during late phases of propulsion, has led to a uniquely derived condition among African apes and humans, namely fusion of the os centrale to the scaphoid which increases midcarpal stability (Corruccini, 1978; Harrison,1986; Lewis,1985; Sarmiento, 1985,1988; Jenkins and Fleagle,1975; Tuttle,1967,1969a,b,1974). Fusion of these two bones in African apes and humans usually occurs in fetal or neonatal stages of development (Schultz, 1936). Orangs and gibbons have retained the primitive anthropoid condition of unfused os centrale. The convex portion of the proximal scaphoid in these two taxa is small in relation to the flattened dorsal extension of the facet. Lewis (1988) states that gibbon morphology is reminiscent of monkeys, in that the proximal surface of the scaphoid retains a dorsal concavity (which is actually more flat than concave, pers. obs.).

Knuckle-walkers and humans typically have capitates that are mediolaterally broad and blocky, expanded distal articular surfaces (linear dimensions), and total proximodistal length that is greater than hamate length (Corruccini *et al,* 1975; Corruccini, 1978). The degree to which the capitate head is expanded laterally is said to be highly variable among hominoids, however it is generally small in gorillas and humans and larger in chimps, the latter more closely resembling terrestrial cercopithecines than other hominoids (Corruccini *et al*, 1975; O'Connor, 1975; Lewis, 1973,1974,1985,1988). Chimps typically have a large, non-articular excavation distal to the capitate head contributing to a so-called "waisted" appearance. Gorilla and human capitates are much blockier in shape than those of chimps, in that the inferior border of the head is filled in. The capitate head of orangs and gibbons is not expanded to the degree seen in African apes, and distal articular surface dimensions of gibbons are similar to that of monkeys. Expansion of the capitate head in African apes is associated with greater contact with the lunate proximally. In orangs and gibbons, much of the distal lunate surface articulates with the hamate (Lewis 1985,1988; Marzke *et al,* 1994).

The hamate is characteristically broad relative to its length in gorillas and monkeys, especially terrestrial monkeys, with a triquetral facet that is situated obliquely and faces proximolaterally. The hamate gets progressively longer and the triquetral facet shifts in a more medial direction in chimps, orangs, and hylobatids respectively. In orangs and gibbons, the hamate is as long or longer than the capitate. The monkey, gorilla and chimp triquetral facets are relatively broad and oriented to faciliate weight transmission through the ulnar aspect of the wrist (Corruccini,1978; Corruccini et al, 1975; O'Connor, 1975; Lewis, 1972,1974,1985,1988; Sarmiento, 1988, 1994). In large hominoids, the articular surface between the hamate and capitate is a linear plane synovial joint taking up the whole flattened surface proximally and extending distally as a dorsally located strip. This articular surface is often split into proximal and distal portions in gibbons (Lewis, 1985,1988) - a condition sometimes seen in chimps as well (pers. obs.).

The preceding summary of hominoid antebrachial joint and selected carpal morphology has demonstrated that African apes share a number of features that can be functionally linked to increased stability of the wrist. Questions that remain unanswered, however, are whether joint surfaces of wrist elements scale isometrically with changes in body size or if there is an allometric pattern in surface area that may be correlated with specific modes of habitual limb usage.

The notion of geometric similarity assumes that animals will have bones that are the same shape regardless of absolute size. Under this assumption, surface areas do not scale directly with body mass, such that joints of larger animals bear relatively greater gravitational loads than those of small animals. Therefore, it is expected that joint surface area would scale positively allometrically with body mass to maintain functional similarity and to compensate for relatively greater loads experienced by large animals (Swartz,1989; see also Biewener,1982; Rubin and Lanyon,1984). Alexander (1980) cautions that geometric similarity also assumes that linear dimensions of articular surfaces are proportional to overall dimensions of the given limb segment of which it is part. According to Jungers and Susman

(1984), such a relationship between joint shape and long bone length does not exit among African apes, and that most joints scale or increase in size at a considerably faster rate than limb length. However, they state that scaling of long bone diameters likely *does* correspond more closely to joint articular size and shape.

In their examination of African apes, Jungers and Susman's (1984) results indicate that forelimb articular dimensions (glenoid fossa, proximal and distal humerus, and radial head) scale positively with body size, whereas hindlimb articular surfaces scale slightly negatively. This finding is corroborated by Godfrey *et* al (1991) in their analysis of anthropoids, insofar as hindlimb articular elements scale close to isometry and forelimb dimensions (proximal and distal dimensions of the humerus, radius and ulna) scale slightly positively. However, these authors contend that functional differences within groups can mask joint surface isometry, in that the presence of functional differences between small and large members of a given taxonomic group can result in patterns of positive or negative allometry or isometry. "If function varies with body size, then positive or negative allometry can occur as a spurious effect of changes in function without having anything to do with scaling *per se*." (p.621). This may be true in analyses using datasets including animals of very small and large size with different locomotor habits (ie: small cercopithecines and large hominoids). A study of closely related species wherein body size does not differ greatly (termed "narrow allometry" by Smith, 1980), may reveal differences in linear dimensions and surface areas that are uncorrelated with body size and likely reflect functionally significant patterns of limb usage.

The questions to be addressed in this analysis are as follows:

1. Do knuckle-walkers have expanded surface areas of the distal radius and proximal articular surfaces of the scaphoid and lunate as compared to other hominoids and cercopithecines, relative to a metacarpal body size surrogate?
2. What is the relative contribution of *actual* surface area of the scaphoid and lunate to the antebrachial joint among knuckle-walkers, other hominoids and cercopithecines? Do knuckle-walkers have expanded areas on the radial side of the forelimb? It is well known that orangs have greatly enlarged lunates, however, does the relative size and scaling of the scaphoid differ in knuckle-walkers?
3. Do knuckle-walkers have expanded surface areas of the scaphoid facet on the capitate, capitate facet on the hamate, and distal surfaces of these elements compared to other hominoids and cercopithecines, relative to a metacarpal body size surrogate and relative to total length of these carpal elements? Increased scaphoid area would be indicative of greater stability along the radial aspect of the wrist, larger hamate areas would be an effective stress reduction mechanism whereby forces are transmitted from the hamate to capitate, and larger distal articular surface areas would be suggestive of weight bearing.
4. Do gorillas, chimps and bonobos exhibit different patterns of scaling in the above measures relative to each other and to other hominoids and cercopithecines.

Measurements

Measurement of the wrist elements under investigation are graphically depicted in

Measurement of the wrist elements under investigation are graphically depicted in figures 1.4-1.13 (pages 26-30. Maximum area of a facet was digitized along the margin of the articular surface, which is clearly visible. The scaphoid and lunate areas on the distal radius were, for the most part, easily discernable by the contours of the articular margin and by a ridge separating the facets within the articular surface. In some cases, this ridge was not clearly visible, and the scaphoid and lunate areas were estimated from the contours of the articular margin on the dorsal and ventral aspect, then digitizing a line between them.

As noted in the summary above, the capitate facet on the hamate is typically split into proximal and distal portions in gibbons (and chimps on occasion, pers. obs.). In this instance, area was measured for both segments and then summed to obtain a total area. Total proximodistal length of the hamate and capitate was obtained with Mititoyo digital calipers, measuring from the most distal projection of the distal articular surface to the most proximal surface of the bone. For the hamate, the most distal projection was taken from the level of the metacarpal four (MIV) and metacarpal five (MV) articular facets when these are in the same plane, and from the ridge separating the two facets when their conformation is on an angle. For the capitate, the level of the distodorsal edge of the bone was taken as its most distal projection. Measurement of the capitate and hamate distal articular surfaces (the MIII and MIV/MV facets respectively) was accomplished by placing each bone such that the distal surface was perpendicular to the lens of the camera. In those cases where the MIV and MV facets on the distal hamate are set on an angle to each other, each was measured separately and the measures added later during the digitizing process to arrive at a total distal articular surface area.

The capitate in chimps has a scaphoid surface that is confluent dorsally with a facet for the trapezoid. Gorillas lack a dorsal articulation with the trapezoid, consequently the distal margins of the scaphoid surface are clearly demarcated. This distal margin is estimated in chimps by comparing the morphology in gorillas, then digitizing a line from the level of the most distal projection of the scaphoid surface ventrally, across the narrow articular strip for the trapezoid to the point where it joins the scaphoid facet ventrally (see figure 1.7).

Results

Descriptive statistics for distal radius articular dimensions, scaphoid and lunate proximal areas, capitate and hamate dimensions by taxon are shown in Tables 3.1-3.6. Coefficients of variation for distal radius and proximal carpal row articular areas tend to be considerably higher in gorillas than most other taxa (if sample size is considered). This wide range of variability can be attributed to the high degree of sexual dimorphism in this taxon. Male and female gorillas differ significantly ($p<=.000$) in all surface dimensions of the antebrachial joint. Male and female chimps differ only in proximal scaphoid area, while bonobos show no size differences between sexes. Interestingly, no intersex differences are evident in terrestrial quadrupeds in any of these dimensions, despite males having substantially heavier body weights. Alternately, humans are not considered to be particularly sexually dimorphic, however significant differences in these joint surfaces do exist.

Spearman Rank Order coefficients show that all variables are significantly correlated with a metacarpal composite body size surrogate. Mann-Whitney U-tests of pairwise comparisons are based on ratios of articular dimensions to the metacarpal composite and to total length of the bone (for the capitate and hamate), as well as Z-scores for raw variables. Comparisons to total length are made in order to facilitate assessment of fossil specimens. Z-scores are standardized scores that determine how many standard deviation units above or below the mean of the total sample a given value falls. These comparisons are graphically depicted in figures 3.1 - 3.26.

In radius distal articular surface z-scores, gorillas are significantly different from all other taxa. Clearly, they have the largest overall size for this variable. The same holds true for scaphoid and lunate areas on the distal radius. Chimps and bonobos are significantly different for total area, but neither differ from humans. *Pongo* total area is somewhat larger, and they differ significantly from bonobos and humans, but not chimps. In scaphoid area, chimps, bonobos, orangs and humans are all similar, however in lunate area only bonobos and humans are not significantly different. Excluding gorillas, orangs have the largest lunate areas, followed by chimps. In all z-scores, brachiators (gibbons and siamangs together) are virtually identical to arboreal quadrupeds, and they both differ significantly from terrestrial monkeys. The latter have larger areas for distal radius dimensions.

Relative to metacarpal dimensions, gorillas and orangs have the largest total surface areas and are not significantly different from each other. Gorillas have significantly larger areas than chimps and bonobos, but the latter two do not differ from orangs. All large hominoids have much larger distal radius surface areas than humans. Among brachiators and monkeys, all differ significantly from eachother in relative radius distal area, with arboreal quadrupeds having the smallest surfaces, and terrestrial quadrupeds the largest.

Scaphoid area on the distal radius relative to metacarpal dimensions shows that gorillas have significantly larger areas than all other taxa, however chimps, bonobos and orangs are all similar. Compared to large apes, humans have much smaller scaphoid areas. Terrestrial monkeys have significantly larger areas than arboreal monkeys, and brachiators and intermediate between these two.

Orangs have the largest relative lunate surface area on the distal radius, but they do not differ significantly from gorillas or chimps. Gorillas, chimps and bonobos all differ significantly from each other and, with the exception of bonobos, from humans as well. Both humans and bonobos have reduced relative lunate surface areas.

In the ratio of scaphoid to lunate area on the distal radius, the range of variation is high for all taxa. The results show that bonobos, humans and gorillas respectively have the highest ratios for this dimension and do not differ significantly from each other in this respect. In other words, they have the largest scaphoid areas relative to lunate area. Among hominoids, orangs have the largest relative lunate area, followed by chimps. Results also indicate that terrestrial and arboreal monkeys are most similar to orangs in this ratio.

Comparision of the radial surface areas of the proximal carpal row produces results that are very similar to those of the distal radius. Z-scores of the proximal surface of the scaphoid (fig. 3.7) show once again that gorillas have the largest overall areas, and that chimps, bonobos and humans are very similar. Orangs have slightly smaller areas, but do not differ significantly from chimps, bonobos or humans. Brachiators have the smallest areas, but do not differ from monkeys overall. Relative to metacarpal size, bonobos do not differ significantly from gorillas or chimps, but are more similar to the former. This is likely an artifact of metacarpal dimension (to be addressed in the discussion), *vis a vis* actual scaphoid area being virtually indistinguishable between chimps and bonobos. Having said that, the mean for proximal scaphoid surface area is marginally bigger in bonobos (see table 3.2). Relative scaphoid area is smaller in humans and orangs, and both differ significantly from gorillas and bonobos. Among brachiators, arboreal and terrestrial monkeys there are no significant differences, however terrestrial quadrupeds do have somewhat larger relative scaphoid areas.

Lunate proximal surface z-scores reveal a pattern that is also similar to that of the distal radius (fig. 3.9). Both gorillas and orangs have much larger lunate radial surfaces compared to other taxa and do not differ significantly from each other. Chimps, bonobos and humans are all similar, but bonobos have the smallest areas whereas the human lunate surface is somewhat larger. Once again, brachiators most closely resemble monkeys, although terrestrial quadrupeds have slightly larger lunates overall. Relative to metacarpal dimensions, lunate proximal surface is greatest in orangs and gorillas, with no significant differences between the two. Chimps, bonobos and humans all have similarly sized lunate proximal surfaces. Terrestrial quadrupeds have significantly larger areas than brachiators or arboreal monkeys.

In the ratio of scaphoid to lunate area, *Pongo* is signifcantly different from all other taxa in the extreme enlargement of the lunate surface. Gorillas, chimps, humans and terrestrial monkeys all differ insignificantly, however humans do, in fact, have slightly larger relative lunate areas. Bonobos have a slightly higher ratio, therefore relatively larger scaphoid than lunate, compared to other larger hominoids and humans. They are significantly different from both chimps and humans, and p=.06 for the comparison to gorillas. The mean for scaphoid to lunate area in bonobos most closely resembles brachiators and arboreal monkeys.

Examining the distal carpal row, z-scores (fig 3.12) for all measures of the capitate show that, not surprisingly, gorillas have the largest overall articular surfaces compared to other taxa. Chimps, bonobos, orangs and humans do not differ significantly from each other however, among large hominoids, humans have the smallest distal articular surface of the capitate. *Pongo* has a very large range of variation for the distal articular surface, as well as the hamate facet area. This may not neccessarily be attributable to small sample size, since samples for brachiators and arboreal monkeys are the same and they do not show this same degree of variability. Gibbons and siamangs are not significantly different from monkeys, however they more closely resemble arboreal quadrupeds in having slightly smaller dimensions.

Comparisons of scaphoid facet area on the capitate relative to metacarpal size and total length reveal a pattern almost identical to that of the proximal surface of the scaphoid. Gorillas and bonobos are not significantly different from each other, and both have significantly larger scaphoid surfaces relative to metacarpal size compared to chimps, orangs and humans (fig 3.15). Relative to total length, gorillas have the largest scaphoid surface areas. Chimps and bonobos are most similar in this aspect, although the latter has slightly larger values. Orangs and human do not differ significantly in this measure and brachiators are comparable to monkeys, although gibbons and siamangs tend to have smaller scaphoid areas.

Hamate area on the capitate relative to metacarpal size is very similar among great apes and humans. Bonobos, however, are significantly different from gorillas and humans in having somewhat larger values for this measure. Orangs possess a very high range of variation in hamate area. Brachiators are virtually identical to arboreal monkeys and both have substantially smaller hamate areas than terrestrial forms. Relative to total capitate length (fig 3.18), hamate area follows a progressive pattern of larger to smaller from gorillas to bonobos, and from terrestrial monkeys to brachiators. In this ratio, only highly terrestrial species (gorillas and terrestrial quadrupeds) are significantly different from other taxa of similar size. Again, *Pongo* shows a very high range of variation.

In distal articular surface area of the capitate relative to metacarpal size, orangs again have a high range of variation, such that they are not significantly different from African apes. The means are quite close however, and all large apes have substantially larger distal surface areas than humans. Gorillas do differ significantly from chimps and bonobos, and the latter two are practically indistinguishable. In the ratio of distal area to capitate total length, there is essentially a trend of decreasing size of the distal surface from gorillas to gibbons (fig 3.19). Compared to large apes, humans have greatly reduced distal surface areas. It should be noted that among great apes and humans, only gorillas have significantly longer capitates and those of brachiators are most similar to arboreal monkeys (see table 3.3).

Pairwise comparisons of hamate distal and capitate articular surfaces show that gorillas have signifcantly larger areas for these dimensions, as indicated by z-scores, compared to all other taxa (fig. 3.21,3.22). Humans have the second largest absolute distal areas compared to great apes, but differ significantly from bonobos only which have the smallest areas. Brachiators have substantially smaller capitate and distal surface areas than monkeys.

Relative to metacarpal size, capitate facet area is greatly reduced in humans and is significantly lower than in great apes. As a ratio of total length, gorillas have enlarged capitate surface area, whereas for chimps, bonobos, orangs and humans it is has almost the same value. Brachiators have the lowest values for this dimension, likely due to their proximo-distally elongated hamates. Table 3.5 shows that gibbons and siamangs have longer hamates than monkeys. Among great apes, orangs have the longest hamates but differ significantly from bonobos only.

Distal articular surface area relative to metacarpal size again shows a high range of variation for orangs. Figure 3.25 demonstrates that distal area is very similar among great apes and humans. Gorillas differ signifcantly from chimps and humans, but not bonobos. The higher value in the latter is an artifact of metacarpal size, since absolute distal area is slightly less in bonobos than chimps (see fig 3.22). Terrestrial quadrupeds have significantly larger hamate distal surfaces than arboreal monkeys and brachiators. As a ratio of total hamate length, gorillas have considerably larger distal surfaces (p<=.000) than all other taxa. Chimps, bonobos and orangs have virtually identical measures, and all differ from humans which have larger distal areas. Terrestrial monkeys have expanded surfaces relative to arboreal forms and brachiators.

To summarize (see also table 3.8), gorillas and orangs both have expanded radius distal articular surface areas. Compared to all large apes, humans have distal surfaces that are much smaller. Lunate surface area is greater in gorillas and orangs, but is particularly noteworthy in the latter. No significant differences in scaphoid area exist among chimps, bonobos, orangs and humans. Therefore the disparity in total distal surface area is accounted for by lunate area. All hominoids except bonobos and humans differ in this respect. *Pongo* has the largest lunate area (in z-scores and relative to metacarpals), and bonobos have somewhat smaller lunate surfaces. Overall, the greatest changes in the radius distal articular surface appear to be occuring in the expansion of the scaphoid area in gorillas, and expansion of the lunate area in orangs. Brachiators are most similar to arboreal monkeys in most dimensions, except for total distal area relative to metacarpal size. This may be due to smaller metacarpal dimensions for gibbons and siamangs. In the ratio of scaphoid to lunate surface areas, orangs and terrestrial monkeys are significantly different from gorillas, *Pan*, and humans in having expanded lunate surfaces.

In the proximal carpal row, gorillas have the largest absolute scaphoid proximal surface areas, and no differences are evident among chimps, bonobos, orangs and humans. Relative to metacarpal dimensions, African apes tend to have larger scaphoid areas than Asian apes and humans. In this measure, bonobos are most similar to gorillas, however this is likey an artifact of metacarpal dimension. Lunate proximal surface areas are largest in gorillas and orangs respectively. Those of chimps, bonobos and humans are most similar, with humans having slightly larger overall surface area. Relative to metacarpal size, orangs have the largest lunate proximal areas, with gorillas being somewhat larger than chimps, bonobos and humans. In the ratio of scaphoid to lunate area, orangs have much larger lunates than scaphoids. Gorillas, chimps, terrestrial monkeys and humans all have slightly larger scaphoids than lunates, however in humans the ratio is more equal. Bonobos are distinct from other African apes and humans in having larger scaphoids relative to lunates, and are most similar .

to brachiators and arboreal monkeys in this respect. Brachiators most closely resemble arboreal quadrupeds in these measures.

In the distal carpal row, relative to metacarpal size gorillas and bonobos have expanded scaphoid areas on the capitate head. However as a ratio of total length, bonobos and chimps are most similar in scaphoid area, although the former still has a slightly larger value. Overall, African apes tend to have expanded scaphoid areas compared to orangs and humans, the latter being most similar to each other. Very few differences are apparent in hamate surface area on the capitate among great apes and humans, however overall gorillas have somewhat larger relative areas (as do terrestrial quadrupeds). In capitate distal articular area, great apes have much larger surfaces than humans, and expansion is most notable in gorillas. As per its counterpart, the capitate facet area on the hamate is not particularly revealing, other than humans having a smaller value than great apes relative to metacarpal size. As a ratio of total length, gorillas have expanded capitate surfaces. Humans are similar to chimps, bonobos and orangs in hamate distal articular size relative to metacarpals. Compared to total length however, humans share with gorillas an expanded distal area. In almost all dimensions, brachiators most closely resemble arboreal monkeys.

The results obtained for the proximal carpal row generally accord well with those obtained for the distal radius, in terms of overall relationships between measures. That notwithstanding, table 3.7 shows that surface area measures, on the ulnar aspect in particular, are grossly overestimated in the distal radius. The female mating surface in modified ovoid joints always has a smaller area than the male mating surface (MacConnaill and Basmajian, 1969). Clearly, measurement error has occurred in obtaining results of surface areas across the antebrachial joint. This error is almost certainly present in the distal radius measures due to difficulties in demarcating the individual scaphoid and lunate components on the video images in many cases. Consequently, final discussion of distal radius measures will be confined to gross overall area.

Regression analyses of the antebrachial joint and selected elements of the distal carpal row clarify the relationships among articular surface variables under investigation. The goal is to determine whether allometric trends in surface morphology are present in the sample as a whole, and within taxonomic subsets which may reveal differential patterns of limb loading associated with locomotor behaviour.

There is considerable debate over the appropriate line-fitting technique in allometric regressions, therefore results from both RMA and OLS regressions are reported. In order to determine if departures from a common trend exist, use of the predictive model of least squares is appropriate (Harvey and Pagel,1991; Jungers,1985), and is the preferred method here since analysis of covariance can be used with OLS as a powerful statistical test for slope and intercept differences (Inouye,1992,1994). Only slope differences that agree between both methods are reported. Furthermore, the use of a body size surrogate(s) is problematic in evaluating the actual slope of a regression. Body weights for all specimens were unavailable, requiring the use of size surrogates. Generally, it is considered acceptable to use a size surrogate from a region of the body anatomically remote from the variables under investigation. However, variables used as size surrogates may be undergoing allometry in the same, or opposite direction as the variable in question. Hence, the biological significance of the actual value of the slopes is confounded by the two regression techniques consistently yielding different results when correlations are below .90 (RMA slopes are usually slightly higher than OLS slopes), and regressions of variables against different size surrogates producing different results.

In this analysis, a metacarpal composite measure is used as a substitute for body size. It is not anatomically remote from the variables under investigation however, considering that all hominoids are characterized by forelimb dominated locomotor behaviour, selection is acting on the forelimb and it is likely that allometric trends are present. Furthermore, it is also likely that patterns of allometry within different components of the forelimb are in the same direction, such that departures from this common trend may reflect unique adaptations to different loading regimes among closely related species.

Discussion of the regression analyses to follow will focus on the *pattern* of change in intertaxonal comparisons of slopes, with the understanding that slope values are either positively or negatively allometric, or isometric relative to the size surrogate in question. Assessing the direction and degree of departure from some common trend among taxonomic subunits over a narrower size range minimizes the impact of disparate adaptive or phylogenetic histories, so that proportional and morphological changes that are essentially related to body size differences (or, in this case, body size surrogates) can be evaluated (Jungers and Susman,1984; Jungers,1985; Smith,1980).

Radius Distal Articular Surface

Regression results for all variables are shown in Table 3.8 and figures 3.27-3.43. Radius distal articular surface for the entire sample is negatively allometric relative to metacarpal size and humerus epicondylar breadth. The pattern produced is the same for both surrogates, and only metacarpal comparisons will be discussed. Scaphoid area increases at a slightly faster rate than lunate area, however the slopes are not significantly different (see fig. 3.30).

For intertaxonal comparisons, arboreal quadrupeds have been omitted due to sampling problems. The sample of arboreal monkeys is comprised primarily of colobus monkeys, plus one *Nasalis*. *Nasalis* is similar to terrestrial quadrupeds in distal radius articular area verses metacarpal size and falls along the regression line with the latter. Colobus monkeys have much smaller dimensions and are most similar to gibbons. It is quite possible that for a larger sample of *Nasalis* monkeys, the regression slope would be similar to that of colobus monkeys, but transposed above the line for the latter indicating that at common sizes, *Nasalis* has larger relative dimensions of the distal radius. Attempting to put a line of best fit through the arboreal monkey sample *as it is* does not accurately reflect the true slope for this group. Results for *Pongo* are also problematic due to very small sample size and uneven distribution of males and females (for the radius, 5 males and 2 females). However, as the only other large hominoid that is not a knuckle-walker (excluding humans), orangs are included in the analysis, although actual slopes are to be interpreted with caution.

Table 3.6 shows the pattern of change in distal radius articular surface area among the taxa under investigation. There are no significant differences in slope for all groups, however y-intercepts do differ. Terrestrial quadrupeds have a slope closest to isometry with metacarpal dimensions. Among hominoids, the pattern of change is most rapid (ie: higher slope) for humans, followed by gorillas. The slopes for chimps, bonobos and orangs are considerably lower, indicating that radial area increases less with increasing metacarpal size. Scaphoid area on the distal radius approaches isometry in terrestrial quadrupeds, and is very close to isometry for brachiators. The slopes for bonobos and orangs are somewhat lower. In the regression of the total sample, bonobos in particular fall above the line, indicating that at common sizes with chimps, for example, bonobos tend to have larger scaphoid dimensions. Recalling the pairwise comparisons discussed earlier, the ratio of scaphoid area to metacarpal size is almost the same among chimps, bonobos and orangs (see fig 3.8). This suggests that an increase in scaphoid surface area may be of greater functional significance than changes in metacarpal size, and that bonobos exhibit very few differences in these dimensions between the sexes. It may also reflect sex-specific differences in behaviour, in that males may load their limbs in a different manner than females (see Ruff, 1988).

Scaphoid area scales faster than lunate area in gorillas, chimps, orangs and brachiators. It might have been expected that *Pongo*, having the largest lunate area relative to scaphoid area (see above), would have a higher slope. This result is likely a function of sampling problems, in that low correlations reflect little more than a constricted range of *x* and *y* variables (Smith,1981). Sampling problems are not the case for chimps, however they too exhibit an extremely low correlation and slope for lunate area. Scaling of scaphoid area is very similar between gorillas and chimps, but the latter have much lower slopes for lunate area compared to gorillas. Again, this may imply differential loading of the limb in chimp males and females. Bonobos, on the other hand, have higher slopes for the lunate than the scaphoid. In the ratio of scaphoid to lunate area (see above), bonobos in fact have the highest value, indicating that they have larger scaphoids than lunates compared to other taxa. Figure 3.29 depicting lunate area shows that there are two specimens distinguished from the rest of the bonobo sample in being somewhat smaller in both lunate and metacarpal dimensions. These two are young individuals and it's possible that the intertaxonal regression has produced an artifically high slope. It is interesting to note, however, that these same specimens are not distinguished in the regression for scaphoid area. There is considerable overlap in scaphoid area between chimps and bonobos, suggesting a size increase in surface area on the radial side of the forelimb independent of body size (metacarpal dimensions) in the latter.

Humans have the highest lunate surface slopes of all hominoids, and are second only to terrestrial quadrupeds. Humans have overall distal radial dimensions that are reduced in size compared to other large apes, and the faster rate of increase of the lunate component suggests greater emphasis on the ulnar aspect of the forelimb. Terrestrial quadrupeds alone have lunate dimensions that are positively allometric. Indeed, they have the largest lunate surfaces relative to scaphoid of all taxa. The forelimb of monkeys is fundamentally different in structure from hominoids however, in having an elongated ulnar styloid process which articulates with the proximal carpal row and, consequently, reduced adduction capabilities. Forces transmitted through the antebrachial joint are evidently concentrated on the ulnar aspect of the limb.

Proximal Carpal Row

The radial articular surface on the proximal scaphoid for the entire sample is negatively allometric (slope=.879) and, in contrast to the results of the distal radius, scales *lower* than that of lunate proximal area (slope=.975). The slopes for these two variables are not significantly different, but the y-intercepts are ($p<=.01$). The regression plot of scaphoid proximal area (fig 3.32) for the total sample shows that bonobos fall well above the line, and that at common sizes with chimps, *P.paniscus* has larger scaphoid proximal areas. Bonobos tend to have smaller body size dimensions, but overlap with chimps in scaphoid area. Two distinct size groupings are evident in gorillas (males and females), however they fall along the regression line. Lunate surface area scales closer to isometry than scaphoid area. As might be expected, orangs fall well above the line (Fig. 3.33), indicating that they possess greatly enlarged lunate surfaces relative to body size dimensions. At common sizes with chimps, bonobos have similar lunate surface areas. Indeed, there is considerable overlap in lunate area in these two taxa, however differences in body size dimensions results in a different pattern of distribution along the regression line. Brachiators and arboreal monkeys tend to have smaller proximal carpal row surface areas relative to body size.

Comparisons by taxon reveal that chimps and humans are most similar in the pattern of scaphoid area increase, having the highest slopes and no significant differences in either slope or y-intercept. The value for chimps (.975) is closest to isometry compared to all taxa. Once again, bonobos exhibit a much lower slope (.538) than all other large hominoids for scaphoid area, indicative of a restricted size range among males and females and possibly reflective of sex-specific differences in habitual limb usage. All taxa have significant correlations of scaphoid area to body size dimensions *except* orangs. Correlations of lunate area to body size are also non-significant in orangs and arboreal monkeys. *Pongo* has the lowest slope for scaphoid area, and the highest slope (1.394) for lunate area. Thus, it is clear that a size dependent increase in proximal carpal row articular surface area is occurring on the ulnar aspect of the antebrachial joint at the expense of the radial aspect in orangs.

Arboreal and terrestrial monkeys have very similar slopes for scaphoid area, but the slope for the latter is transposed above that of arboreal forms, indicating that at all sizes terrestrial monkeys have larger scaphoid areas. The pattern of increase is the same however. Lunate area tells a different story (figure 3.34). It is positively allometric in arboreal monkeys, having a slope of 1.21, and the correlation between lunate area and body size is non-significant. It is possible that the position of one large arboreal monkey (*Nasalis*) is confounding the true slope value for a very small sample size (in the same way as in the distal radius), although it is intriguing that this particular specimen did not cause a dramatic deviation away from the common arboreal monkey trend in scaphoid area. Accordingly, it may also be possible that there *is* a positively allometric increase in lunate surface area in arboreal monkeys that is functionally related to limb postures requiring more varied hand positions. Unfortunately, this is difficult to ascertain with such a small sample size.

Slopes for lunate proximal surface area are very similar among African apes, humans, and terrestrial monkeys. In comparing the rate of change of scaphoid to lunate area among taxa, it is demonstrated that lunate area scales faster in bonobos, orangs, arboreal and terrestrial monkeys. Scaphoid area, on the other hand, scales faster in gorillas, chimps and humans. This implies a shift in emphasis to the radial aspect of the forelimb in chimps and gorillas associated with high frequencies of terrestrial locomotor behaviour. The fact that lunate area scales faster in *both* arboreal and terrestrial monkeys suggests that this is the primitive condition, one that is elaborated on to the extreme in *Pongo*, and is retained in bonobos.

Distal Carpal Row

Regression results for capitate and hamate measures are shown in table 3.8. Scaphoid facet area on the capitate regressed against metacarpal dimensions for the total sample has a value close to isometry (.912), and scaphoid area relative to total capitate length is positively allometric (1.181). Figure 3.35 demonstates that all bonobos fall above the line for scaphoid area relative to body size measures, as do many chimps, indicating that these two taxa possess enlarged scaphoid surfaces on the capitate. Most humans and orangs fall below the line. Relative to total length the distribution is somewhat more even about the regression line (figure 3.36).

Comparisons by taxon reveal that chimps are positively allometric for scaphoid area relative to metacarpal size (slope=1.213), and are significantly different ($p<=.05$) from gorillas, humans and bonobos whose slopes are considerably lower. Whereas bonobos have the flattest slope (.466) for the regression against metacarpal size, in scaphoid area compared to total capitate length they are slightly positively allometric (slope=1.093), while gorillas and chimps have identical slopes of 0.901. The pattern of change for all large hominoids is similar, and at all sizes gorillas have the largest scaphoid areas and *Pongo* has the smallest.

Hamate area on the capitate for the total sample is negatively allometric (.843) relative to metacarpal dimensions, and approaches isometry (.935) compared to total capitate length. Figure 3.37 shows that all bonobos and many chimps are transposed above the regression line for metacarpal size, and a large portion of gorillas, arboreal monkeys and brachiators fall below the line. The distribution is more equal in hamate area relative to total capitate length (figure 3.38).

Comparisions by taxon reveal no significant differences in slope for hamate area on the capitate. The correlation between hamate area and metacarpal size is significant in all taxa except orangs and terrestrial monkeys, however compared to total length hamate area is significant only in gorillas and chimps. Thus, neither body size nor capitate length have any influence on hamate area in *Pongo* and terrestrial monkeys. Regressions for hamate area relative to size and length variates demonstrate that *Pongo* has the highest slope and terrestrial monkeys the lowest (Table 2.6), implying a functionally relevant role of the capitate-hamate joint in these two taxa, but in fundamentally different directions. There is considerable overlap in hamate area among all large hominoids, including humans. Once again, however, the restricted size range of metacarpal dimensions in bonobos has produced a very shallow slope. Gorillas and humans area most similar to each other in hamate area verses metacarpal size, and chimps exhibit a somewhat faster rate of change. For all taxa except orangs, slopes are well below isometry, suggesting that hamate facet area is a rather conservative trait and does not change in response to increasing body size.

Compared to capitate total length, hamate facet area in all taxa except *Pongo* exhibits slopes well below isometry. In this case, humans are most similar to terrestrial quadrupeds in having very low slopes and gorillas have the fastest rate of change. Fig. 3.38 shows that all large hominoids (to the exclusion of male gorillas) are tightly grouped for hamate area regressed against capitate length reflecting a narrow range of sizes for these two variables. The fact that terrestrial monkeys have low slopes in regressions against metacarpal size and total capitate length is likely a function of proximodistally reduced hamates which are almost always excluded from contact with the lunate proximally by a laterally expanded capitate head (Marzke, 1994 and see above).

Capitate distal articular surface area relative to metacarpal dimensions for the total sample (figure 3.39) is negatively allometric (slope = .898), but closer to isometry compared to total length (slope = .972, figure 3.40). All bonobos, and most chimps and orangs fall above the regression line for metacarpal size, indicating they have enlarged distal areas. All humans and arboreal monkeys fall well below the line. Distal area relative to total length demonstrates that almost all gorillas fall above the line, indicating that they have larger distal surfaces than would be expected given the total capitate length. Humans still fall below the line, therefore in both comparisons they have much smaller distal surfaces than other great apes.

No significant differences in slope exist in intertaxonal comparisons of capitate distal area, however chimps are closest to isometry relative to metacarpal size (.901) and again bonobos have the lowest slope (.403). Gorillas are most similar to terrestrial monkeys in the rate of change, although the former are transposed above the line of the latter, and humans are similar to orangs. Relative to total length, terrestrial monkeys (.910) and gorillas (.859) respectively have the highest slopes for distal area. Humans and *Pongo* show almost identical rates of change, however orangs are transposed above humans, indicating that at common sizes (for capitate length) orangs have much larger distal areas. The slope for bonobos is slightly lower than that of chimps, however the higher slope here compared to the regression against metacarpal size demonstrates that there is a greater degree of variation in metacarpal dimensions in the bonobo sample than there is for capitate length.

Finally, figure 3.41 illustrates that capitate length does not differ greatly among large hominoids. Chimps, bonobos and humans in particular are very similar in overall length. Regressing total capitate length against metacarpal dimensions reveals a pattern that is almost identical among gorillas, chimps, humans and *Pongo*. Bonobos again have much lower slopes, indicating that there is very little variation between males and females in capitate length, and that at common sizes of capitate length, *P.paniscus* has greatly reduced metacarpal dimensions compared to other hominoids. Terrestrial quadrupeds also possess a limited range of variation in capitate length, but are shifted well below the regression line of bonobos, indicating that at common sizes terrestrial monkeys have much shorter capitates.

The hamate distal articular surface is negatively allometric (.834) with metacarpal dimensions for the total sample, and approaches isometry relative to hamate proximodistal length (.906). Figure 3.42 illustrates that there is considerable overlap in distal area among bonobos, chimps and humans but bonobos have relatively larger distal areas given their metacarpal size. In the plot of distal area verses total hamate length, it is clearly demonstrated that brachiators have greatly reduced areas compared to other taxa, and virtually all gorillas and most terrestrial monkeys fall above the regression line, indicating they have larger distal areas than would be expected given their hamate lengths (figure 3.43). Capitate area on the hamate follows a pattern similar to its counterpart (hamate area on capitate), in that area relative to total length (slope=1.036) scales faster than relative to metacarpal dimensions (slope=.892). The distribution of taxa around the regression line for capitate area relative to total length mirrors that of distal articular surface area. This is primarily a function of extreme hamate elongation in brachiators, and greatly reduced hamate length in gorillas and terrestrial monkeys.

Comparisons by taxon for capitate area on the hamate relative to metacarpal size show that chimps and terrestrial monkeys are similar to each other in having the highest slopes, although chimps are shifted above terrestrial monkeys. Humans most closely resemble gorillas and bonobos have the lowest slopes of all taxa. Relative to hamate total length, capitate area increases at a rate close to isometry (.906) for gorillas, and is followed by *Pongo* which has a slightly lower slope. Chimps, bonobos and humans are most similar to each other, and all have considerably lower slopes than gorillas and orangs. There is a wide range of overlap in hamate total length among all great apes and humans, however it is gorillas that are distinguished on the basis of much greater capitate areas with increasing hamate length.

Distal articular surface area of the hamate relative to metacarpal size produces an interesting set of relationships. Although no significant differences in slope exist, terrestrial quadrupeds, gorillas and chimps are all very similar in slope values and are distinguished from bonobos, orangs and humans which have much lower slopes (figure. 3.43). These two distinct groupings are clearly separated on the basis of highly terrestrial locomotor behaviour in gorillas, chimps and monkeys, resulting in modification of the hamate distal surface in response to increased stresses incurred along the ulnar aspect of the wrist in a forelimb habitually loaded in compression.

Distal articular surface area relative to hamate total length produces a slightly different result. In gorillas, the distal area increases at a rate close to isometry (.917), however the slope for terrestrial monkeys is extremely low. Again, this is a function of extreme proximodistal reduction in hamate height in the latter which, in conjuction with an expanded distal surface, results in the "blocky" overall shape of the hamate. The rate of change in humans for distal area is reduced compared to bonobos and chimps, however at common hamate lengths with chimps and bonobos, humans have larger distal areas.

Summary of Carpal Regressions

To summarize the regression analysis of articular surface areas of the distal radius, and proximal and distal carpal row, the following trends have been noted:

Distal Radius

- Distal articular surface area is negatively allometric relative to metacarpal size for the total sample
- Gorillas, humans and terrestrial quadrupeds are most similar and scale closest to isometry for distal area whereas chimps, bonobos and orangs have lower slopes

- Bonobos have larger distal areas than would be expected given their body/metacarpal size
- For the total sample, scaphoid area scales faster than lunate area
- By taxon, scaphoid area scales faster in gorillas, chimps and orangs while lunate area scales faster in bonobos, humans and terrestrial monkeys

Proximal Carpal Row

- Scaphoid and lunate areas are negatively allometric relative to metacarpal dimensions
- Bonobos have larger scaphoid areas than would be expected given their metacarpal size
- Orangs have much larger lunate areas than would be expected given their metacarpal size
- For the total sample, scaphoid area scales *lower* than lunate area (contra the result of the distal radius)
- By taxon, scaphoid area scales faster in gorillas, chimps and humans whereas lunate area scales faster in bonobos, orangs and monkeys (AQ and TQ)

Distal Carpal Row

- Scaphoid area on the capitate scales close to isometry for the total sample
- Bonobos and chimps have larger scaphoid areas than would be expected given their metacarpal dimensions, and chimps are positively allometric in this feature
- Hamate facet area on the capitate is negatively allometric for the total sample
- All bonobos, and large numbers of chimps and orangs have hamate facet areas that are greater than would be expected given their metacarpal size, however bonobos

have lower slopes

- Gorillas and humans are most similar in the pattern of scaling of hamate area
- For all taxa except *Pongo*, hamate area scales well below isometry and does not change dramatically with increasing body size
- Hamate facet area is not influenced by body size or capitate length in orangs and terrestrial monkeys, however it scales fastest in orangs and slowest in monkeys
- Capitate distal articular area is negatively allometric for the total sample
- All bonobos and most chimps have enlarged distal areas given their metacarpal size
- Chimps scale closest to isometry for distal area verses metacarpal size and, although the values for bonobos overlap, the latter have much lower slopes
- Chimps and bonobos are most similar to each other in the pattern of scaling for distal area and capitate length
- Gorillas and terrestrial monkeys are similar to each other in the pattern of scaling of distal area relative to metacarpal size and capitate length
- Humans resemble orangs in the pattern of scaling of distal area, however at common sizes *Pongo* has much larger surface areas
- Absolute capitate length does not differ greatly among great apes and humans, and is most similar among chimps, bonobos and humans
- Relative to metacarpal size, the pattern of scaling of capitate length is very similar among gorillas, chimps, orangs and humans
- Bonobos and terrestrial monkeys both have little variation in capitate length
- Capitate area on the hamate is negatively allometric for the total sample

- Humans and gorillas are most similar to each other in the pattern of scaling of capitate area relative to metacarpal size, and chimps resemble terrestrial monkeys in this feature
- Relative to total hamate length, gorillas and orangs have slopes closest to isometry for capitate area, and chimps, bonobos and humans are most similar in having much lower slopes
- Among great apes and humans, there is a wide range of overlap in hamate length, however gorillas have larger capitate areas with increasing hamate length
- Gorillas and terrestrial monkeys have greatly enlarged hamate distal articular surface areas relative to total length, but area scales close to isometry in gorillas and does not in monkeys
- Chimps, bonobos and humans overlap in hamate distal articular surface areas, but bonobos have larger distal areas given their metacarpal size
- The pattern of scaling (high slopes) of distal hamate area relative to metacarpal size is very similar among gorillas, chimps and terrestrial monkeys, and clearly distinguishes this group from bonobos, humans and *Pongo*

Finally, bonobos are characterized in having the lowest or flattest slopes compared to other African apes and humans in the following features:

- Radius distal articular surface
- Scaphoid proximal surface
- Scaphoid area on the capitate

- Hamate area on the capitate
- Distal articular surface of the capitate
- Total capitate length

Discussion

The preceding analysis has attempted to answer several questions about hominoid wrist morphology that may be functionally linked with knuckle-walking in African apes. First, compared to other hominoids and monkeys, do knuckle-walkers have expanded articular surface areas of the distal radius and proximal carpal row. Second, is the relative size and scaling of the scaphoid proximal surface distinctive in knuckle-walkers.

The results show that all great apes have significantly larger radius distal articular surface areas than humans, however chimps, bonobos and orangs are not different from each other in this respect. It is only gorillas that exhibit a dramatic increase in this joint surface and they are, in fact, significantly larger than both chimps and bonobos relative to body size surrogate (metacarpal) measures. Terrestrial monkeys also have enlarged distal radius areas compared to arboreal animals. The pattern of scaling in this feature demonstrates that gorillas, terrestrial monkeys, and *humans* have distal areas that increase at a rate close to isometry (although slightly negative), whereas chimps, bonobos and *Pongo* have much lower slopes. Insofar as the female joint mating surface in modified ovoid joints always has a smaller area than the male mating surface (MacConnaill and Basmajian, 1969), the former represents the minimum amount of joint surface area needed to reduce joint stress and thus, conveys information about joint loading and stability (Godfrey *et al*,1991). Therefore, the faster rate of increase of radius distal area in gorillas, terrestrial monkeys and humans implies that antebrachial joint stability is of greater importance to these taxa than to more arboreal animals like chimps, bonobos and orangs.

Observations from behavioural studies have shown that gorillas are almost exclusively terrestrial and possess many characters of the wrist and hand associated with stability, weight transmission and distribution. For example, a cartilage covered, articular ulnar styloid process enclosed in its own synovial cavity; a semi-lunar mensicus that is fully fused and indistinguishable from the fibrocartilaginous triangular articular disc, resulting in a single, convex and expanded articular surface for the proximal carpal row; reduced adduction capabilities; ray lengths of the metacarpals and phalanges that are roughly equal so that all four lateral digits are used for support in knuckle-walking stance. All these characters help to distribute body weight evenly across the antebrachial joint, which is of paramount importance to an extremely large-bodied animal habitually loading the forelimb in compression during terrestrial locomotion. Studies of human wrists have shown that under small compressive loads, there is initial contact with the scaphoid, lunate and distal radius (Volz *et* al, 1980). With increasing loads, the area of contact is extended to the fibrocartilaginous triangular disc underlying the ulna. Removal of the triangular disc results in greater stress per unit area in the radio-lunar joint and trauma (Volz *et* al, 1980). Therefore it is clear that complete fusion of the triangular disc and meniscus in gorillas is an unique adaptation and effective stress dispersal mechanism.

Terrestrial monkeys have a scaling pattern of the distal radius that is similar to gorillas, although stability and weight distribution is achieved through somewhat different means. The ulnar styloid process, for example, is elongated and directly articular with the triquetrum distally. Terrestrial monkeys are not nearly as massive as gorillas, however they generally have larger body sizes than arboreal forms, and a scaling pattern that more closely approximates isometry is reflective of joint stress reduction mechanisms neccessitated by a terrestrial habitus. Humans, on the other hand, do not utilize the forelimb in locomotion. The human hand is adapted for maximum manipulatory capabilities (see Marzke,1993,1997; Napier,1959). A complete analysis of human hand function is beyond the scope of this paper, however it is likely that with the advent of tool use and manufacture, requirements for antebrachial joint stability arose.

In overall distal radius articular area chimps, bonobos and orangs scale at a rate much lower than that of gorillas, terrestrial monkeys and humans. This implies that stresses are not as great across the antebrachial joint in these more arboreal forms, and that mobility is favoured over stability. Chimps tend to be more terrestrial than bonobos, nevertheless it is clear the forces generated across the wrist joint are not as great as in gorillas, and that high frequencies of arboreal activity in chimps precludes expansion of the distal radius articular surface which would compromise mobility. Chimps have a range of adduction of the wrist similar to that of gorillas (Tuttle, 1969a, 1970), but the semi-lunar meniscus is (in most cases) not fused to the triangular articular disc. This permits the ulnar styloid process to participate with the proximal carpal row in positions of extreme adduction. The fact that the triangular disc and meniscus are not completely fused suggests that weight distribution across the antebrachial joint is not even as in gorillas. Chimps tend to use more varied hand positions in knuckle-walking than gorillas, and manual rays are not of equal length, such that chimps typically support the body on digits three and four. All these features imply differential loading across the hand and wrist.

At present it is not known what the conformation of the semi-lunar meniscus and triangular disc is in bonobos, but in the characters just described they are similar to chimps. In fact, bonobos overlap considerably with chimps in distal radius articular size, however, bonobos have larger distal areas than would be expected given their metacarpal dimensions. Indeed, in this feature bonobos have the lowest slope of all great apes and humans, indicating an extremely restricted size range in distal radius area within this taxon. Given that bonobos are characterized by high male/female affinity in their social structure, less sexual differentiation in postcranial linear dimensions, and higher frequencies of arboreal travel than common chimps, (Doran,1993; Jungers and Susman,1984;Kuroda,1979; Kano,1980; Zihlman and Cramer,1978), the implication is that there are fewer sex-specific differences in locomotor behaviour and patterns of limb loading within bonobos as compared to other great apes. However, this may not be the case.

In their assessment of African ape limb morphology, Jungers and Susman (1984) conclude that flat slopes and nonsignificant correlations they observed for limb length scaling within bonobos is due to "significant sexual dimorphism in body weight combined with the absence of sexual dimorphism in linear variables" (p.162). The same is apparently true in this analysis, in that variation in metacarpal dimensions in bonobos (as a substitute for body size) is comparable to that of chimps, but variation in radius distal area is greatly reduced in the former. Jungers and Susman (1984) suggest the possibility of "genetic uncoupling" of size and linear (in this case, articular area) dimensions, such that selection for an increase in linear (or area) measures may not neccessarily be correlated with increasing body size. Numerous authors have reported on the skeletal differences between common chimps and *Pan paniscus*. For example, compared to chimps, bonobos have: minimal sexual dimorphism; a lower intermembral index (ie: relatively longer hindlimbs); a more gracile upper body; a smaller chest girth; narrower scapula in males; more curved proximal and intermediate phalanges; metacarpal heads with less pronounced "dorsal ridges"; and thicker cortices in the metacarpals and phalanges (Coolidge,1933; Coolidge and Shea,1982; Jungers and Susman,1984; Roberts,1974; Shea,1986; Susman,1979; Zihlman and Cramer,1978). These differences in the postcranial skeleton may be a consequence of random genetic drift, resulting from bonobos' isolation, as well as adaptation to forest dwelling and more arboreal habits (Doran,1993; Horn,1979; Johnson,1981; Lande,1979; Latimer *et al*,1981; MacKinnon, 1978; Susman,1979).

Regardless of whether these differences between *P.troglodytes* and *P.paniscus* are genetic in origin, the results thus far demonstrate that in the pattern of scaling of radius distal articular area, these two taxa are similar to each other, and are distinguished from the more terrestrial gorillas and monkeys. As noted previously, the antebrachial joint morphology of gorillas reflects even weight distribution. Chimps utilize more varied hand positions during knuckle-walking, and are more arboreal than gorillas. Behavioural observations of bonobos and chimps reveal that, while both are knuckle-walkers when on the ground, arboreal travel is a more significant component in bonobo locomotion (Doran,1993). In addition, both male and female bonobos use more arboreal quadrupedalism and less climbing/scrambling than chimps. Within bonobos, females use less climbing/scrambling than males and more quadrupedalism. Bonobos typically use palmigrade quadrupedal postures on boughs, while chimps will knuckle-walk on branches that are big enough. On smaller boughs, chimps characteristically use climbing, scrambling, and aided bipedalism but are reluctant to adopt palmigrade postures (Doran,1993). Male bonobos engage in higher frequencies of suspensory behaviour than their male chimp counterparts.

Thus, it is clear that within *Pan*, arborealism is a significant component of daily activity, and is reflected in the lower scaling pattern of the distal radius articular surface. This feature is shared with *Pongo* (which is almost exclusively arboreal) to the exclusion of gorillas and terrestrial monkeys. That chimps have a somewhat higher scaling pattern than bonobos might be indicative of increased frequencies of terrestriality, and size dependent enlargement of the distal radius surface for stress reduction. Previous studies of linear dimensions of limbs and fingers have concluded that a pattern of ontogenetic scaling is present within *Pan*, whereby proportions of adult chimps are the same as those predicted if the growth pattern of bonobos is extended to larger terminal sizes (Inouye, 1992; Shea, 1984). Evidence presented here shows that, although slopes for distal radius area are not statistically significantly different, the pattern is somewhat distinct in these two taxa and bonobos are not ontogenetically scaled versions of chimps.

As noted above, variation within *Pan* in arboreal postures and behaviours, and among bonobos, chimps and gorillas in frequencies of terrestrial verses arboreal locomotor habits would be expected to result in differential loading across the proximal carpal row. This leads to the second question to be addressed - does the relative size and scaling of the scaphoid distinguish knuckle-walkers? Fusion of the os centrale to the scaphoid is a uniquely derived character shared between African apes and humans to the exclusion of all other anthropoid taxa. It has been hypothesized that this feature is functionally linked to knuckle-walking and the comcomitant requirement of greater wrist stability (Begun 1992,1994; Begun *et al.*, 1997; Corruccini,1978; Harrison,1986; Jenkins and Fleagle,1975; Lewis,1985; Sarmiento, 1985,1988; Tuttle,1967,1969a,b,1974). Jenkins and Fleagle (1975) observed that the proximal carpal row remains essentially static during knuckle-walking, and as body weight passes over the forelimb the axis of rotation shifts from between digits three and four, toward the radial side. It is expected that emphasis on the radial aspect of the forelimb during weight bearing would result in larger relative scaphoids in knuckle-walkers, an observation that has been noted by earlier researchers based on linear measures (Corruccini, 1978; Jenkins and Fleagle,1975; Sarmiento, 1988,1994). Specifically, the question to be addressed is whether scaphoid area increases at a rate consistant with increasing body size, and the nature of the relationship between scaphoid and lunate proximal surface areas and their respective scaling patterns.

Comparative analysis of the scaphoid and lunate radial articular surfaces shows that relative to metacarpal dimensions, African apes have larger scaphoid areas than Asian apes and humans. In fact, bonobos are most similar to gorillas in this respect, however this is likely an artifact of relatively smaller metacarpal dimensions in bonobos. As expected, *Pongo* has a greatly enlarged lunate proximal surface. In conjunction with other features of the wrist such as an extremely reduced and non-articular ulnar styloid process, a proximal carpal row that is more curved in mediolateral plane than the distal radius surface, and equal development of the flexor and extensor muscles of the wrist, accords orangs with the widest range of radioulnar deviation capability of all hominoids. Needless to say, this is extremely important to a large-bodied animal engaging in quadrumanus climbing and suspensory activity. Gorillas also have an expanded lunate proximal surface, and this is relatively larger than chimps, bonobos and humans. This is consistent with the overall antebrachial joint area enlargement discussed above, and the requirement for joint stress reduction in gorillas across the whole antebrachial surface.

In comparing the ratio of scaphoid to lunate proximal areas, the results show that bonobos, brachiators and arboreal monkeys are most similar to each other in having relatively larger scaphoids. Gorillas, chimps and terrestrial quadrupeds all share expanded lunate surface areas, so that their ratios are somewhat smaller. Humans have slightly larger lunate surfaces still, but there are no significant differences among gorillas, chimps, humans and terrestrial monkeys in scaphoid to lunate area. Orangs are unique in having extremely enlarged lunates, and are different from all other taxa in this respect.

It might be posited that, since a relatively larger scaphoid area is characteristic of arboreal monkeys and brachiators, this trait represents the primitive condition for anthropoids and is retained in bonobos. Previous research has established that hylobatids are very primitive in characters of the wrist and are more similar to arboreal monkeys than they are to other hominoids. Moreover, many gibbons have second metacarpals (MII's) that are the most robust of all metacarpals (Susman, 1979), and all gibbons typically have large humero-radial joints (Rose, 1993). Hence, these traits imply a reliance on radial side loading of the forearm. Behavioural observations outlined earlier have shown that bonobos are more arboreal than chimps, and that often they behave much like arboreal quadrupeds in using palmigrade quadrupedal postures. Gripping a branch with the thumb abducted and the lateral digits adducted, ground reaction forces would be concentrated through the radial side of the wrist. Thus, selection for a larger scaphoid in both bonobos and arboreal quadrupeds would be favoured. As discussed above, bonobos do have larger scaphoids relative to metacarpal dimensions than chimps.

According to Godfrey *et al* (1991), there is a "tendency for larger animals in general and hominoids in particular to shift medially the transmission of force through the elbow" (p.619). Great apes have larger humeral trochlear surfaces relative to capitulum surfaces, therefore much of the load is borne through the humero-ulnar joint. The opposite is true of cercopithecoids, wherein the capitulum area is enlarged, and load bearing is shared more evenly between the humero-ulnar and humero-radial joints (Rose,1988). The analysis presented here demonstrates that expansion of the lunate surface, as seen in the reduction in the ratio of scaphoid to lunate proximal surface areas, does occur with increasing body size and therefore supports the conclusions of Godfrey *et* al (1991).

During knuckle-walking and terrestrial quadrupedalism (digitigrady), the forelimb acts as a supporting prop, the wrist is held in line with the forelimb, and the weight of the body is transmitted down through the carpals to the metacarpal heads. During stance phase in knuckle-walking, chimps support the body on digits three and four and weight is transmitted directly through the capitate and hamate to the proximal carpal row. As described earlier, weight distribution is likely more even in gorillas, wherein digits two and five are used with greater frequency in knuckle-walking support (Inouye, 1994). What would appear to be happening is that the axis of weight transmission has shifted from the radial side, as in bonobos and arboreal monkeys, toward the ulnar side and the lunate surface. African apes are characterized by having "inflated" capitate heads, which increases surface area contact with the lunate proximally. In addition, Marzke *et al* (1994) have shown that, with few exceptions, all African apes have extensive contact between the proximal pole of the hamate and distal lunate, permitting effective weight transmission through these two bones.

The shift in the axis of weight transmission is achieved through slightly different means in terrestrial monkeys. Weight of the body passes through the elongated ulnar styloid process directly to the triquetrum, which then articulates with the hamate. The triquetral facet on the hamate faces medially, and the hamate itself is very short and medio-laterally broad. This morphology reflects reduced rotational capability between the triquetrum and hamate, but an efficient weight transmission mechanism. The monkey capitate head is "swollen" medially, increasing surface area contact with the lunate proximally, but excluding the hamate from contact with the lunate.

Humans also have expanded lunate surfaces that are, in fact, relatively larger than those of African apes. In humans, the ratio of scaphoid to lunate area is almost 1:1. This similarity to African apes may be due to a shared phylogenetic history and a shared ancestral pattern of locomotion, or merely a reflection of larger body size. Greater elaboration of the lunate surface as compared to African apes may have occurred as an adaptive response to mobility requirements arising from tool making and manipulation. One marked difference in the wrist morphology of humans as compared to African apes is the frequency of contact between the hamate and lunate. In their study, Marzke *et al* (1994) found that in only 65% of humans in their sample was there contact between the hamate and lunate, and in most cases this contact was associated with pathology. They cite evidence of degenerative joint changes resulting from repetitive impulsive loading, such as hammering, associated with rapid ulnar deviation of the wrist. These authors suggest the possibility of an evolutionary process that began with an African ape-like lunatohamate contact in early hominids, possibly linked to midcarpal stability requirements of weight transmission through the forelimb, which then progressed through a reduction in lunatohamate contact as tool use and manufacture increased.

Elaboration of the lunate is taken to extreme proportions in *Pongo*, and undoubtedly arose from the requirement for wide ranges of wrist adduction. In absolute size and relative to metacarpal dimensions, orangs have the smallest scaphoid surfaces of all great apes and humans. Thus, expansion of the proximal carpal row surface area in total is accomplished through enlargement of the lunate, at the expense of the scaphoid.

Regression analyses for the total sample reveal that scaphoid and lunate areas are negatively allometric relative to metacarpal size. Slopes do not differ significantly, however scaphoid area scales slightly lower than lunate area. The latter approaches isometry and is shifted downward resulting in a signficant difference in y-intercept. This finding for the sample as a whole is consistent with the pattern described above, in that lunate area increases rapidly with increasing body size.

Intertaxonal comparisons of scaphoid to lunate surface area scaling patterns produce a somewhat different result. Lunate area increases at a faster rate than scaphoid area in bonobos, orangs and both arboreal and terrestrial monkeys. This fits the pattern described above wherein increases in body size are accompanied by a similar rate of increase in lunate proximal surface area and, thus, more reliance on loading across the ulnar aspect of the forelimb. On the other hand, scaphoid area scales faster than lunate area in gorillas, chimps and humans. Despite the fact that hominoids in particular are purportedly characterized by a medial shift in load bearing resulting from greater weight transmission through the humero-ulnar joint, it is clear that among knuckle-walkers (excluding bonobos for the moment) a faster rate of increase in scaphoid area has functionally significant implications, and overall expansion of the proximal carpal row surface area is accounted for primarily by enlargement along the radial aspect.

As noted earlier, during initial stance phase in knuckle-walking, forces are directed primarily through the capitate and hamate. In the latter phases of propulsion, the axis of rotation shifts toward the radial side (Jenkins and Fleagle, 1975). Although no significant differences in slope exist, chimps and humans are most similar in their slope values for scaphoid area, and these are somewhat higher than for gorillas. In chimps and gorillas, this small diffference in slope pattern may be due to kinematically distinct modes of knuckle-walking. As described previously, chimps typically utilize hand postures that are oblique to the forward line of progression. Doing so increases the degree of radial deviation of the wrist during the latter phases of propulsion, as opposed to a hand that is held in a position perpendicular to the line of travel.

Why bonobos should have a lower rate of scaling of the scaphoid compared to the lunate is unclear. In fact, scaling of the lunate is very similar in all African apes and humans. It is the considerably lower slope of the scaphoid that distinguishes *P.paniscus*. The scaphoid proximal surface area is not reduced in size compared to chimps, for example. It is simply that there does not appear to be as great a size dependent increase in scaphoid area in bonobos as in chimps. This may be due to sex-specific differences in behaviour within bonobos, and/or species-specific variations in locomotor habits between bonobos and chimps.

Bonobo females engage in more quadrupedalism and less climbing/scrambling than males, and both males and females are generally more arboreal and use more quadrupedalism and less climbing/scrambing than chimps. Palmigrade postures would place substantial loads through the radial aspect of the wrist and a large scaphoid surface would be adaptive to palmigrade quadrupedal behaviours, but would not hinder knuckle-walking capabilities.

Bonobos do, however, follow the pattern typical among catarrhines examined in this study, in that lunate proximal surface area increases at a rate consistent with increasing body size, which in turn empasizes ulnar loading across the forelimb. This is important for a large bodied hominoid engaging in suspensory activities. The bonobo wrist, therefore, reflects a compromise morphology. *P.paniscus* is indeed a knuckle-walker when on the ground, and consequently requires stability across the radial aspect of the forelimb. As a result, bonobos share with other African apes a fused os centrale. It is likely that higher frequencies of knuckle-walking in gorillas and chimps has resulted in a shift to more rapid enlargement of the scaphoid as compared to the lunate and greater reliance on loading of the radial side of the forelimb. Moreover, bonobos are characterized by having a higher intermembral index and reduced forearm elongation as compared to gorillas and chimps. This might imply differential weight distribution across the forelimb as compared to the hindlimb among these taxa, although studies have shown that the contribution of forelimb support during walking is similar among primates possessing grossly different interlimb proportions (Jungers, 1985). Bonobos are purportedly ontogenetically scaled with chimps in linear dimensions of the postcranial skeleton, however this does not appear to be the case for articular surface area of the scaphoid or the distal radius.

In the distal carpal row, African apes tend to have larger scaphoid areas on the capitate heads compared to Asian apes, monkeys and humans. This pattern is consistent with the analysis of the scaphoid and lunate proximal surface areas, in that African apes have larger relative scaphoid proximal surface areas, and scaphoid proximal surface scales faster than lunate proximal surface in gorillas and chimps. These factors are indicative of weight transmission through the radial aspect of the wrist being an important functional component of knuckle-walking behaviour.

Scaling of scaphoid area on the capitate is close to isometry for the total sample, although bonobos and chimps have larger areas than would be expected given their metacarpal dimensions. The rate of scaling, however, is positively allometric for chimps, but is much lower in gorillas, humans and bonobos respectively. Why chimps should have such a high rate of increase is unclear. It is evident from examination of capitates that many chimps possess an anterior extension of the scaphoid surface. This ventral "bulge" clearly delineates the lunate articulation from the scaphoid surface, such that the anterior aspect of the bone has a marked inconguity and separation of articular surfaces. In functional terms, this may be related to kinematically distinct knuckle-walking progression in chimps as compared to gorillas. Chimps use more varied hand positions and the hand is typically placed obliquely to the foreward line of progression, rather than perpendicular to it as in gorillas. The scaphoid itself extends obliquely in a distoventral fashion and lies between the centre of rotation of the lunate and capitate. It's position, in conjunction with numerous ligmentous connections, enables the scaphoid to act as a radial "strut", stabilizing the midcarpal joint (Linscheid,1986; Feipel *et al*,1994). In radial deviation, the scaphoid undergoes palmar flexion (Linscheid, 1986). Thus, a ventral extension of the scaphoid facet on the capitate implies a greater potential for palmar movement of the scaphoid as the wrist undergoes radial deviation. Such deviation likely occurs in the latter phases of propulsion during knuckle-walking with a forelimb held obliquely to the forward line of progression. That this morphology is more characteristic of chimps rather than bonobos is correlated with greater frequency of terrestriality in the former. In general, an enlarged scaphoid and articular area for the capitate head would confer greater stability to the midcarpal joint in the transmision of forces through the capitate to the proximal carpal row.

The distal capitate articular surface area is much larger in all great apes compared to humans, however the distal hamate does not show the same disparity. It's clear that capitate distal area does not distinguish knuckle-walkers from slow climbers, although the relative area is somewhat larger in gorillas. Insofar as humans are distinct from great apes in having substantially smaller distal capitate areas, the same is not true of the distal hamate. Humans are virtually indistinguishable from chimps, bonobos and orangs in distal hamate area. Gorillas have slightly larger relative areas, as do terrestrial monkeys compared to brachiators and arboreal monkeys. Human hands are designed for maximum manipulatory capability and possess an number of unique anatomical characters that attest to this. The conformation of the hamate distal articular surface, for example, has a convex contour rather than one that is concave like in apes. A broad convex surface accords the fourth and fifth digits the ability to oppose the thumb. Articulating with the distal capitate, the base of the third metacarpal has a proximally projecting dorsal styloid process which likely serves to stabilize the capitate-MIII joint without increasing the conjoining surface areas.

The scaling pattern of capitate distal area demonstrates that chimps are closest to isometry relative to metacarpal dimensions, and all other taxa are more negatively allometric. The rate of increase is almost identical between gorillas and terrestrial monkeys, however the regression line for monkeys is transposed below that of gorillas, so at common sizes gorillas have much larger distal area. Similarly, humans are most similar to orangs, but shifted down. Overall, terrestrial species have somewhat faster rates of increase in capitate distal area. More even weight distribution across the antebrachial joint in gorillas and terrestrial monkeys may account for the slightly lower slopes in these two taxa compared to chimps. Again, bonobos have the lowest slopes of all taxa, indicative of a low range of variation in capitate distal area, despite considerable overlap with chimps in this feature.

Scaling of distal hamate area is somewhat more revealing. There is a clear separation between terrestrial and arboreal species. Gorillas, chimps and terrestrial monkeys have higher rates of change in surface area and form a unit distinct from bonobos, orangs and humans. Thus, a size dependent increase (although still negatively allometric) is present in species engaging in high frequencies of terrestrial locomotion. Increase in surface area, as a means to dissipate forces generated through compressive loading along the ulnar aspect of the forelimb, is evidently a more functionally distinctive feature across the hamate than across the capitate. Terrestrial quadrupeds possess uniquely shaped hamates, in that the triquetral facet faces more proximo-medially than in apes, permitting more direct weight transmission from the ulnar styloid through the triquetrum to the hamate, and finally to the metacarpals. Gorillas also posses anatomical features, such as relatively equal ray lengths, which help to more evenly distribute body weight through the metacarpals to the hamate and capitate. Chimps typically support the body on digits three and four, so that forces are not as evenly dissipated across the ulnar aspect as in gorillas. Nonetheless, expansion of the fourth digit articular surface area on the hamate is sufficient to contribute to overall articular size increase that is more rapid than in arboreal species.

Finally, the joint between the capitate and hamate acts as a shock absorber to compressive loads placed on the ulnar aspect of the forelimb, transmitting forces to the more stable capitate via the hamatocapitate ligaments (Weber,1984). Comparisons among taxa for hamate area on the capitate, and capitate on the hamate produce results that are virtually identical and demonstrate very little difference among great apes in these features. Humans have somewhat reduced relative areas for these measures, and terrestrial quadrupeds have larger surfaces than arboreal monkeys or brachiators. Thus, in terms of overall size, capitate-hamate articulation does not distinguish knuckle-walkers from slow climbers, but terrestrial monkeys are distinct from more arboreal forms. This is compatible with the notion discussed earlier, wherein ulnar loading increases with increasing body size. This is particularly true of large hominoids, which have much larger humeral trochlear surfaces that maintain integrity of the humero-ulnar joint. Therefore, a large area of contact between the hamate and capitate is neccessary in both quadrupedal and suspensory animals.

Scaling patterns for capitate-hamate articulation are very similar among chimps, gorillas and humans. Chimps, however, are most similar to terrestrial monkeys in having more rapid increase in this articular surface than gorillas or humans. Again, structural features of the antebrachial joint and metacarpals that act to distribute body weight more evenly in gorillas may be responsible for the lower scaling pattern in this taxon. In addition, bonobos have much lower slope values despite considerable overlap in capitate-hamate articular surface area with chimps, which is suggestive of differences in loading patterns across the wrist between these two species.

Conclusions

This analysis has attempted to answer several questions pertaining to knuckle-walking behaviour and its potential morphological correlates. It has been demonstrated that all large hominoids are characterized by having expanded distal radius articular surface areas as compared to lesser apes, monkeys and humans, and this feature alone does not distinguish knuckle-walkers from slow climbers. For a sample comprised of species ranging in size from arboreal cercopithecines to gorillas, comparison of proximal carpal row elements shows that lunate area scales faster than scaphoid area, which is consistent with the notion that a shift to forelimb loading on the ulnar aspect with increasing body size occurs. Analysis of individual species however, reveals that scaphoid proximal area scales faster in gorillas, chimps, and humans. This finding is also compatible with known traits that are derived and uniquely shared between African apes and humans - in particular the fused os centrale - as well as with a shift in transmission of forces toward the radial side of the wrist associated with knuckle-walking.

Overall scaphoid facet size on the capitate distinguishes African apes, and scaling of this feature is distinctive in chimps. Enlargement of the distal articular surface area of the capitate is shared among all great apes to the exclusion of humans. Relative size of the hamate distal area does not significantly differ among great apes and humans, however the pattern of scaling in this feature separates terrestrial species (chimps, gorillas and terrestrial monkeys) from more arboreal ones (bonobos, orangs) and humans.

Differences in size and scaling patterns of certain elements between *Gorilla* and *Pan* have been attributed to larger body size, greater frequency of terrestrial behaviour, and anatomical structures within the wrist and hand that distribute forces more evenly in gorillas. Size and scaling differences between *Pan troglodytes* and *Pan paniscus* are attributed to variation in arboreal verses terrestrial behaviours, as well as greater frequencies of palmigrade quadrupedal postures on the part of bonobos. In several features, notably radius distal area, scaphoid proximal area, and all articular surfaces on the capitate, regression analyses have demonstrated very low ranges of variation in these characters within bonobos. These elements are all integral to the transmission of forces through the carpus and antibracial joint. This implies some fundamental alteration in the loading regime across the forelimb in bonobos, possibly due to species-specific and sex-specific differences in locomotor behaviours.

TABLE 3.1 Descriptive Statistics for Radius and Proximal Carpal Row

Taxon	Radius Distal Area	Radius Scap Area	Radius Lun Area	Radius Scap/lun	Scaphoid Area	Lunate Area	Scap / lun Ratio
Gorilla							
N	35				38	29	27
mean	654.16	330.78	317.92	1.05	366.87	292.97	1.24
S.D.	161.09	90.03	80.75	.203	96.38	80.45	.235
C.V.	24.63	27.34	25.40	19.36	26.27	27.46	18.91
Pan troglodytes							
N	23				20	22	20
mean	409.11	191.82	206.87	.933	226.41	184.51	1.24
S.D.	57.75	35.36	28.57	.151	40.37	29.66	.185
C.V.	14.12	18.43	13.81	16.17	17.83	16.08	14.93
Pan paniscus							
N	13				13	12	12
mean	366.28	177.91	168.09	1.12	227.03	162.06	1.38
S.D.	53.21	32.22	44.95	.313	35.73	22.57	.148
C.V.	14.53	18.11	26.74	28.01	15.74	13.93	10.72
Pongo							
N	7				7	5	3
mean	454.17	204.42	241.58	.871	190.08	267.58	.775
S.D.	53.99	41.74	41.74	.216	53.38	68.12	.112
C.V.	11.89	11.28	17.28	24.78	28.08	25.46	14.50
Human							
N	10				10	10	10
mean	364.40	185.37	177.46	1.06	221.05	201.68	1.10
S.D.	57.71	35.61	36.58	.205	43.63	36.45	.124
C.V.	15.84	19.21	20.62	19.38	19.74	18.07	11.24
Gibbon							
N	11				4	5	4
mean	80.91	38.69	39.95	.975	46.46	32.11	1.41
S.D.	11.86	8.96	5.94	.217	8.45	3.63	.262
C.V.	14.66	23.16	14.87	22.26	18.16	11.30	18.61
Siamang							
N	3				1	1	1
mean	116.14	58.36	54.62	1.07	57.14	35.08	1.63
S.D.	16.59	14.22	11.18	.219	na	na	na
C.V.	14.28	24.37	20.47	20.47	na	na	na
Arboreal monkey							
N	4				5	5	5
mean	78.11	36.82	41.23	.895	63.99	43.88	1.50
S.D.	4.57	4.76	4.30	.09	10.34	13.51	.190
C.V.	5.85	12.93	10.43	10.06	16.16	30.79	12.65

Taxon	Radius Distal Area	Radius Scap Area	Radius Lun Area	Radius Scap/lun	Scaphoid Area	Lunate Area	Scap / lun Ratio
Terrestrial monkey							
N	11				10	10	10
mean	144.25	64.12	78.18	.842	93.83	76.26	1.24
S.D.	36.54	18.81	22.51	.223	18.72	14.49	.148
C.V.	25.33	29.33	28.79	25.56	19.95	19.00	11.96

TABLE 3.1 continued * Means of raw measures in mm^2

TABLE 3.2 Ratios for the Distal Radius and the Proximal Carpal Row

Taxon	Rad Das-MC	Rad Scap-MC	Rad Lun-MC	Scapoid -MC	Lunate-MC
Gorilla					
N	35			38	29
mean	48.48	24.46	23.63	27.82	22.66
S.D.	6.25	4.01	3.73	4.43	3.59
C.V.	12.89	16.39	15.79	15.92	15.84
Pan troglodytes					
N	23			19	22
mean	42.96	20.11	21.77	23.17	18.59
S.D.	4.98	3.14	2.76	2.85	2.38
C.V.	11.59	15.61	12.68	12.30	12.80
Pan paniscus					
N	13			13	12
mean	43.38	21.00	19.95	26.83	19.45
S.D.	5.63	2.95	5.69	3.23	1.78
C.V.	12.85	14.05	28.52	12.03	9.15
Pongo					
N	7			7	5
mean	46.26	20.79	24.67	18.91	27.01
S.D.	4.07	1.23	4.35	4.22	5.32
C.V.	8.80	5.92	17.63	22.32	19.70
Human					
N	10			10	10
mean	34.33	17.45	16.68	20.76	18.98
S.D.	3.15	2.44	2.32	2.67	2.12
C.V.	9.18	13.98	13.91	12.86	11.17
Gibbon					
N	11			4	5
mean	18.01	8.57	8.90	10.54	7.35
S.D.	2.25	1.67	1.18	1.42	.7776
C.V.	12.49	19.48	20.22	13.47	10.58
Siamang					
N	3			1	1
mean	23.41	11.73	10.88	12.90	7.92
S.D.	3.47	2.84	.5016	na	na
C.V.	14.82	24.21	4.61	na	na
Arboreal monkey					
N	4			5	5
mean	15.34	7.22	8.10	12.00	8.12
S.D.	.9126	.8333	.8467	.8176	1.42
C.V.	5.95	11.54	10.45	6.81	17.49

Taxon	Rad Das-MC	Rad Scap-MC	Rad Lun-MC	Scapoid -MC	Lunate-MC
Terrestrial monkey					
N	11			10	10
mean	23.57	10.48	12.73	15.32	12.45
S.D.	4.14	2.39	2.43	1.78	1.09
C.V.	17.56	22.81	19.09	11.62	8.76

* Rad Das-MC = Radius Distal Area/metacarpal composite; Rad Scap-MC = Radius scaphoid area/metacarpal composite; Rad Lun-MC = Radius Lunate area/metacarpal composite

TABLE 3.2 Continued

TABLE 3.3 Descriptive Statistics for the Distal Carpal Row

Taxon	Cap Sfa	Cap Hfa	Cap Das	Cap Length	Ham Cfa	Ham Das	Ham Length
Gorilla							
N	30				29	30	
mean	237.62	175.17	250.95	26.62	165.00	215.60	19.71
S.D.	63.69	46.30	62.52	3.20	43.82	61.04	2.39
C.V.	26.80	26.43	24.90	12.02	26.56	28.31	12.13
Pan troglodytes							
N	22				21		
mean	161.74	136.21	172.75	23.55	132.50	146.97	20.43
S.D.	33.58	23.32	29.46	1.92	21.14	25.60	1.81
C.V.	20.76	17.12	17.05	8.15	16.15	17.42	8.86
Pan paniscus							
N	13	12			11	12	13
mean	162.41	123.80	148.35	22.79	118.43	133.71	18.32
S.D.	23.30	17.91	17.96	1.15	17.28	18.85	1.04
C.V.	14.35	14.47	12.11	5.05	14.59	14.10	5.68
Pongo							
N	5				8		
mean	142.43	145.15	185.65	24.59	129.43	148.13	21.55
S.D.	24.36	35.79	39.11	1.95	28.83	27.15	1.47
C.V.	17.10	24.66	21.07	7.93	22.27	18.33	6.82
Human							
N	10				10		
mean	145.56	134.78	128.80	23.36	119.96	156.73	19.11
S.D.	24.22	17.91	17.01	1.86	14.91	16.88	2.39
C.V.	16.64	13.29	13.21	7.96	12.43	10.77	12.51
Gibbon							
N	4				4		
mean	27.17	27.00	36.67	11.50	21.47	30.61	12.77
S.D.	.5383	5.70	5.65	.5092	3.03	4.09	.6069
C.V.	1.98	21.11	15.41	4.43	14.11	13.36	5.24
Siamang							
N	1				1		
mean	25.12	-	32.98	10.43	28.63	31.33	12.19
S.D.	-	-	-	-	-	-	-
C.V.	-	-	-	-	-	-	-
Arboreal monk							
N	1	5			5		
mean	49.28	32.29	40.70	10.68	31.17	44.92	10.36
S.D.	-	9.95	9.15	2.46	4.46	10.59	2.21
C.V.	-	30.81	22.48	23.03	14.30	23.58	21.33

Taxon	Cap Sfa	Cap Hfa	Cap Das	Cap Length	Ham Cfa	Ham Das	Ham Length
Terrest monk							
N	5	10			10		
mean	45.10	53.35	63.01	13.83	44.49	64.19	10.88
S.D.	13.26	7.36	12.52	1.21	10.46	12.47	2.21
C.V.	29.38	14.06	19.87	8.75	23.51	19.43	20.31

• Cap = capitate; Ham = hamate; Sfa = scaphoid facet area; Das = Distal articular surface; Hfa = hamate facet area; Cfa = capitate facet area; Means of raw measures = mm^2

TABLE 3.4 Ratios of Distal Carpal Row Variables and Metacarpal Size

Taxon	Cap Sfa-MC	Cap Hfa-MC	Cap Das-MC	Ham Cfa-MC	Ham Das-MC	MC
Gorilla						
N	30			29	30	29
mean	18.41	13.56	19.38	12.84	16.64	12.70
S.D.	3.22	2.31	2.57	2.30	3.05	1.92
C.V.	17.49	17.04	13.26	17.91	18.33	7.24
Pan troglodytes						
N	22			21		18
mean	16.36	13.82	17.50	13.40	14.88	9.28
S.D.	2.68	1.98	2.23	1.69	2.16	1.07
C.V.	16.38	14.33	12.74	12.61	14.52	11.53
Pan paniscus						
N	13	12	13	11	12	13
mean	19.22	14.72	17.57	13.99	15.75	8.46
S.D.	2.11	1.77	1.66	1.66	1.57	.8036
C.V.	10.98	12.02	9.45	11.87	9.97	9.53
Pongo						
N	5			8		8
mean	14.46	14.67	18.88	13.16	14.85	9.74
S.D.	1.79	2.74	3.69	2.29	2.95	1.30
C.V.	12.38	18.68	19.54	17.40	19.86	13.34
Human						
N	10			10		10
mean	13.67	12.72	12.15	11.33	14.84	10.57
S.D.	1.67	.8692	.8028	.8179	1.25	.9659
C.V.	12.22	6.83	6.61	7.22	8.42	9.14
Gibbon						
N	4			4		12
mean	6.19	6.13	8.32	4.88	6.97	4.41
S.D.	.2543	1.17	.9005	.5705	.8950	.4138
C.V.	4.10	19.08	10.94	11.69	12.84	9.38
Siamang						
N	1		1	1		3
mean	5.67	-	7.44	6.46	7.07	5.01
S.D.	-	-	-	-	-	.9262
C.V.	-	-	-	-	-	18.48
Arboreal monk						
N	1	5	5	5		5
mean	7.71	5.98	7.59	5.86	8.37	5.44
S.D.	-	1.17	.7871	.3771	1.20	.6141
C.V.	-	19.57	10.37	6.44	14.34	11.29

Taxon	Cap Sfa-MC	Cap Hfa-MC	Cap Das-MC	Ham Cfa-MC	Ham Das-MC	MC
Terrest monk						
N	5	10	10	10		10
mean	8.11	8.62	10.28	7.24	10.47	6.09
S.D.	1.98	1.04	1.10	1.02	.9420	.7189
C.V.	24.44	12.18	10.70	14.09	9.00	11.80

• MC = Metacarpal composite measure comprised of midshaft breadth and ventral head breadth of metacarpals II-V

TABLE 3.4 continued

TABLE 3.5 Ratios of Distal Carpal Row Variables and Total Length (Capitate and Hamate)

Taxon	Cap Sfa-TL	Cap Hfa-TL	Cap Das-TL	Ham Cfa-TL	Ham Das-TL
Gorilla					
N	30			29	30
mean	8.23	6.52	9.33	8.34	10.81
S.D.	1.49	1.14	1.47	1.50	2.07
C.V.	16.89	17.48	15.76	17.99	19.15
Pan troglodytes					
N	22			21	
mean	6.83	5.77	7.32	6.48	7.21
S.D.	1.09	.7960	1.03	.8532	1.12
C.V.	15.82	13.80	14.07	13.17	15.53
Pan paniscus					
N	13			11	12
mean	19.22	5.45	6.5	6.45	7.30
S.D.	2.11	.6966	.6351	.8515	.8956
C.V.	10.98	12.79	9.77	13.20	12.27
Pongo					
N	5			8	
mean	5.77	5.86	7.54	5.98	6.94
S.D.	.6502	1.11	1.45	1.10	1.25
C.V.	11.27	18.94	19.23	18.39	18.01
Human					
N	9	10		10	
mean	6.13	5.77	5.51	6.30	8.25
S.D.	.7417	.6204	.5053	.5750	.8177
C.V.	12.10	10.75	9.17	9.13	9.91
Gibbon					
N	4			4	
mean	2.37	2.36	3.19	1.68	2.40
S.D.	.097	.5384	.4956	.2504	.3586
C.V.	4.09	19.09	15.55	14.90	14.94
Siamang					
N	1	-	1	1	1
mean	2.41	-	3.16	2.35	2.57
S.D.	-	-	-	-	-
C.V.	-	-	-	-	-

Taxon	Cap Sfa-TL	Cap Hfa-TL	Cap Das-TL	Ham Cfa-TL	Ham Das-TL
Arboreal monkey					
N	1	5		5	
mean	3.27	3.00	3.82	3.08	4.45
S.D.	-	.4325	.1756	.2898	1.02
C.V.	-	14.43	4.61	9.41	22.92
Terrestrial monkey					
N	5	10		10	
mean	3.38	3.79	4.53	4.09	5.96
S.D.	.9805	.4300	.6197	.8083	1.23
C.V.	29.00	11.35	13.69	19.76	20.64

•TL = total length

TABLE 3.5 continued

Table 3.6: Summary of Raw variable Z-scores and ratios for the Distal Radius, Proximal and Distal Carpal Rows

Radius	Gorilla and orang have largest distal area; relative scaphoid area is larger in gorilla, relative lunate area is larger in orang
Scaphoid	Relative to MC's, African apes have larger scaphoid areas than Asian apes and humans
Lunate	Relative to MC's, orangs have larger proximal areas than African apes and humans; in the ratio of scaphoid-lunate area bonobos have the largest relative scaphoid area compared to gorillas, chimps, orangs and humans; Bonobos resemble brachiators and AQ in scaphoid-lunate area
Capitate	African apes have expanded scaphoid facet areas compared to Asian apes and humans; humans share with great apes an expanded hamate facet area; great apes have expanded distal surfaces to the exclusion of humans
Hamate	Humans share with great apes an expanded distal surface; relative to total hamate length humans have larger distal areas than chimps, bonobos and orangs

TABLE 3.7 Comparision of Distal Radius and Proximal Carpal Row Mean Values For Areas

Taxon	Rad Scap	Scap	*Scap - Rad scap	Rad Lun	Lun	*Lun - Rad lun	% scap	% lun
Gorilla	330.78	366.87	36.09	317.92	292.97	-24.95	110.91	92.15
Chimp	191.82	226.41	34.59	206.87	184.51	-22.36	118.03	89.19
Bonobo	177.91	227.03	49.12	168.09	162.06	-6.03	127.61	96.41
Orang	204.42	190.08	-14.34	241.58	267.58	26.00	92.99	110.76
Human	185.36	221.05	35.69	177.46	201.68	24.22	119.25	113.65
Gibbon	38.69	46.46	7.77	39.95	32.11	-7.84	120.08	80.38
Siamang	58.36	57.14	-1.22	54.61	35.08	-19.53	97.91	64.23
AQ	36.82	63.99	27.17	41.23	43.88	2.65	173.79	106.43
TQ	64.12	93.83	29.71	78.17	76.26	-1.92	146.33	97.54

* Scaphoid area minus radius scaphoid area; lunate area minus radius lunate area; Negative values indicate that the female surface (as measured) is larger than the male surface, a condition which should not occur in any modified ovoid joints.
% scap = (scaphoid/radius scaphoid)*100;
% lun = (lunate/radius lunate)*100

TABLE 3.8 Regression Results

Sample	Measure	*r*	*Slope	95% CI	y-int	95% CI	% SEE
Total(117)	Radius Das	.963	.936	.887 - .984	.364	.316 - .411	4.35
			(.969)	(.920 - 1.018)	(.332)	(.284 - .379)	
(117)	Radius Scap	.962	.979	.928 - 1.031	.162	.112 - .212	4.62
			(1.02)	(.967 - 1.072)	(.124)	.073 - .175)	
(117)	Radius Lun	.952	.917	.862 - .971	.229	.176 - .281	4.87
			(.962)	(.907 - 1.018)	(.185)	(.132 - .238)	
Gorilla(35)	Radius Das	.884	.668	.543 - .793	.653	.513 - .793	2.60
Chimp(23)		.599	.562	.221 - .903	.754	.421 - 1.088	2.53
Bonobo(13)		.555	.426	.002 - .844	.889	.499 - 1.279	2.70
Orang(7)		.696	.438	-.082 - .967	.894	.379 - 1.409	2.12
Human(10)		.846	.715	.348 - 1.082	.547	.172 - .923	1.90
BR(14)		.616	.633	.123 - 1.142	.551	.214 - .888	2.93
TQ(11)		.819	.975	.460 - 1.490	.312	-.090 - .715	3.56
Gorilla(35)	Radius Scap	.861	.722	.571 - .873	.442	.273 - .612	-
Chimp(23)		.603	.756	.303 - 1.210	.399	-.045 - .842	-
Bonobo(13)		.616	.595	.091 - 1.100	.571	.104 - 1.038	-
Orang(7)		.867	.518	.177 - .860	.641	.302 - .979	-
Human(10)		.757	.780	.231 - 1.330	.332	-.230 - .895	-
BR(14)		.648	.953	.249 - 1.65	.178	-.288 - .644	-
TQ(11)		.719	.988	.268 - 1.71	.124	-.438 - .686	-

Sample	Measure	*r*	*Slope	95% CI	y-int	95% CI	% SEE
Gorilla(35)	Radius Lun	.793	.602	.438 - .765	.570	.386 - .754	-
Chimp(23)		.394	.358	-.021 - .736	.806	.436 - 1.17	-
Bonobo(11)		.592	.710	.029 - 1.39	.437	-.195 - 1.07	-
Orang(7)		.312	.311	-.779 - 1.40	.880	-.201 - 1.961	-
Human(10)		.794	.866	.325 - 1.41	.235	-.319 - .788	-
BR(14)		.700	.681	.245 - 1.12	.363	.074 - .652	-
TQ(11)		.868	1.101	.625 - 1.578	.079	-.292 - .452	-
Total(107)	Scaphoid	.956	.897 (.921)	.826 - .931 (.867 - .975)	.299 (.257)	.247 - .351 (.204 - .311)	3.96
Gorilla(38)	Scaphoid	.869	.813	.657 -.969	.372	.198 - .546	2.9
Chimp(20)		.775	.975	.568 - 1.381	.209	-.195 - .613	2.4
Bonobo(13)		.636	.538	.104 - .972	.677	.275 - 1.079	2.8
Orang(7)		.535	.455	-.372 - 1.282	.679	-.148 - 1.506	4.9
Human(10)		.865	.948	.500 - 1.395	.199	-.259 - .657	2.3
AQ(5)		.922	.659	.152 - 1.165	.424	.057 - .792	1.5
TQ(10)		.841	.698	.332 - 1.064	.436	.150 - 1.064	2.4
Total(98)	Lunate	.964	.975 (1.008	.912 - 1.029 (.953 - 1.063)	.164 (.132)	.112 - .217 (.079 - .185)	3.93

Sample	Measure	*r*	*Slope	95% CI	y-int	95% CI	% SEE
Gorilla(29)	Lunate	.860	.751	.575 - .927	.398	.204 - .593	3.0
Chimp(22)		.608	.704	.275 - 1.132	.430	.004 - .856	2.8
Bonobo(12)		.783	.714	.315 - 1.113	.447	.081 - .814	1.9
Orang(5)		.833	1.394	.308 - 3.096	-.174	-1.861 - 1.514	3.7
Human(10)		.825	.776	.343- 1.210	.355	-.088 - .799	2.2
BR(6)		.455	.684	-1.173 - 2.54	.317	-.873 - 1.507	2.4
AQ(5)		.985	1.210	.821 - 1.599	.061	-.343 - .221	1.2
TQ(10)		.938	.754	.528 - .981	.348	.170 - .525	1.5
Total(85)	Cap Sfa	.919	.912	.829 - .996	.184	.100 - .267	5.05
			(.998)	(.915 - 1.081)	(.099)	(.016 - .181)	
(85)	Cap Sfa(TL)	.960	1.181	1.108 - 1.254	-.515	-.614 - -.416	3.72
			(1.201)	(1.132 - 1.270)	(-.538)	(-.631- -.444)	
Gorilla(30)	Cap Sfa	.736	.637	.410 - .864	.478	.227 - .729	3.81
Chimp(22)		.774	1.213	.751 - 1.676	-.103	-.562 - .356	2.94
Bonobo(13)		.622	.466	.077 - .855	.672	.311 - 1.033	2.49
Orang(5)		.737	.769	-.528 - 2.066	.312	-.974 - 1.599	2.88
Human(10)		.698	.610	.050 - 1.170	.454	-.120 - 1.028	2.79
Gorilla(30)	Cap Sfa(TL)	.835	.901	.671 - 1.131	-.101	-.428 - .227	3.10
Chimp(22)		.714	.901	.489 - 1.313	-.135	-.699 - .430	3.26
Bonobo(13)		.778	1.093	.508 - 1.679	-.380	-1.175 - .414	2.0
Orang(5)		.817	.860	-.256 - 1.975	-.120	-1.671 - 1.430	2.39
Human(10)		.726	.873	.133 - 1.613	-.120	-1.136 - .896	2.67

Sample	Measure	*r*	*Slope	95% CI	y-int	95% CI	% SEE
Total(98)	Cap Hfa	.931	.843 (.905)	.776 - .911 (.839 - .972)	.207 (.147)	.141 - .273 (.082 - .211)	4.5
(98)	Cap Hfa(TL)	.961	.935 (.999)	.881 - .990 .948 - 1.050)	-.219 (-.305)	-.291 - -.146 (-.373 - -.236)	3.5
Gorilla(30)	Cap Hfa	.788	.664	.464 - .865	.382	.161 - .604	3.37
Chimp(22)		.624	.822	.341 - 1.303	.249	-.228 - .726	3.06
Bonobo(12)		.620	.483	.052 - .913	.599	.201 - .996	2.67
Orang(5)		.842	1.243	-.221 - 2.707	-.156	-1.607 - 1.296	3.16
Human(10)		.876	.637	.350 - .923	.412	.119 - .705	1.48
TQ(10)		.620	.361	-.011 - .734	.575	.283 - .867	2.49
Gorilla(30)	Cap Hfa (TL)	.791	.831	.582 - 1.079	-.066	-.420 - .288	3.35
Chimp(22)		.629	.667	.282 - 1.052	.149	-.378 - .677	3.04
Bonobo(12)		.472	.714	-.225 - 1.653	-.076	-1.196 - 1.349	3.0
Orang(5)		.765	1.139	-.622 - 2.900	-.507	-2.955 - 1.941	3.77
Human(10)		.584	.497	-.066 - 1.059	.384	-.386 - 1.153	2.48
TQ(10)		.579	.463	-.069 - .996	.330	-.277 - .937	2.59
Total(99)	Cap Das	.948	.898 (.949)	.837 - .959 (.890 - 1.009)	.206 (.156)	.146 - .265 (.098 - .214)	4.20
(99)	Cap Das(TL)	.957	.972 (1.029)	.913 - 1.031 (.975 - 1.084)	-.216 (-.293)	-.295 - -.138 (-.365 - -.221)	3.91

Sample	Measure	*r*	*Slope	95% CI	y-int	95% CI	% SEE
Gorilla(30)	Cap Das	.885	.726	.579 - .874	.393	.230 - .556	2.48
Chimp(22)		.704	.901	.465 - 1.337	.221	-.211 - .652	2.58
Bonobo(13)		.631	.403	.075 - .732	.711	.407 - 1.015	2.10
Orang(5)		.454	.662	-1.724 - 3.047	.474	-1.891 - 2.840	5.15
Human(10)		.899	.669	.404 - .934	.369	.098 - .640	1.37
TQ(10)		.885	.739	.422 - 1.057	.318	.068 - .567	2.12
Gorilla(30)	Cap Das(TL)	.840	.859	.644 - 1.073	-.028	-.333 - .278	2.89
Chimp(22)		.824	.800	.536 - 1.065	.014	-.348 - .377	2.06
Bonobo(13)		.591	.707	.066 - 1.348	.125	-.746 - .995	2.19
Orang(5)		.445	.654	-1.763 - 3.072	.221	-3.140 - 3.581	5.18
Human(10)		.745	.648	.175 - 1.121	.167	-.480 - .814	2.09
TQ(10)		.792	.910	.338 - 1.482	-.141	-.793 - .511	2.78
Total(98)	Ham Cfa	.940	.892 (.948)	.827 - .957 (.882 - 1.014)	.144 (.090)	.080 - .207 .025 - .155)	4.59
(98)	Ham Cfa(TL)	.876	1.036 (1.178)	.921 - 1.150 1.063 - 1.293)	-.281 (-.457)	-.424 - -.137 (-.600- -.314)	6.50
Gorilla(29)	Ham Cfa	.761	.662	.439 - .884	.373	.128 - .618	3.68
Chimp(21)		.675	.826	.392 - 1.260	.238	-.193 - .669	2.68
Bonobo(11)		.594	.431	-.009 - .871	.635	.227 - 1.043	2.59
Orang(8)		.743	.717	-.025 - 1.459	.351	-.384 - 1.086	3.06
Human(10)		.828	.569	.254 - .883	.456	.135 - .778	1.62
TQ(10)		.842	.818	.392 - 1.245	.179	-.156 - .513	2.85
Gorilla(29)	Ham Cfa(TL)	.831	.906	.667 - 1.146	-.066	-.376 - .243	3.16
Chimp(21)		.558	.507	.145 - .869	.395	-.078 - .869	3.01
Bonobo(11)		.363	.422	-.394 - 1.238	.502	-.530 - 1.533	3.00
Orang(8)		.611	.816	-.398 - 2.030	-.029	-1.651 - 1.593	3.62
Human(10)		.735	.372	.092 - .651	.563	.205 - .921	1.96
TQ(10)		.538	.456	-.126 - 1.037	.348	-.254 - .950	4.46

Sample	Measure	*r*	*Slope	95% CI	y-int	95% CI	% SEE
Total(100)	Ham Das	.954	.834 (.877)	.782 - .887 (.823 - .932)	.247 (.201)	.195 - .298 (.151 - .258)	3.76
(100)	Ham Das(TL)	.823	.906 (1.101)	.782 - 1.031 (.970 - 1.231)	-.072 (-.314)	-.228 - .084 (-.476 - -.151)	7.09
Gorilla(30)	Hamate Das	.792	.742	.521 - .963	.340	.096 - .584	3.71
Chimp(21)		.541	.695	.176 - 1.214	.390	-.125 - .906	3.20
Bonobo(12)		.677	.469	.109 - .828	.627	.293 - .960	2.25
Orang(8)		.676	.479	-.245 - 1.203	.625	-.089 - 1.339	2.64
Human(10)		.664	.396	.033 - .759	.691	.320 - 1.063	1.87
TQ(10)		..942	.750	.533 - .967	.314	.143 - .484	1.45
Gorilla(30)	Ham Das(TL)	.917	.917	.653 - 1.180	-.251	-.365 - .315	3.63
Chimp(21)		.388	.370	-.052 - .792	.596	.044 - 1.148	3.51
Bonobo(12)		.386	.435	-.297 - 1.168	.512	-.413 - 1.436	3.81
Orang(8)		.335	.470	-.853 - 1.793	.719	-1.301 - 2.216	1.90
Human(10)		.651	.286	.014 - .557	.731	.384 - 1.078	
TQ(10)		.234	.162	-.387 - .712	.247	.164 - 1.301	4.22

All measures are relative to metacarpal size unless specified as relative to total length (TL)
*** OLS results are reported above, RMA results are reported in brackets below**

Figure 3.1 Radius Distal Area Z-Scores*

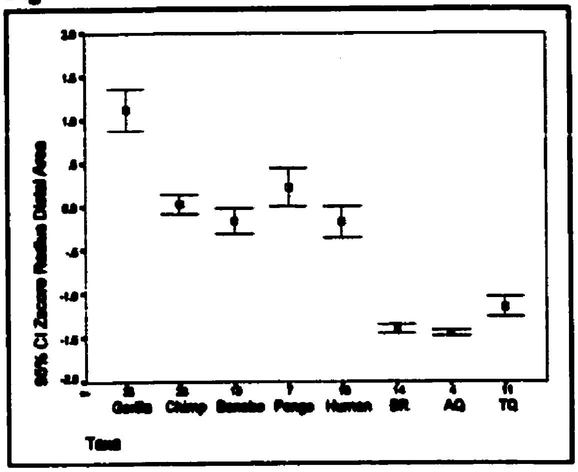
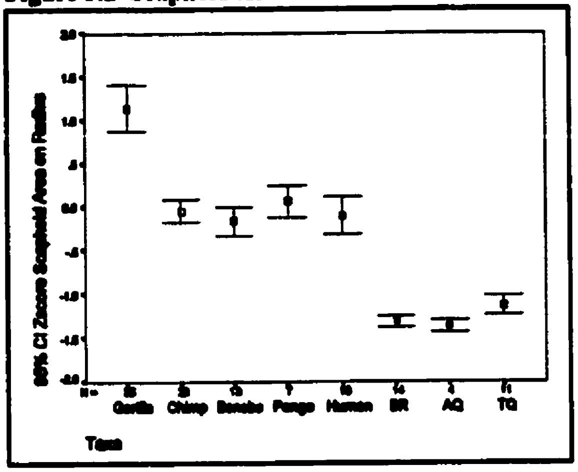


Figure 3.2 Scaphoid Area on Radius Z-Scores



*Center = mean, bars represent 95% confidence interval (a range of values based on the mean that, with 95% liklihood, include the population mean).

Figure 3.3 Lunate Area on Radius Z-Scores

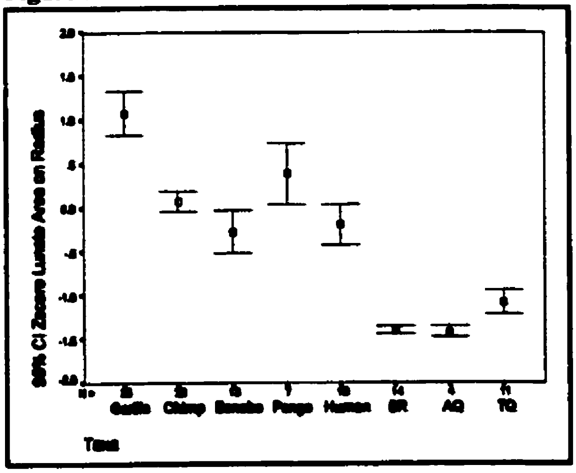


Figure 3.4 Radius Distal Area / Metacarpal Size

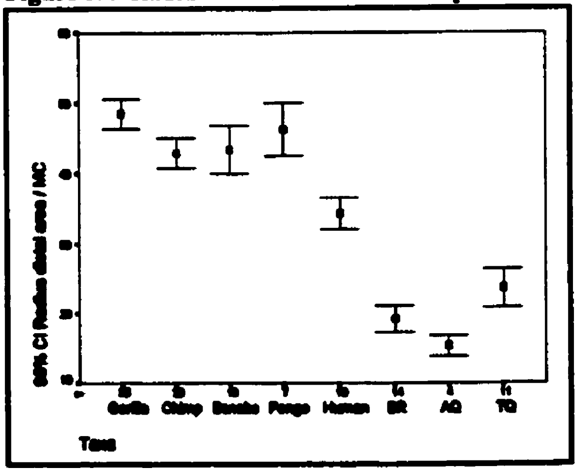


Figure 3.5 Scaphoid Area on Radius /Metacarpal Size

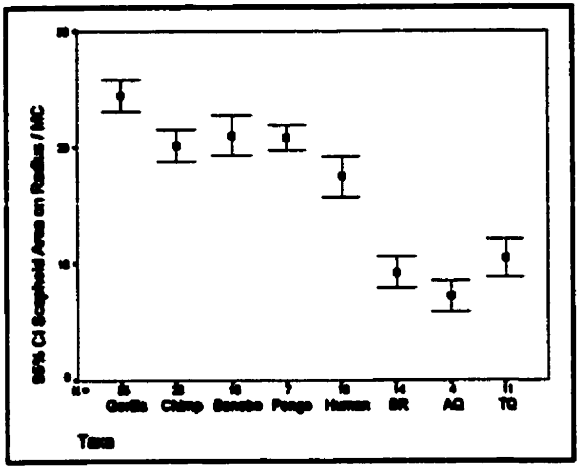


Figure 3.6 Lunate Area on Radius / Metacarpal Size

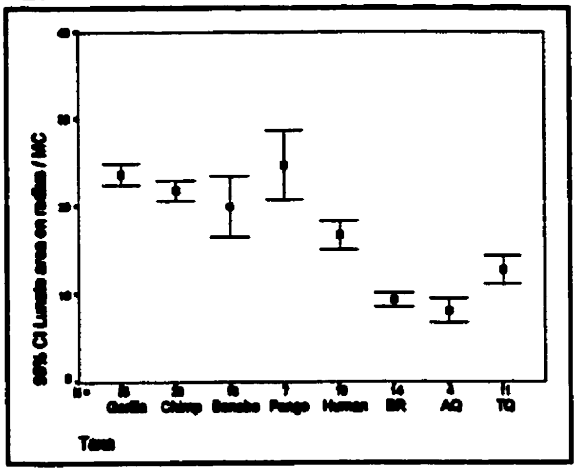


Figure 3.7 Scaphoid Proximal Area Zscores

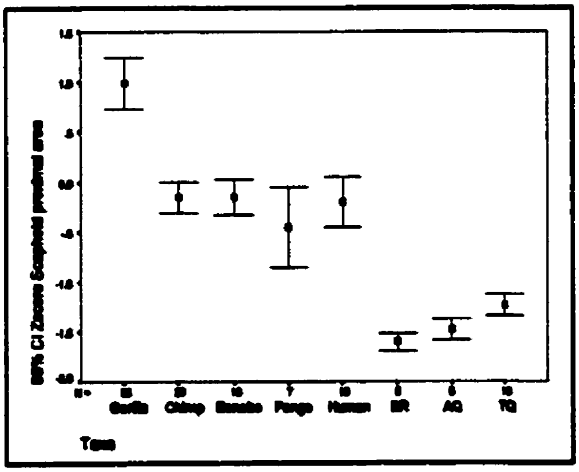


Figure 3.8 Scaphoid Proximal Area Relative to Metacarpal Size

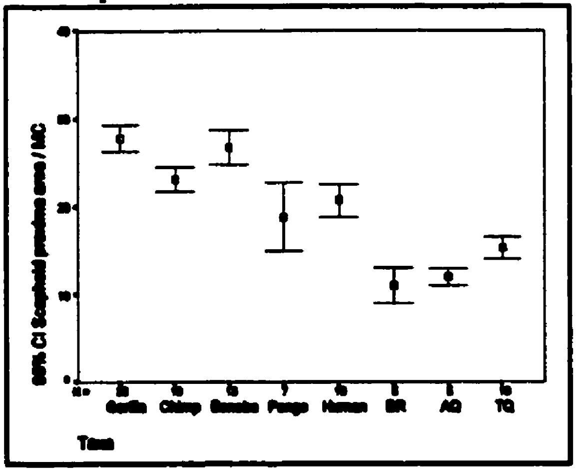


Figure 3.9 Lunate Proximal Area Zscores

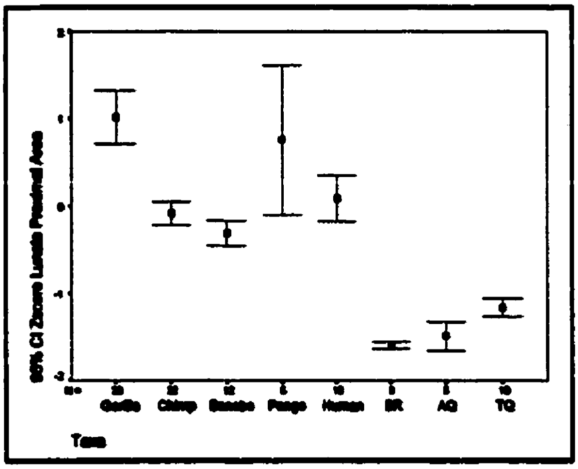


Figure 3.10 Lunate Proximal Area Relative to Metacarpal Size

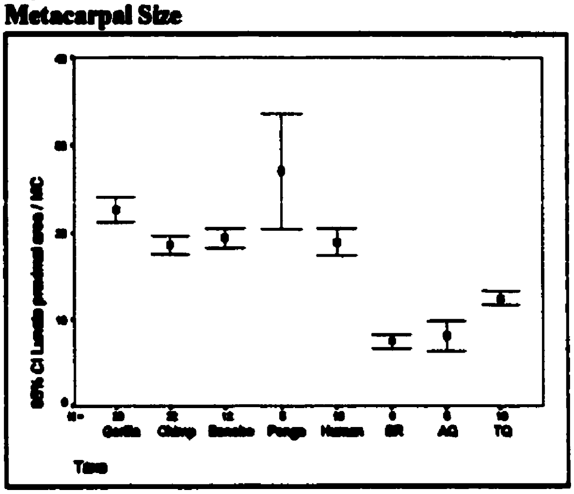


Figure 3.11 Ratio of Scaphoid to Lunate Area

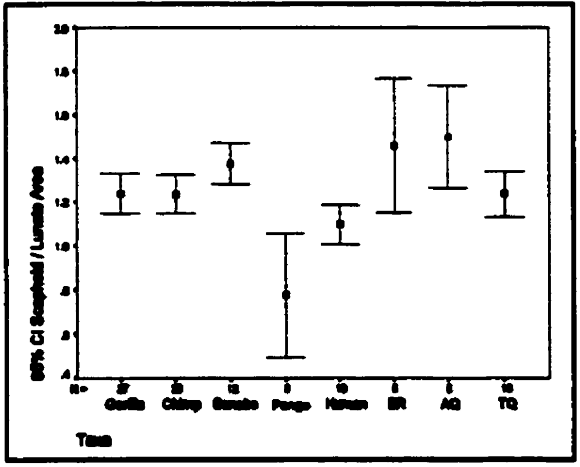


Figure 3.12 Capitate Distal Area Z-Scores

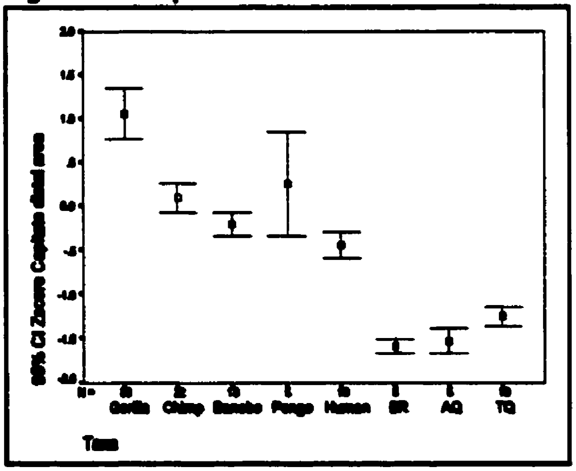


Figure 3.13 Scaphoid Facet Area on Capitate Z-Scores

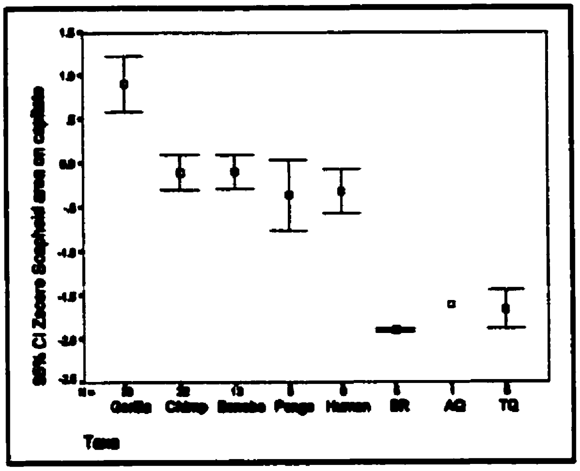


Figure 3.14 Hamate Facet Area on Capitate Z-Scores

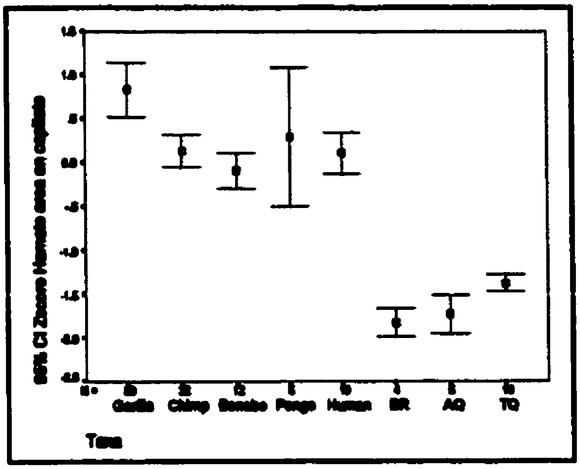


Figure 3.15 Scaphoid Area on Capitate Relative to Metacarpal Size

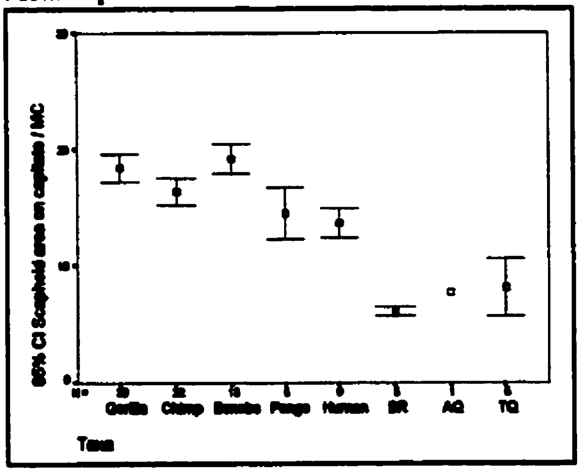


Figure 3.16 Scaphoid Area on Capitate Relative to Total Capitate Length

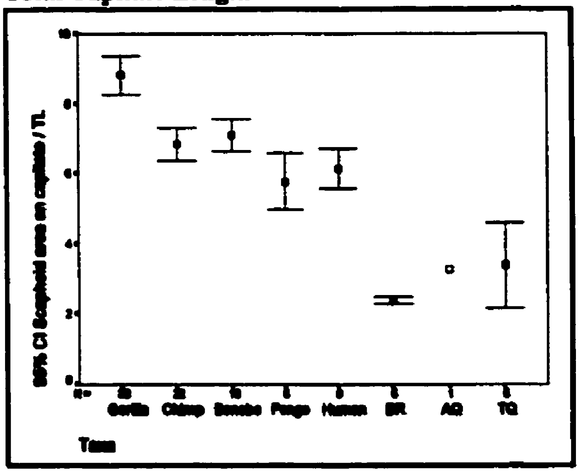


Figure 3.17 Hamate Facet Area on Capitate Relative to Metacarpal Size

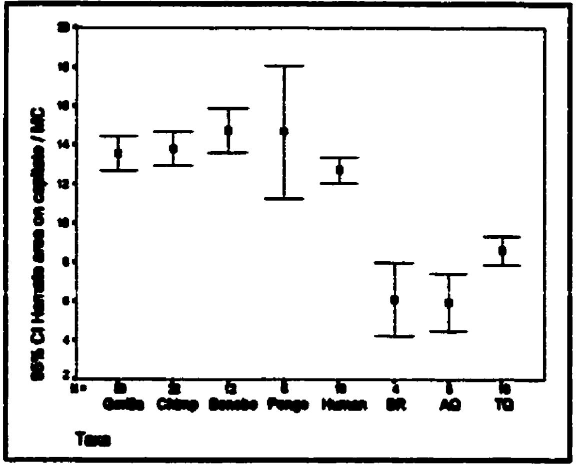


Figure 3.18 Hamate Facet Area on Capitate Relative to Total Capitate Length

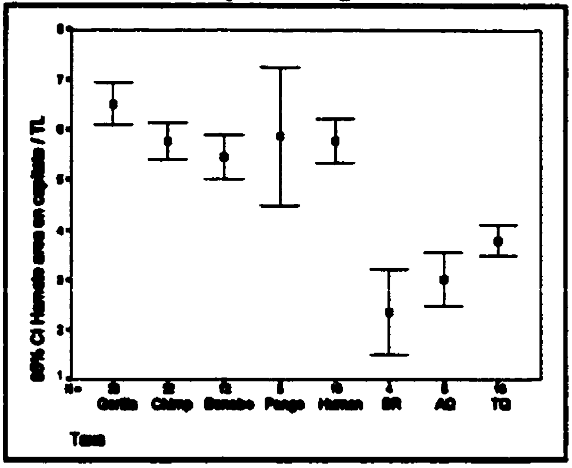


Figure 3.19 Capitate Distal Area Relative to Metacarpal Size

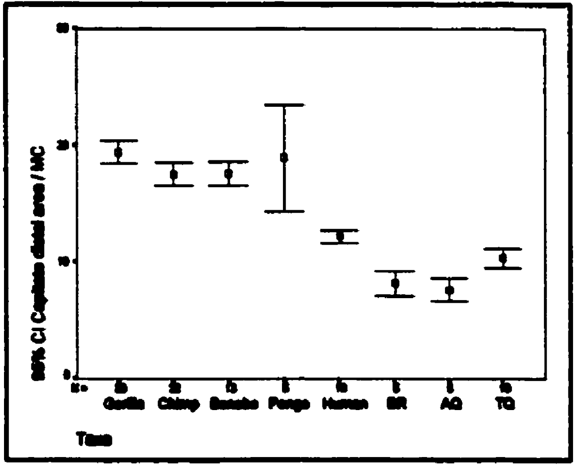


Figure 3.20 Capitate Distal Area Relative to Capitate Total Length

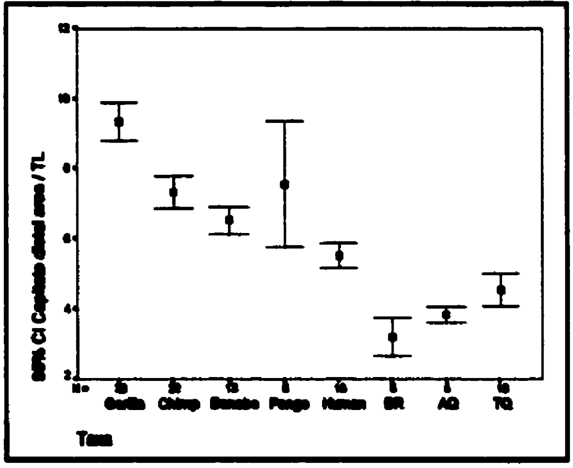


Figure 3.21 Capitate Area on Hamate Z-Scores

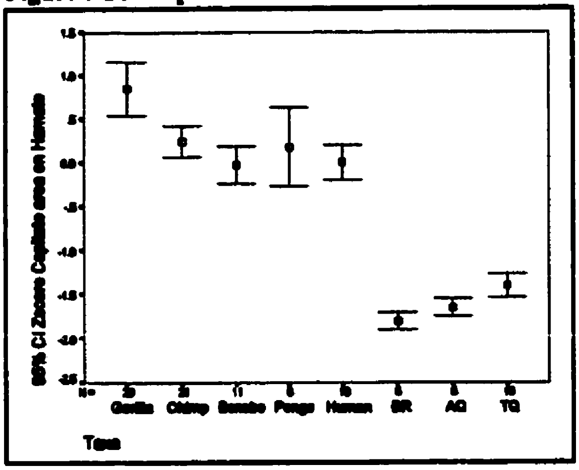


Figure 3.22 Hamate Distal Area Z-Scores

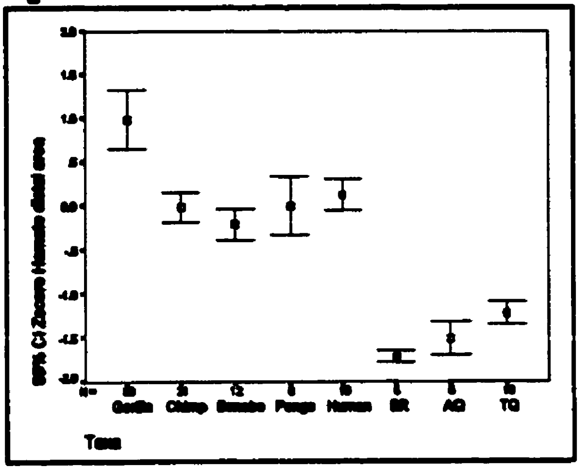


Figure 3.23 Capitate Area on Hamate Relative to Metacarpal Size

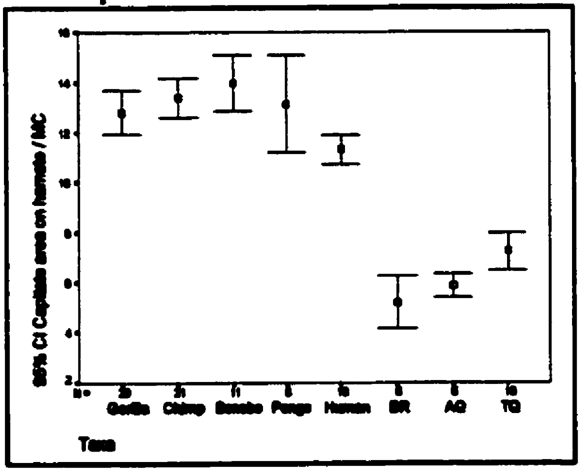


Figure 3.24 Capitate Area on Hamate Relative to Hamate Total Length

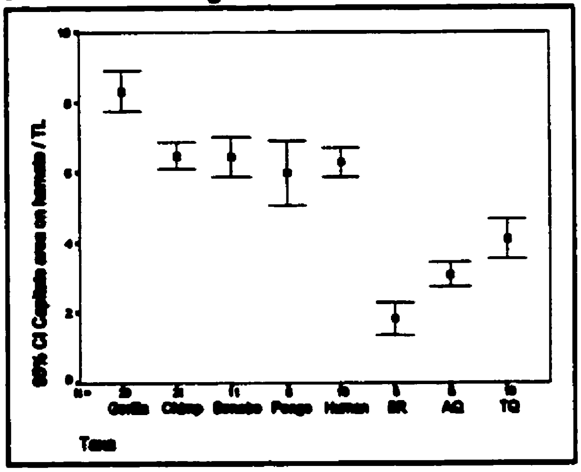


Figure 3.25 Hamate Distal Area Relative to Metacarpal size

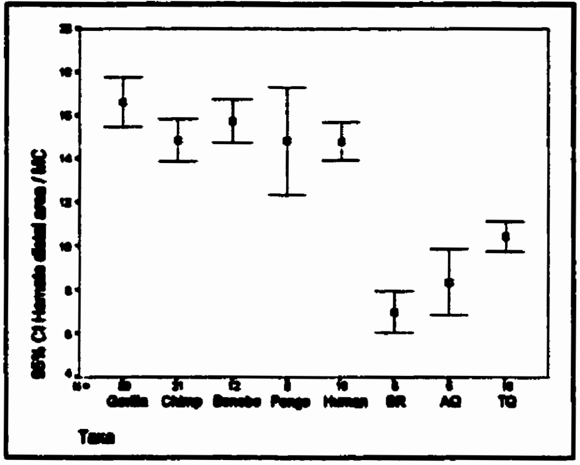


Figure 3.26 Hamate Distal Area Relative to Hamate Total Length

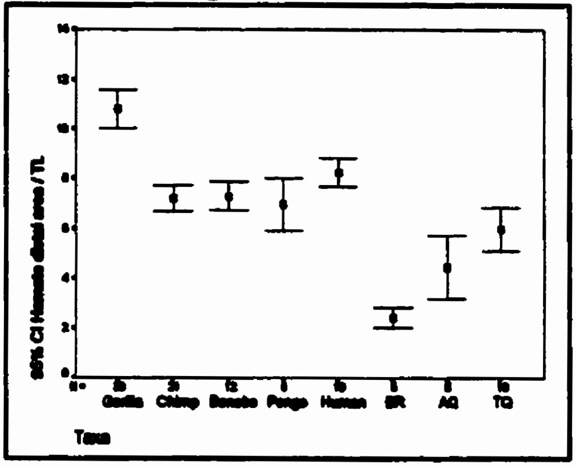


Figure 3.27 Regression Plot of Radius Distal Articular Area versus Metacarpal Size For Total Sample

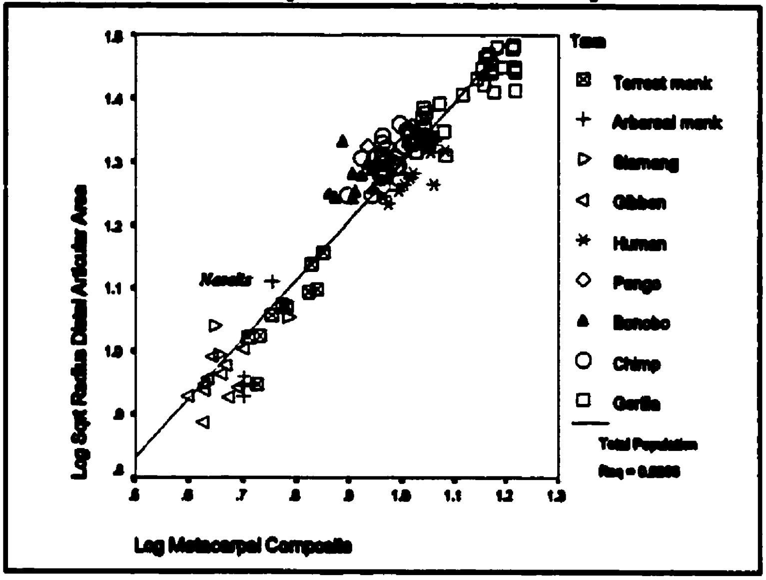


Figure 3.28 Regression Plot of Scaphoid Area on the Radius versus Metacarpal Size For the Total Sample

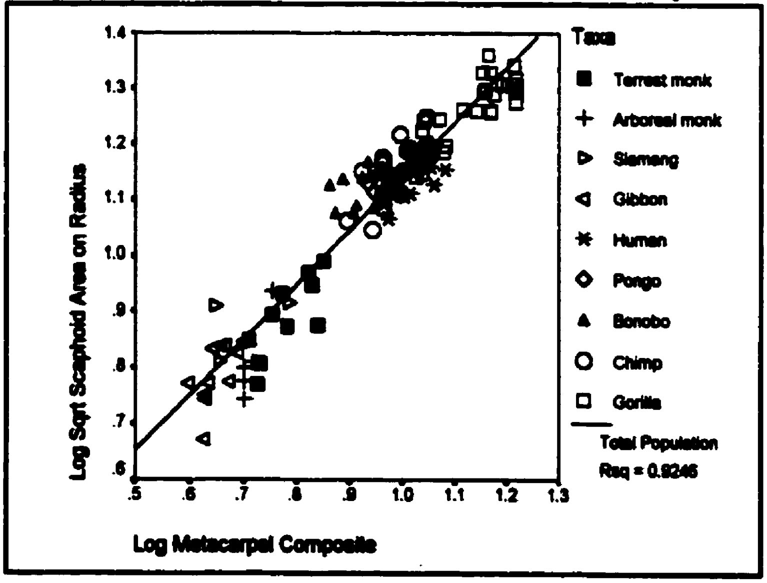


Figure 3.29 Regression Plot of Lunate Area on Radius versus Metacarpal Size For Total Sample

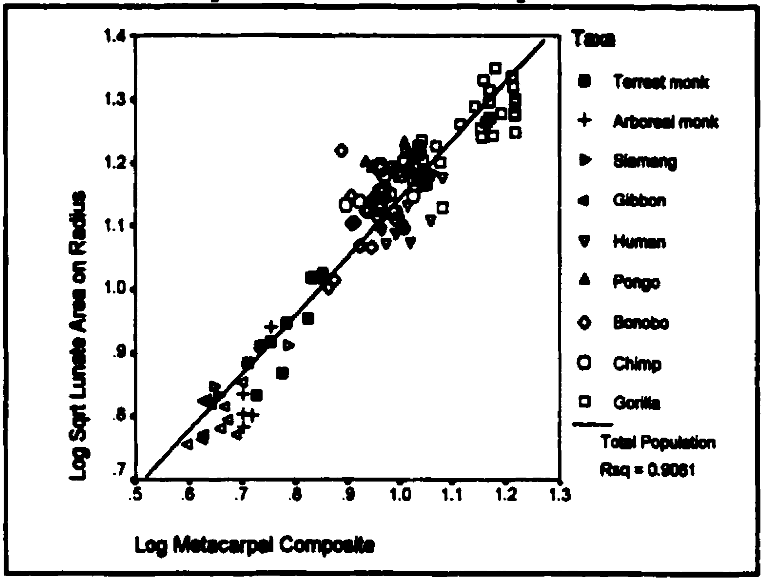
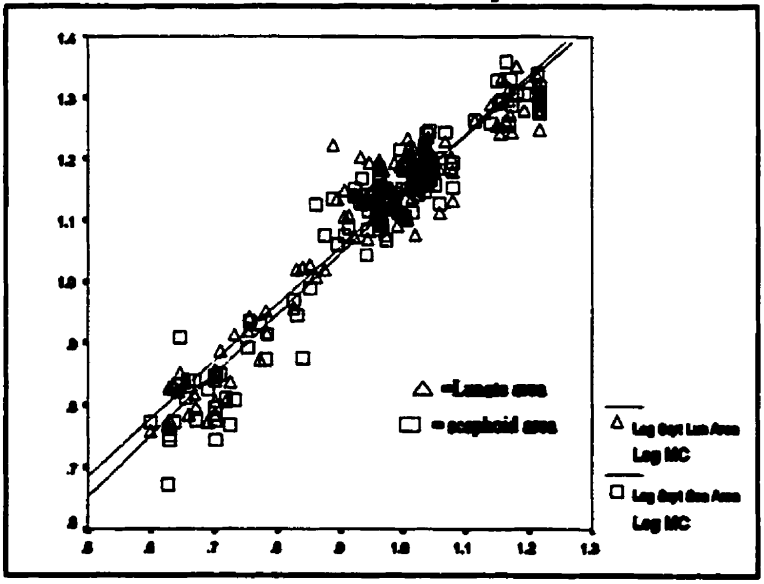


Figure 3.30 Regression Plot of Scaphoid and Lunate Areas on the Radius versus Metacarpal Size



clarify

Figure 3.31: Regression Plot of Scaphoid and Lunate Proximal Areas versus Metacarpal Size

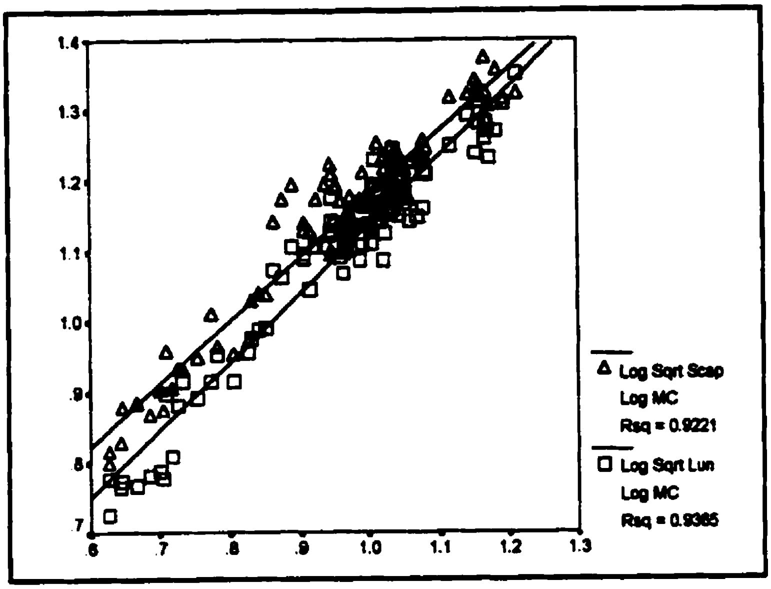


Figure 3.32: Scaphoid Proximal Area Versus Metacarpal Size

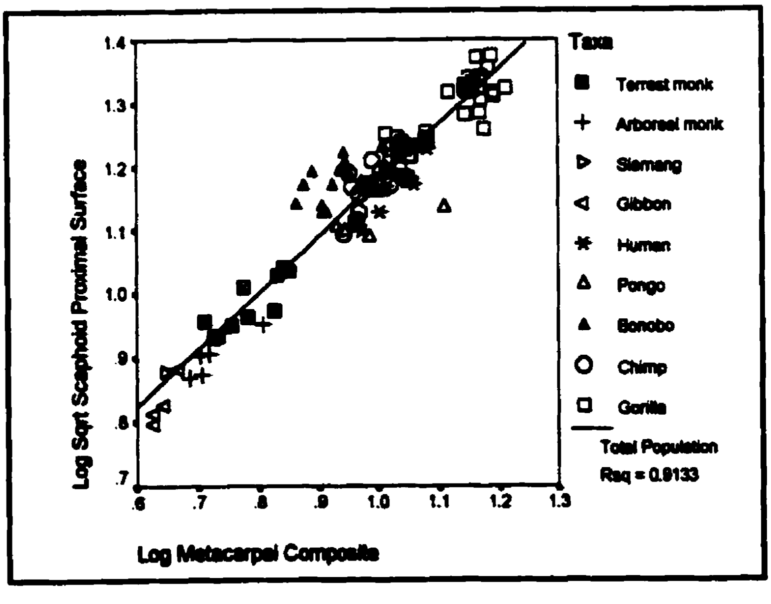


FIGURE 3.33 Regression of Lunate Proximal Area versus Metacarpal Size

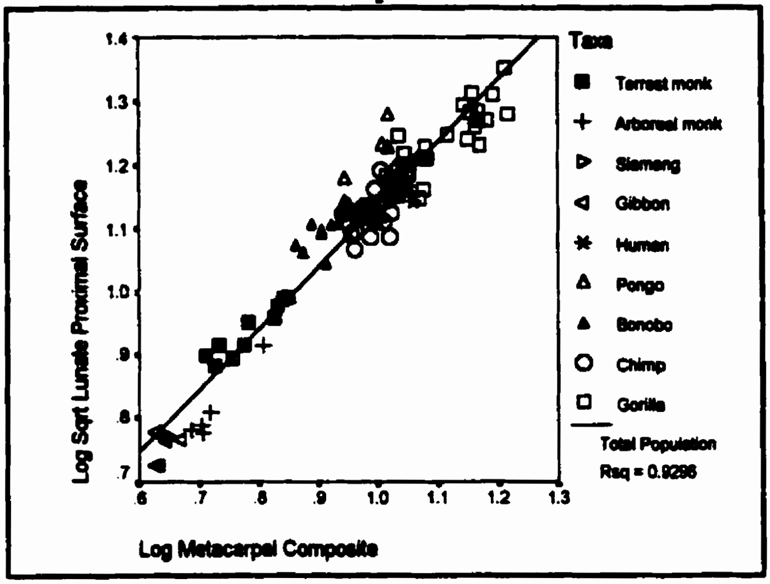


Figure 3.34: Regression Plot of Lunate Proximal Area versus Metacarpal Size By Taxon

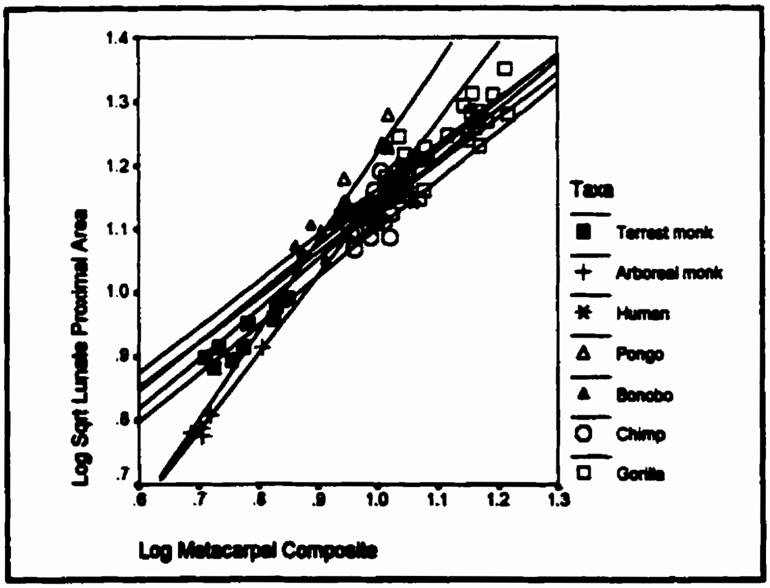


Figure 3.35: Regression Plot of Scaphoid Area on the Capitate versus Metacarpal Size For the Total Sample

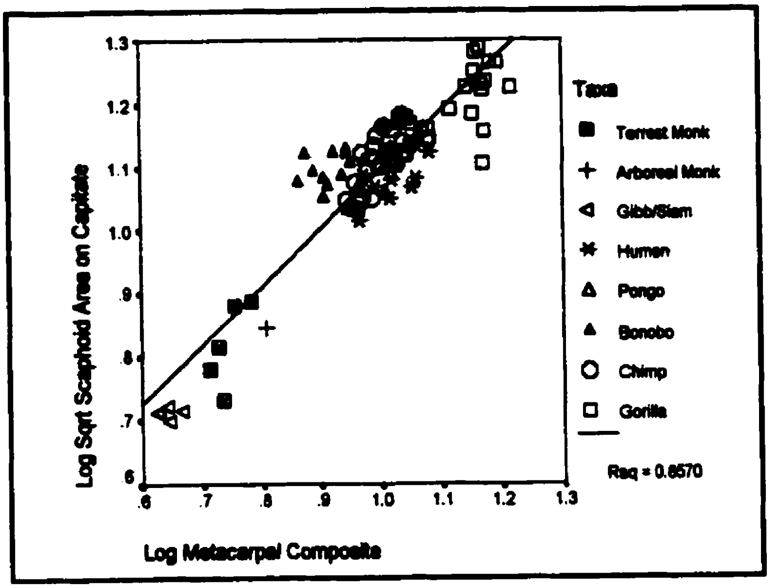


FIGURE 3.36: Regression of Scaphoid Area on Capitate versus Capitate Total Length For the Total Sample

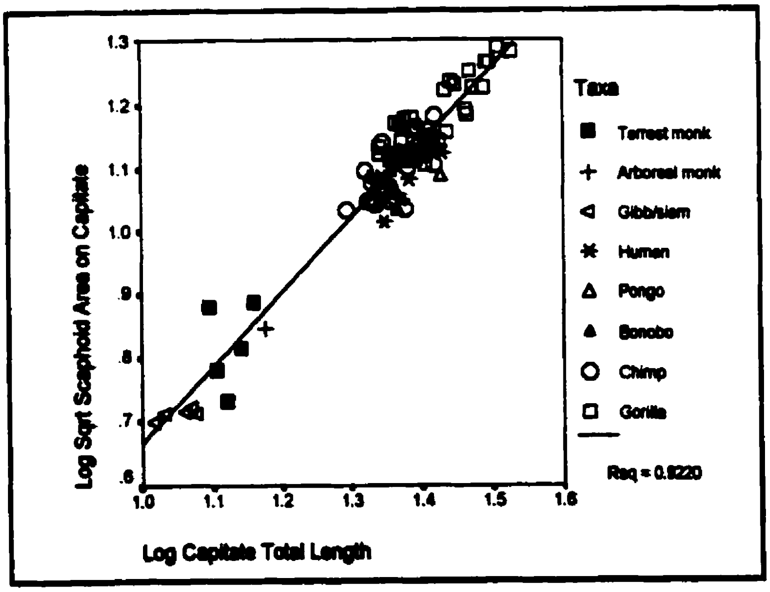


Figure 3.37: Regression Plot of Hamate Area on the Capitate versus Metacarpal Size for the Total Sample

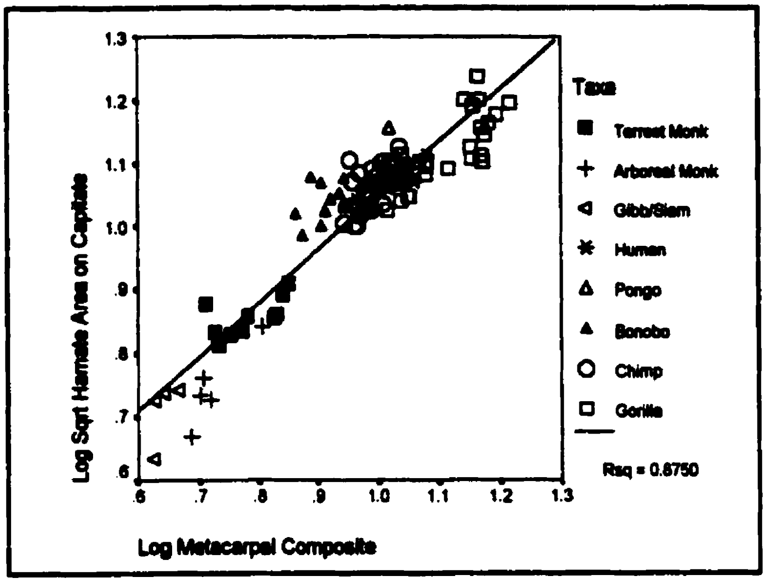


Figure 3.38: Regression Plot of Hamate Area on the Capitate versus Capitate Total Length for the Total Sample

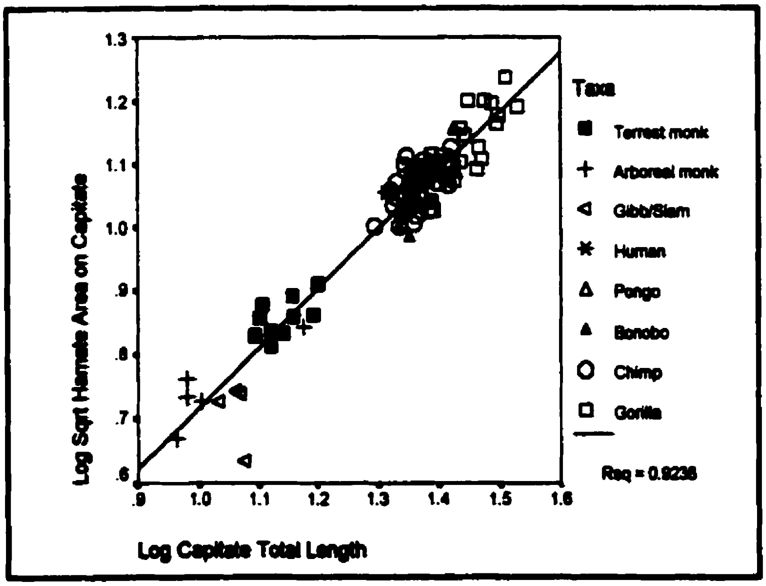


Figure 3.39: Regression Plot of Capitate Distal Area versus Metacarpal Size for the Total Sample

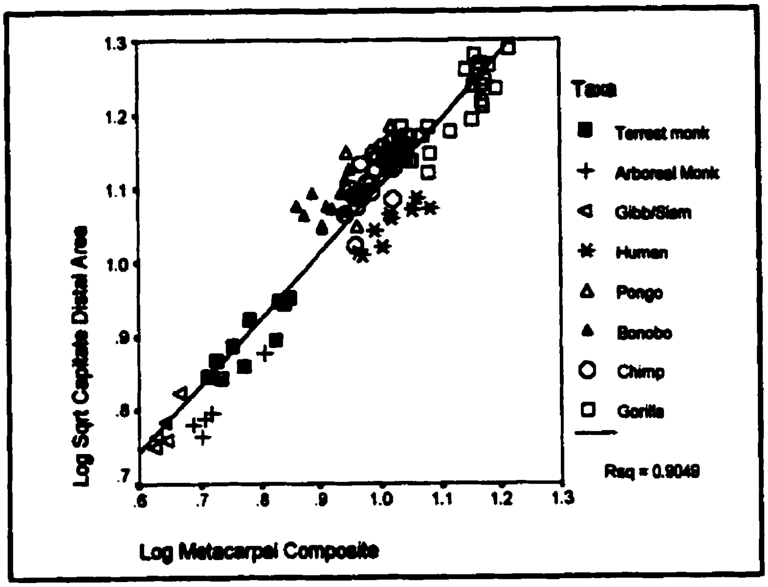


Figure 3.40 Regression Plot of Capitate Distal Area versus Capitate Total Length for the Total Sample

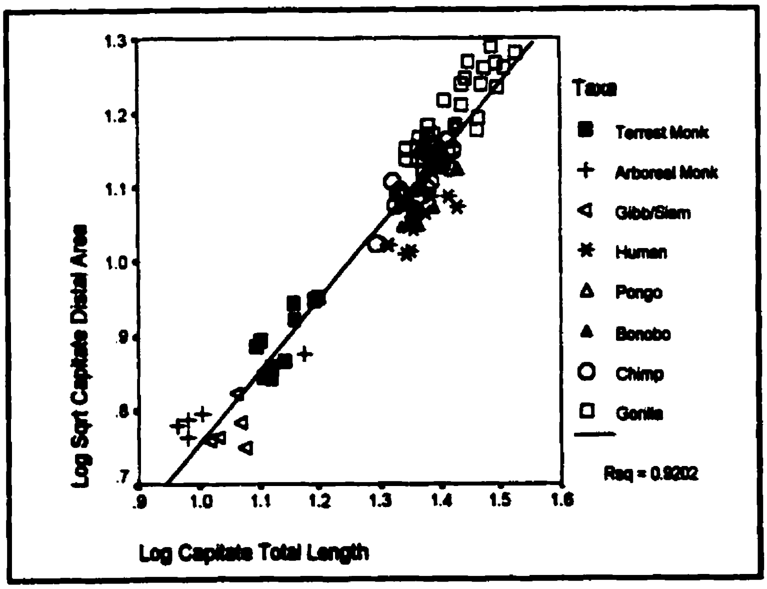


Figure 3.41: Regression Plot of Hamate Distal Area versus Metacarpal Size for the Total Sample

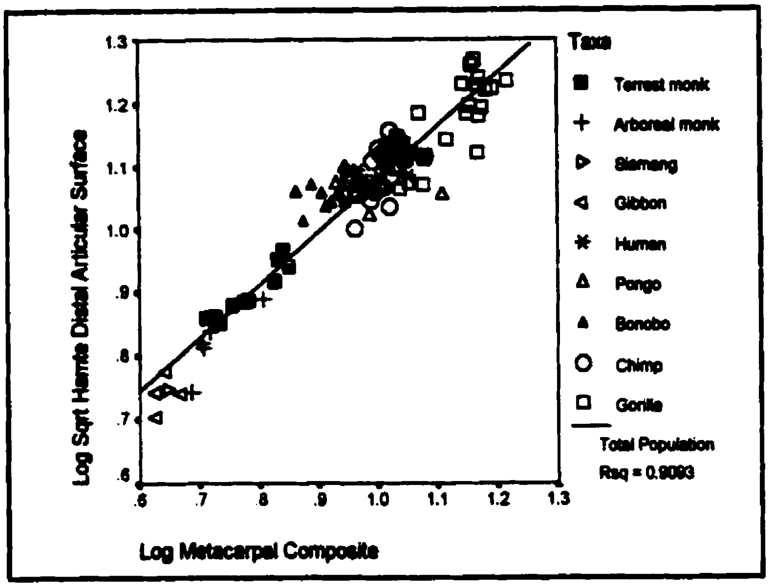


FIGURE 3.42: Regression Plot of Hamate Distal Area versus Hamate Total Length for the Total Sample

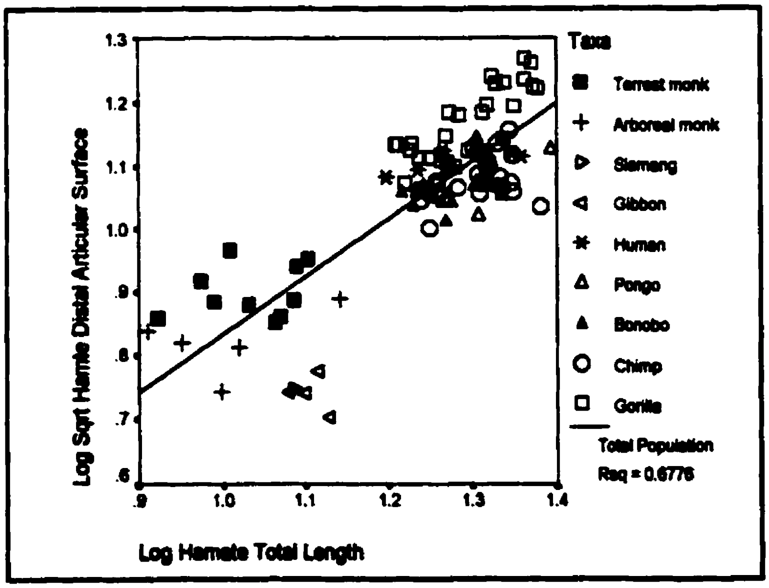
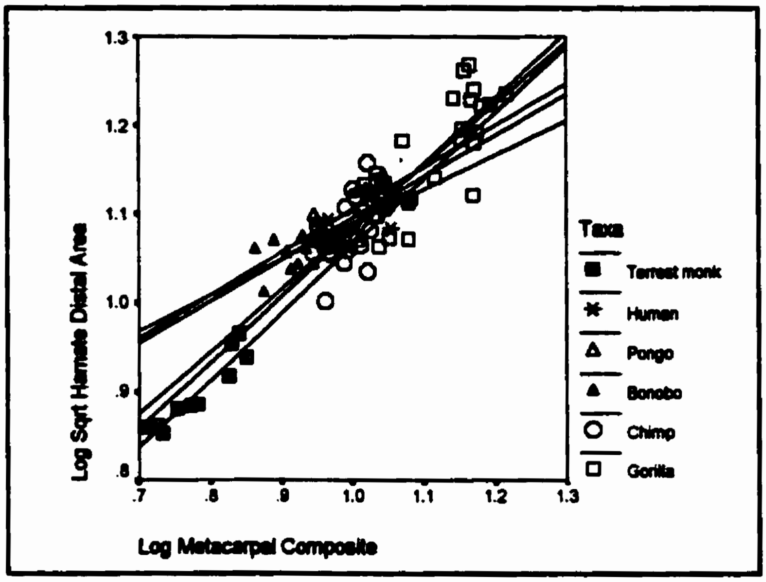


Figure 3.43: Regression Plot of Hamate Distal Area versus Metacarpal Size By Taxon



CHAPTER 4

The Metacarpophalangeal Joint

Background of Hominoid Hand Morphology

Studies of the comparative anatomy of hominoid hands have been numerous. Of primary interest initially were analyses of features viewed within a phylogenetic context (Gregory,1928a,b; Huxley, 1893; Strauss, 1940,1949) and comparative descriptions of fossil taxa (Brain et al, 1988; Bush et al, 1982; Napier, 1959; Ricklan, 1986; Susman, 1988a,b, 1989; Susman and Creel, 1979). Much of the early research focussed on basic hand shape (Erikson, 1963; Midlo, 1934; Schultz, 1927,1936,1956) and relative ray lengths among hominoids (Napier, 1959; Schultz, 1956; Susman, 1979). Subsequently, a more functional approach to the analysis of hands has been adopted (Inouye, 1989,1990,1991a,b; Lewis, 1969,1972a, 1973,1977,1989; Napier, 1959,1960a,1962; Sarmiento 1988,1994; Smith, 1990; Susman,1979,1988a,b, 1989; Susman and Creel,1979; Susman and Stern, 1980; Susman et al, 1982; Tuttle, 1967, 1969a,b,c).

As mentioned, much of this work has emphasized hand shape and relative ray lengths and dimensions. Many of the differences among living great apes are attributed to varying degrees of arboreality verses terrestriality (Erikson, 1963; Preushchoft, 1973; Straus, 1940; Schultz, 1927; 1936;1956; Susman, 1979; Tuttle, 1967,1969a,b; Tuttle and Cortright, 1988; Tuttle and Watts, 1985). It has been noted that gorillas are the most terrestrial of all great apes, orangs are the most arboreal, and that chimps are intermediate in the frequencies of arboreal verses terrestrial locomotor behaviours (Fleagle, 1976; Tuttle, 1977, 1986). Consequently, chimp hand morphology reflects a compromise between terrestrial knuckle-walking and arboreal grasping behaviours (Erikson, 1963; Schultz, 1927,1936,1956; Susman, 1979). Bonobos are said to engage in higher frequencies of arboreal postures and travel than chimps (Badrian and Badrian, 1977; Doran, 1993). The finger morphology of *Pan paniscus* is described as intermediary between chimps and orangs, suggesting more arboreal characteristics of the hand in this taxon (Susman, 1979).

Gorillas are characterized as having very broad hands relative to body size (Erikson, 1963; Midlo, 1934; Schultz, 1927,1936,1956), with metacarpals and proximal phalanges that are short and stout compared to chimps and orangs (Sarmiento, 1994; Susman, 1979, 1983; Susman *et al* 1984). It has been clearly demonstrated by Inouye (1992) however, that in most metacarpal dimensions, gorillas and chimps are ontogenetically scaled. For example, metacarpal midshaft width scales isometrically with body size, and there are no significant differences between gorillas and chimps in this variable at common sizes. Metacarpal and proximal phalangeal length, as well as proximal phalangeal midshaft width, do depart from the pattern of ontogenetic scaling. At common sizes, gorillas have shorter metacarpals and phalanges, and wider phalanges. The relatively shorter proximal phalanges of gorillas compared to metacarpal length reflect a pattern of negative allometry (Inouye, 1992). At common metacarpal lengths, gorillas and chimps have proximal phalanges of similar length, however as gorillas surpass chimps in size, their proximal phalanges get proportionately shorter (Inouye, 1992). Additionally, the proximal phalanges of gorillas are heavily constructed and lacking in longitudinal curvature, with well developed basal tubercles and marked flexor sheath ridges.

Orang hands are described as being elongated and slender (Erikson,1963; Midlo, 1934; Schultz, 1927,1936,1956; Susman, 1979). Compared to all African apes, orangs have the longest proximal phalanges. Metacarpal length, however, does not differ between chimps and orangs at common sizes, but chimps have wider midshaft diameters (Inouye, 1992). Thus, in comparison to gorillas, orangs have longer metacarpals and phalanges, with smaller midshaft diameters. Compared to chimps, orangs have smaller metacarpal shaft diameters and longer phalanges. According to Susman (1979), *Pongo* metacarpal shafts also have thicker cortices than those of chimps and gorillas, but this feature is shared with bonobos. In addition, all Asian apes are characterized by having extremely curved proximal phalanges, particularly orangs (Susman, 1979; Susman and Stern, 1984; Stern and Susman, 1983). In most cases (orangs), the volar surface of the phalangeal shaft is raised above the level of the flexor sheath ridges, contra chimps and gorillas, but a condition also found in many bonobos (Susman, 1979).

As mentioned, chimp hands have been described as morphologically intermediate between gorillas and orangs (see above). In comparing chimps and bonobos, it becomes apparent that the latter are morphological intermediaries between chimps and orangs. For example, bonobos have smaller midshaft diameters of both metacarpals and proximal phalanges (Inouye, 1992), the metacarpals are lacking in well developed secondary features such as muscle markings and ligamentous attachment sites that are present in chimps, and the metacarpal cortices are thicker as in orangs (Susman, 1979), the curvature of the proximal phalanges is intermediate between that of chimps and orangs (Susman and Stern, 1984; Stern and Susman, 1983), and the ventral surface of the phalangeal shaft is often raised above the level of flexor sheath insertion (Susman, 1979).

Several biomechanical models have been proposed to explain these differences in hominoid hand proportions. Long ray segments increase the compass of the hand and facilitate the "hook" grip utilized in grasping large branches (Preuschoft, 1973; Napier, 1967; Susman, 1979). Increased curvature is a modelling reponse to strong bending moments incurred by long fingers (Preuschoft, 1973; Susman, 1979). In orangs and brachiators, elongation of the manual rays results in increased phalangeal curvature. As noted by Hunt (1991), curvature typically parallels the degree of arboreal activity and frequency of suspensory postures in animals. It reduces not only bending moments, but tissue strain as well by maintaining a constant distance between the ventral aspect of the phalanx and support, thus assuring similar pressures along the length of the digit (Hunt, 1991). Since metacarpals are sometimes subjected to strong bending moments, orangs resist these forces through increased cortical thicknes and greater shaft curvature (Susman, 1979; although strong curvature does not usually characterize or distinguish orangs from chimps, pers.obs.). Bonobo hand morphology reflects a greater propensity for arboreal and suspensory activity in this taxon as compared to chimps, in having greater phalangeal curvature and thicker metacarpal shaft cortices.

The knuckle-walking stance characteristic of African apes exerts numerous stresses across the hand, particularly in the metacarpophalangeal joint. Close-packed positioning during stance is achieved through hyperextension of the joint, and knuckle-walkers possess a number of features that are hypothesized to reduce joint stress. One of these features is a reduction in length of the proximal phalanx. During knuckle-walking stance, ground reaction forces tend to hyperextend the metacarpophalangeal joint even further. To prevent its total collapse, passive resistance is provided across the joint by the long digital flexors, as well as by bony and ligamentous structures (Tuttle, 1967; Tuttle *et al*, 1972; Tuttle and Basmajian, 1974). Reducing the length of the phalanx effectively reduces the moment arm of the torque produced around the joint by the ground reaction force (Susman, 1979), and increases the mechanical advantage of those structures responsible for passive resistance.

In addition to stresses exerted across the joint, Prueschoft (1973) has suggested that bending stresses also occur on the metacarpals and proximal phalanges during knuckle-walking. To counteract this, African apes have wider shaft dimensions compared to orangs at common body sizes (Inouye, 1992).

This brief review of overall hand proportions in hominoids lays the foundation for the true purpose of this chapter, namely a description and analysis of metacarpophalangeal joint morphology. More specifically, the goal is to investigate metacarpal head surface geometry and proximal articular surface area and shape of the proximal phalanx in an effort to identify knuckle-walking correlates in African apes. It has already been demonstrated that African apes possess a number of characters that reduce stresses incurred in the hand during knuckle-walking, however these traits are variable in their degree of expression, reflecting a continuum from highly terrestrial species, such as gorillas, to strictly arboreal animals in the form of orangs.

Metacarpophalangeal Joint Morphology

Old World monkeys retain what is considered by Lewis (1989) to be the primitive metacarpal head morphology. The metacarpal heads are deeply grooved laterally and medially on the ventral aspect with a crest in between. These grooves act as tracks for sesamoid bones embedded in the glenoid plate situated ventrally at the base of the proximal phalanx. This plate is a fibrocartilaginous structure, and forms a major component of the articular surface of the proximal phalanx (Lewis, 1989). The glenoid plate has thickened lateral margins in which sesamoids are embedded for reinforcement. The margins of the glenoid act as runners travelling in the grooves along the metacarpal head. During flexion, the plate moves forward over the metacarpal head, guiding the proximal phalanx behind it. Movement at the joint is fundamentally that of a hinge, with some adduction/abduction occurring with extension. The second and fifth metacarpals are typically asymmetrical, MII being bevelled on the radial side and MV bevelled on the ulnar side. Thus, in extension MII undergoes some degree of ulnar deviation, while MV experiences some radial deviation (Lewis, 1989).

Gorilla metacarpal heads are deep dorsoventrally, and have a high flexion set (ie: the head appears to be tilted forward). They are typically heavily constructed with well developed muscle markings and deep excavations for insertion for collateral ligaments. The presence of a dorsal ridge is characteristic of gorillas (Tuttle, 1967,1969a,1969b), however this trait is variably expressed. The ridge is very prominant on large males, less so on smaller females and may be absent in young individuals all together. It is normally most pronounced on MIII and MIV, and the articular surface of the head flattens prior to the dorsal ridge. In dorsal view, the articular surface of MIII/MIV is extended on the ulnar aspect, resulting in slight axial rotation and radial deflection when the proximal phalanx is hyperextended (Susman, 1979). In addition, the greatest breadth of these metacarpal heads is located dorsally. MII is twisted axially, so that the dorsal aspect faces MIII, and the head is somewhat bevelled on the dorsoradial side. The results in some degree of ulnar deviation and supination as the phalanx is brought into extension (Lewis, 1989). The morphology of MV mirrors that of MII, in that the head is bevelled on the dorso-ulnar side, and slight radial deviation and pronation accompany extension of the phalanx. MII and MV heads normally have the broadest portion of the articular surface on the ventral aspect. In general, the articular surface of all metacarpal heads is extended proximally on the dorsal aspect (Tuttle, 1967, 1969a,b). Finally, gorilla metacarpals also have a well developed glenoid plate situated on the ventral aspect of the joint capsule (Susman, 1979).

The metacarpal head morphology of *Pan troglodytes* is very similar to that of gorillas, however some characters are expressed to a lesser degree. For example, the dorsal ridge on MII may be lacking in some cases, dorsal flattening prior to the ridge on MIII is reduced, and the dorsal asymmetry of the MIII head is less marked (Susman, 1979). Chimps have smaller dimensions of MII and MV heads relative to MIII and MIV (Sarmiento, 1994).

Bonobos depart somewhat from the pattern typical of gorillas and chimps. The metacarpal heads overall are less robustly constructed, with reduced epicondyle size, muscle markings and excavations for collateral ligament insertion. Dorsal ridges, when present, are weakly developed. If present, distribution of the ridges differs from that of other African apes. In some cases, ridges may be visible on all four lateral metacarpals, in others it may occur on both MIII and MIV, or only on MIII. Most third and fourth metacarpals have their greatest breadth along the dorsal aspect, as in gorillas and chimps, however some have broader ventral surfaces. MII's have wider ventral surfaces, however some MV's have wider dorsal aspects (Susman, 1979). Nonetheless, bonobos do share with other African apes a proximal extension of the articular surface dorsally, as well as dorsoventrally deeper metacarpal heads as compared to Asian apes.

Pongo metacarpal heads exhibit an entirely different morphology. Although Lewis (1989) states that orang morphology resembles that of young chimps and gorillas, in that dorsal ridges are lacking, this is not truly accurate. Dorsal ridges are lacking in *Pongo*, but the metacarpal heads overall are more gracile, with smaller epicondyles, reduced markings for muscle insertions and excavations for ligament attachment, and are less deep dorsoventrally. The articular surface of the head is not extended on the dorsal aspect as in African apes, and it does not end in a ridge, but rather in bipartite extensions (Susman, 1979). In almost all cases, the greatest breadth of the metacarpal head is on the ventral aspect. The appearence of the metacarpal head in profile is somewhat flatter, or less inflated distally, as compared to African apes. Orangs do possess a pattern of asymmetry across the MII and MV heads similar to that of gorillas and *Pan*, suggesting similar functional implications (Lewis, 1989). Orangs, however, are lacking the fibrocartilaginous glenoid plate on the ventral aspect of the joint capsule (Susman, 1979).

The metacarpal heads of gibbons and siamangs are non-distinctive, lacking in the pattern of asymmetry typical of large hominoids (Lewis, 1989; Susman, 1979). The metacarpals are lightly built, with poorly developed markings for muscle insertions and excavations for ligament attachment. The articular surface of the head is truncated dorsally, and its general appearence is relatively shallow, lacking the inflation seen in African apes. While the metacarpal head has a less fluted appearence ventrally as in monkeys, the joint capsule does contain sesamoid bones, unlike other hominoids (Calhoun, 1977).

In humans, the metacarpals are very robust, with well developed muscle markings and "globular" heads (Susman, 1979). The greatest breadth of the articular surface is ventral. The second and fifth metacarpal heads are highly asymmetrical (Lewis, 1989; Susman, 1979). MII is markedly twisted, with considerable bevelling dorsally and radially (ie: the edge of the articular surface is rounded, shaved off or has a "routered" appearence). From the ventral aspect, the articular surface of MII has a small convexity on the ulnar side, and a large bulbous protruberence radially (Lewis, 1989). In full extension, the digit is medially deviated and supinated, while in flexion it deviates laterally and pronates . In humans, MIII is unique in that it is also asymmetrical across its articular surface. It is similar to MII in being axially rotated, such that during flexion MII and MIII rotate and deviate radially as a unit, enhancing opposition with the thumb in the precision grip (Susman, 1979). MII is unique in that it is the most robust of all the lateral metacarpals, a condition similar to many brachiators, but contra other large hominoids wherein MIII is the most robust. Indeed, in humans MII/MIII and MIV/MV form two distinct size and functional groupings, reflecting their different roles in precision and power gripping. Great apes, on the other hand, have a functional grouping comprised of MII, MIII/MIV, and MV (Susman, 1979).

This review of general hand proportions, metacarpal head morphology, and proximal phalangeal morphology has shown that African apes possess a number of traits that are considered to be adaptations to a knuckle-walking mode of locomotion. These traits include: relatively shorter and/or wider metacarpals and phalanges; a higher flexion set of and dorsoventrally deeper metacarpal head; well developed epicondyles and (variably developed) dorsal ridges; extension of the articular surface proximally on the dorsal aspect; and well developed palmar glenoid plates. It has been noted how shorter proximal phalanges, wider phalangeal and metacarpal midshafts help to decrease the moment arm of the ground reaction force and reduce bending stresses during knuckle-walking stance. All hominoids have relatively free flexion at the metacarpophalangeal joint, however Asian apes are limited in hyperextension capabilities (Tuttle, 1967,1969a,b). Extension of the articular surface proximally along the dorsal aspect of the metacarpal head permits a greater range of hyperextension potential in African apes. Passive hyperextension is achieved in knuckle-walking hand postures. Certain structures present in African ape hands are said to prevent extreme hyperextension and maintain the integrity of the metacarpophalangeal joint. These structures include the dorsal ridges, well developed palmar ligaments, and shortened tendons of the long digital flexors (Napier, 1969; Preuschoft, 1973; Tuttle, 1967,1969a,b). In addition to this, deeper and more flexed metacarpal heads, as well as well developed glenoid plates, increase the moment arm of the long digital flexors and thereby increase their mechanical efficiency in resisting the torque of ground reaction forces acting about the metacarpophalangeal joint (Susman, 1979). The mediolaterally expanded dorsal articular surface, particularly notable in MIII and MIV in African apes, serves to reduce compressive joint stress in normal loading during knuckle-walking stance. Finally, the enlarged epicondyles and flattened dorsal portion prior to the dorsal ridge provide a mechanism for tightening the collateral ligaments and inhibiting axial rotation of the proximal phalanx while in a position of hyperextension (Susman, 1979).

In light of the previous research outlined above, nothing has been said about joint surface geometry of the metacarpal head, or the size and shape of the articular surface at the the base of the proximal phalanx. Modified ovoid joints, such as the metacarpophalangeal joint, have male surfaces that larger in area than the female mating surface (MacConnaill and Basmajian, 1969). The larger male surface conveys information about joint mobility, insofar that it represents the maximum area over which movement can occur (Gomberg, 1981, cited in Godfrey *et* al, 1991). The smaller female surface provides information on joint stability and loading, in that it represents the minimum amount of joint surface area needed to reduce joint stress (Godfrey *et al*, 1991).

Furthermore, modified ovoid joints (such as the metacarpophalangeal joint) that are weight bearing or sustain high pressures will have a male surface profile that departs greatly from a perfect circle (Barnett *et al*, 1961). In other words, the change in curvature from one part of the surface to another is great. Joints that are not weight bearing will have profiles that more closely approximate a perfect circle. Moreover, a curved male surface resting on a relatively flatter female surface will undergo swing movement and sliding translation (Barnett *et al*, 1961). In this way, attrition of the female surface is reduced. Thus, weight bearing joints characteristically possess free translation associated with a swing movement, resulting from changes in curvature from one point to another, and there is typically a great disparity in curvature between the male and female mating surfaces (Barnett *et al*, 1961).

As discussed previously, African apes have the greatest hyperextension capabilities at the metacarpophalangeal joint of all hominoids. This is due, in part, to the proximally extended articular surface on the dorsal aspect of the metacarpal head. However, it is also possible that hyperextension is enhanced by sliding translation, resulting from unequal curvature of the metacarpal head in profile along the sagittal plane in African apes. The questions to be addressed in this analysis are the following:

1. Does the profile of the metacarpal heads in African apes differ from that of other primates?
2. Does the metacarpal head profile in African apes depart greatly from a perfect circle, indicating (a) a weight bearing joint, and (b) sliding translation at the metacarpophalangeal joint?
3. Gorillas have relatively equal ray lengths of the hand, therefore they bear weight more evenly across all four lateral metacarpal heads than chimps or bonobos, who typically utilize digits three and four for support in knuckle-walking stance. Thus, is the pattern of curvature across all four lateral metacarpal heads more consistant in gorillas than in chimps or bonobos, indicating a different pattern of hand usage or kinemetically distinct mode of knuckle-walking?
4. Knuckle-walkers possess certain features that inhibit axial rotation of the proximal phalanx while in a hyperextended position. For example, the enlarged epicondyles and flattened dorsal portion of the metacarpal head prior to the ridge enables tightening of the collateral ligaments, providing greater stability at the metacarpophalangeal joint in close packed position. A more rounded articular surface will permit a greater degree of rotary movement, whereas an oval surface limits such rotation. Hence, is the shape

of the proximal articular surface of the proximal phalanx more oval in African apes as compared to Asian apes, indicative of reduced axial rotation in close packed position of the metacarpophalangeal joint?

Measurements

Metacarpal heads were video taped and digitized in profile from the ulnar aspect for MII - MIV, and from the radial side for MV. For all large hominoids and humans, MII is bevelled on the dorsoradial side. Thus, in order to achieve the least distorted image of sagittal curvature from ventral to dorsal, images were recorded from the ulnar aspect. MIII and MIV show very little asymmetry, so they were also recorded from the ulnar side for consistency with MII. Similarly, MV is typically bevelled on the dorso-ulnar aspect, so images were recorded from the radial side. For each metacarpal head, a line was digitized from the most ventral extent of the articular surface to the most dorsal extent of the surface for which a *convex* curvature was present (see figure 1.14, p.30). In large male gorillas, for example, the articular surface of the metacarpal head continues beyond the convex portion dorsally as a concave section initially, which then flattens out to join with the dorsal ridge. Only that portion of the head which is continuously convex from ventral to dorsal is included in the analysis. A second line, drawn perpendicular to the first, bisects the head into ventral and dorsal halves.

The curvature of each half of the metacarpal head was calculated from measurements of l, a, and h, where l represents the chord length, $a = l/2$, and h is the height of the arc from the chord to the articular surface. The radius of curvature was calculated as: $r = h^2 + a^2 / 2h$. Since metacarpal size and, comcommitantly, arc length differs among taxa, the radius was normalized by dividing by arc length (see Jellema *et* al, 1993). There is some debate regarding the appropriate method of measuring curvature (for example, see Jellema *et al*, 1993; Ohman and Latimer, 1986; Stern *et al*, 1995; Susman *et al*, 1984). Although normalized radius of curvature (henceforth NRC) accounts for the effects of overall size, it does not adequately convey the compass of the subtended arc (Jellema *et* al, 1993). Therefore, included angle for each ventral and dorsal segment is also reported. Included angle is calculated as: $ø = 2 * \arcsin(l/2r)$.

Area of the proximal articular surface of the proximal phalanx was measured by digitizing around the boundary of the joint surface (see Appendix I). Mediolateral breadth and dorsoventral width were also measured in order to obtain a breadth/width ratio. *Mocha* calculates a shape variable, which determines how closely a surface area or perimeter approximates a perfect circle. A value of 1.0 indicates a circle, any value less than that reflects a more oval shaped surface.

Results

Descriptive statistics for metacarpal measures of curvature, arc lengths, and proximal phalanx articular surface areas and shape variables are shown in Tables 4.1 and 4.2. Spearman Rank Order correlation coefficients for the entire sample show that some differences exist in the pattern of correlations among rays. These are summarized in Table

4.3. Results for included angle and NRC were essentially the same, therefore only NRC is reported here.

The results demonstrate that ventral and dorsal arc lengths are significantly correlated with body size for all metacarpals, as is expected. Ventral and dorsal head curvature is also significantly correlated with body size for MIII and MIV, but not MV and only dorsally for MII. Ventral arc length is signficantly correlated with curvature only for MIV, and dorsally arc length is correlated with head curvature for all metacarpals. Curvature of the ventral portion of the metacarpal head is not significantly correlated with dorsal curvature in MIII-MV.

Pairwise comparisons between taxa where performed using non-parametric Mann-Whitney U-tests (tables 4.4- 4.6, p. 196-199). Values for normalized radius of curvature (NRC) approach 1.0 as the surface becomes flatter. Conversely, the more curved a surface is, the lower the value for NRC.

MII

Humans have the flattest ventral head surfaces and are significantly different from all other taxa in this regard. Among large hominoids, chimps have slightly flatter ventral aspects and are significantly different from gorillas, orangs, bonobos and humans (figure 4.1). In dorsal curvature, all large hominoids and monkeys have significantly lower values (ie: are more curved) than gibbons and humans (figure 4.2). In the ratio of ventral to dorsal curvature, gibbons differ from the pattern exhibited in all other taxa in having dorsal surfaces that are flatter than the ventral surfaces, and depart significantly from everything else except arboreal quadrupeds. Chimps have slightly higher ratios than other large hominoids due to the relatively flatter ventral aspects (figure 4.3). Figure 4.4 illustrates the means for each taxon in ratio of ventral to dorsal curvature for MII. It clearly shows that chimps are separate from the group consisting of gorillas, bonobos, orangs and terrestrial quadrupeds. Humans are most similar to arboreal quadrupeds, and gibbons (as well as siamangs) have a completely different pattern.

Z-scores for arc length, which indicate how many standard deviations away from the total sample mean the value for any taxon lies, show that gorillas and orangs respectively have the largest ventral and dorsal arc lengths (see figure 4.5). Relative to metacarpal size (ie: body size surrogate), humans, monkeys and gorillas respectively have reduced arc lengths as compared to chimps, bonobos and Asian apes (figure 4.6).

Regression analyses of log transformed values of metacarpal composite size and arc length were performed and results for both OLS and RMA are reported in Table 4.7. For the purposes of this analysis, RMA results are discussed since the goal is not to compare slopes among taxa, but rather to determine the slope of a particular character for the whole sample and assess its relationship to isometry. Results for MII show that arc length dorsally is essentially isometric with metacarpal dimensions, and the ventral slope is slightly lower. Humans fall well below the regression line, and are most similar to terrestrial quadupeds in arc length relative to metacarpal size (see figure 4.7).

MIII

On examining the curvature across the MIII head, a pattern similar to that of the second metacarpal emerges (figures 4.8-4.10). Again, humans have the flattest ventral curvatures, and are significantly different from all other taxa. Among hominoids, chimps have slightly flatter ventral aspects, and bonobos are most similar to *Pongo*. In dorsal curvature, all knuckle-walkers have significantly more curved metacarpal heads compared to humans and Asian apes. Chimps are not significantly different from monkeys, however gorillas and bonobos have more curved dorsal aspects than terrestrial monkeys.

In the ratio of ventral to dorsal head curvature, all knuckle-walkers have significantly higher values than humans, Asian apes and arboreal quadrupeds, indicating a greater disparity in head curvature from ventral to dorsal aspect. In other words, the profile of the metacarpal heads in African apes is much more curved dorsally not only in absolute terms, but also with respect to the ventral surface. Figure 4.11 depicts species' means for the ratio of ventral to dorsal MIII head curvature. It clearly shows that gorillas, chimps and bonobos form a group distinct from all others. Humans group with arboreal and terrestrial monkeys, and are intermediate between knuckle-walkers and Asian apes in the degree of dorsal head curvature.

Z-scores for arc length are shown in figures 4.12. They demonstrate a fairly continuous size progression in arc length from gorillas to gibbons, however the pattern is slightly different from that of MII. In the second metacarpal, orangs have somewhat larger arc lengths than chimps and bonobos. This is not the case for MIII, wherein orangs have ventral arcs of similar size to bonobos, and dorsal arcs of smaller size than either chimps or bonobos. Nonetheless, when compared relative to metacarpal composite size, the pattern that emerges is virtally identical to that of MII (figure 4.13). Once again, humans have the smallest arc lengths relative to metacarpal dimensions and are most similar to terrestrial monkeys in this repect (differerence is insignificant). Gorillas most closely resemble orangs and gibbons in relative arc lengths, and they have substantially smaller values than those of chimps and bonobos.

Regressions of arc length against metacarpal composite size show that the ventral slope is isometric, while dorsally the value is slightly positively allometric. Humans again fall well below the regression line for both ventral and dorsal arcs, whereas bonobos tend to fall above the line (figure 4.14). This is likely a function of more robust metacarpal size in humans, and slender, more gracile bonobo metacarpal dimensions. However, there is considerable overlap in metacarpal size between humans and chimps, but the latter do have much smaller arc lengths.

MIV

Humans continue the pattern seen in MII and MIII, in that human MIV's possess the flattest ventral surfaces (figure 4.15) and are significantly different from all other taxa. Gorillas, chimps and orangs are very similar to each other and all differ significantly from bonobos, which possess somewhat more curved ventral MIV heads. Bonobos, in fact, most closely resemble gibbons in ventral curvature. Dorsally, however, African apes and monkeys have much more curved surfaces than humans or Asian apes (figure 4.16). Gibbons have the flattest metacarpal heads dorsally. In the ratio of ventral to dorsal curvature, African apes have higher ratios, or greater dorsal curvature relative to ventral curvature, than humans, Asian apes and monkeys. Gorillas and chimps are significantly different from all other taxa, and bonobos differ insignificantly only from humans (figure 4.17). The plot of species means of ventral to dorsal ratio (figure 4.18) illustrates that although African apes do have the greatest curvature dorsally, the groupings are not as distinctive as for MIII. Gibbons still have flatter dorsal aspects than ventral surfaces, and orangs are grouped together with monkeys.

In z-scores for arc length, there is a continuous decreasing size progression from gorillas to gibbons (figures 4.19). Humans are significantly different from all other taxa for arc length, having smaller sizes than large hominoids, and larger arcs than gibbons and monkeys. Relative to metacarpal size, humans have the smallest arc length given their metacarpal dimensions and are significantly different from all other taxa. Overall, humans, terrestrial monkeys and gorillas have the lowest ratios for relative arc length, whereas chimps and bonobos have expanded arcs given their metacarpal dimensions (figures 4.20).

Regressing arc length against metacarpal size reveals a pattern similar to that of MII and MIII, wherein the dorsal slope is higher than the ventral slope. Dorsally, arc length is slightly above isometry, while the ventral slope falls just below isometry. Despite considerable overlap in metacarpal size for chimps and humans (figure 4.21), the latter fall well below the regression line, indicating that humans possess greatly reduced arc lengths given their metacarpal dimensions.

MV

The pattern of curvature over ventral and dorsal halves of MV closely resembles that of MII. Ventrally, very little difference exists among the different species in the degree of head curvature. Dorsally, humans and gibbons are distinctive in having flatter surfaces than all other taxa (figures 4.22-23). In the ratio of ventral to dorsal curvature, humans are most similar to gibbons and monkeys, and differ significantly from chimps, bonobos and *Pongo* (figure 4.24-25).

The pattern for arc length across the MV head is virtually identical to MII as well (figures 4.26). Gorillas and orangs have the greatest arc lengths, while humans have values that are less than those of great apes. Relative to metacarpal dimensions, humans have the smallest arc lengths given their metacarpal size, and chimps, bonobos and orangs all share expanded arc lengths compared to other taxa (figure 4.27).

Regressions of arc length verses metacarpal size shows that ventrally the slope is isometric, whereas dorsally the slope is slightly higher. For ventral and dorsal measures, humans fall well below the regression line (figure 4.28).

Figures 4.29-4.31 show the raw measures of ventral and dorsal metacarpal head cuvature for each taxon and the relationship of ventral to dorsal curvature across metacarpal heads two through five. It is clearly demonstrated that orangs and gibbons, in particular, possess very little differentiation in ratio of curvature along the profile of the lateral metacarpals. Gibbons typically have dorsal aspects that are flatter than ventral aspects, and this is consistent in metacarpals II through V. Orangs have ratios that are just above 1.0, indicating that their dorsal aspects are slightly more curved than the ventral surfaces, but the ratio is fairly consistent for all lateral metacarpals. Although the actual values of the ratios are different, the pattern of change in head curvature is very similar among gorillas, chimps and humans and contrasts with that of Asian apes. In gorillas, chimps and humans MIII is markedly more curved dorsally relative to the ventral aspect than MII, and MIV is even more curved dorsally than MIII. The change in ventral to dorsal curvature is most notable in gorillas. Moreover, the profile of MV changes dramatically, in becoming even less curved dorsally than MII. This overall pattern is exaggerated in gorillas, and virtually identical in chimps and humans. Furthermore, the morphological profile of bonobo metacarpal heads does not match that of other knuckle-walkers or humans, but rather more closely resembles that of monkeys. Bonobos share with monkeys an MIII that is relatively more curved dorsally than MII (as in gorillas, chimps and humans), but the disparity in MIV is less than MIII. Looking at figure 4.29 (and figure 4.15), it becomes apparent that the reason for the lower ratio in bonobos as compared to other African apes is because the ventral aspect of MIV is more curved than in other great apes. The dorsal curvature, however, is the same as in other knuckle-walkers. Consequently, the ratio of ventral to dorsal curvature for MIV in bonobos will be lower only because the overall profile of the metacarpal head is more rounded overall.

Thus, although the actual ratio of ventral to dorsal curvature in MIII is very similar among gorillas, chimps and bonobos as a group, and humans and monkeys as a group, it is the profile of MIV that separates gorillas, chimps and humans from other taxa in having the greatest disparity in curvature across all metacarpal heads.

Summary

- Arc length is correlated with metacarpal size and with dorsal curvature, but not ventral curvature
- Ventral angle is correlated with metacarpal size in MIII and MIV, but not MII or MV
- Dorsal angle is correlated with metacarpal size in MII, MIII and MIV but not MV
- Ratio of ventral to dorsal angle is correlated with metacarpal size in MII, MIII and MIV, but not MV
- Humans have relatively and absolutely the smallest arc lengths compared to great apes
- Chimps, bonobos and orangs all share the longest arc lengths relative to metacarpal size for MII and MV
- Chimps and bonobos have the longest arc lengths relative to metacarpal size for MIII and MIV
- Knuckle-walkers in general have significantly more curved dorsal segments for MIII and MIV, as well as a greater disparity of ventral to dorsal curvature. This is particularly true of MIV in gorillas and chimps.
- The *pattern* of curvature across the metacarpal head is shared among African apes and humans

Proximal Phalanx

Descriptive statistics for proximal phalangeal measures are presented in Table 4.5. Spearman Rank Order correlation coefficients show that proximal articular surface area, both the raw variable and relative to metacarpal midshaft diameter, is significantly correlated with the metacarpal composite dimension (ie: body size), but not with the ratio of breadth to width of the facet. Proximal articular surface shape (both the ratio of breadth/width and the shape variable) is, however, significantly correlated with metacarpal size.

Z-scores for proximal articular surface area are depicted in figure 4.32. As expected, gorillas have the largest overall area, followed by orangs. Chimps, bonobos and humans are most similar to each other, and all have slightly smaller areas than orangs. Gibbons are virtually indistinguishable from monkeys. The pattern is quite similar for area relative to metacarpal dimensions (figure 4.33), however humans have relatively smaller areas than great apes and are significantly different from them. In this respect, gibbons also differ from monkeys in having slightly larger areas given their metacarpal dimensions. In the ratio of area to midshaft breadth (figure 4.34), orangs have the highest value, followed by gorillas. Bonobos are identical to humans in this measure, and chimps have slightly smaller areas relative to phalangeal midshaft breadth. Since chimps have somewhat larger absolute areas than bonobos (see table 3.6), the lower ratio of area to midshaft breadth indicates the greater robusticity of the chimp proximal phalanx. Comcomitantly, the higher ratio of orangs is indicative of their more gracile phalangeal morphology.

In the ratio of proximal articular surface mediolateral breadth to dorsoventral width, a pattern separating arboreal species from more terrestrial ones emerges (figure 4.35). Bonobos are most similar to orangs and gibbons in this variable and these three do not differ significantly from each other. They do, however, all differ from gorillas, chimps, humans and monkeys. Thus, it is clear that bonobos and Asian apes all share more rounded proximal articular surfaces of the phalanx compared to other African apes, humans, and monkeys. The shape variable generated by *Mocha* produces almost identical results. Figure 4.36 shows a continuum of increasing shape variable values from gorillas to orangs and gibbons (1.0 equals a perfect circle, lesser values represent more elliptical shapes). Again, bonobos have much more rounded articular facets than gorillas, chimps or humans and most closely resemble orangs and gibbons in this regard. Terrestrial quadrupeds have the most elongated or elliptical articular surfaces of all taxa.

Regression analysis of proximal articular area verses metacarpal size reveals a relationship that closely approximates isometry (figure 4.37). Humans and monkeys tend to fall somewhat below the regression line, indicating they all have slightly reduced areas given their metacarpal dimensions. Most bonobos and *Pongo* fall above the regression line, indicating that they possess somewhat enlarged proximal articular surfaces of the proximal phalanx relative to metacarpal dimensions. Although Spearman Rank Order coefficients demonstrated a significant correlation between the ratio of breadth/width and metacarpal size, the regression of these variables failed to indicate such a relationship.

Discussion

From the results presented above, it is clear that knuckle-walking has altered the morphology of metacarpal heads, but in subtle ways. This analysis attempts to answer several questions. First, does the profile of the metacarpal heads in African apes differ from that of other primates? Investigation of curvature across the sagittal profile of metacarpal heads has demonstrated that African apes are distinctive in the degree of dorsal curvature. This a particularly true of metacarpals III and IV, wherein the dorsal half of the metacarpal head is much more highly curved than in either humans or other hominoids. This corroborates Susman's (1979) findings that many of the "classic" knuckle-walking characters, like dorsal ridges for example, have their greatest expression in the third and fourth digit. The degree of dorsal curvature in African apes is matched by monkeys, however the latter also have more curved ventral halves of the metacarpal head, yielding a profile that is much more rounded overall.

This leads us to the second question to be addressed: does the metacarpal head profile in African apes depart greatly from a perfect circle, indicating (a) a weight bearing joint, and (b) sliding translation with hyperextension of the metacarpophalangeal joint. Analysis of the ventral curvature of the metacarpal head compared to the dorsal curvature has also demonstrated that all African apes share a greater disparity between the two halves than is present in other taxa. Again, this is most evident in MIII and MIV. As noted by Tuttle (1967,1969,1970), flexion at the metacarpophalangeal joint is very free in all apes. This analysis shows that ventral curvature across all metacarpal heads differs very little among hominoids or monkeys for that matter. It is the degree of *change* in curvature, from a somewhat flatter ventral aspect to more highly curved dorsal surface, that distinguishes knuckle-walkers from all other taxa. Arboreal and terrestrial monkeys also possess some disparity in curvature across the head of MIII, however the ratio, and hence *degree* of change, is much higher in knuckle-walkers.

A ratio of 1.0 for ventral to dorsal curvature would indicate a profile that is rounded or circular. African apes have ratios that are greater than 1.0, particularly in MIII and MIV, indicating that the profiles of these metacarpals do indeed depart from a perfect circle. If disparity in curvature from one point to another is indicative of a weight bearing joint, then the implication is that the third and fourth rays are the primary weight bearing rays. Tuttle (1969a,b,1970) has noted that gorillas and chimps respectively are capable of greater hyperextension of the metacarpophalangeal joint as compared to Asian apes. His measurements are apparently based on passive hyperextension of all four lateral digits simultaneously, with no discrimination between individual rays. This analysis demonstrates that differences in head profiles of metacarpals II-V do exist. Furthermore, the greater degree of hyperextension possible in African ape finger joints is said to be the result of proximally extended articular surfaces on the dorsal aspect of the metacarpal heads (Tuttle, 1969a,b,c, 1970; Susman, 1979). This is most certainly true, however by virtue of the fact that African ape metacarpal heads are also more curved dorsally, with a marked disparity in curvature from ventral to dorsal aspect, the results of this analysis suggest that sliding translation of the proximal phalanx on the metacarpal head facilitates extreme hyperextension in close packed knuckle-walking stance. Although measurement of the actual curvature of the articular surface of the proximal phalanx was beyond the scope of this project, visual inspection of proximal phalangeal facet morphology clearly showed that the highly curved male articulating surface of the dorsal metacarpal head riding over the much shallower female surface of the proximal phalanx indeed makes sliding translation possible at this joint. All African apes possess a high disparity in curvature along the profile of MIII, and even more so along MIV in gorillas and chimps, implying that hyperextension capability through sliding translation is greatest in these rays.

Addressing the third question in this analysis: in light of the fact that gorillas have more equal ray lengths than all other hominoids and, therefore, distribute body weight more evenly across the hand, is the pattern of curvature across all four lateral metacarpal heads more consistent in gorillas than in chimps or bonobos, indicating a different pattern of hand usage or kinematically distinct mode of knuckle-walking? The results presented here suggest, in part at least, that this is not the case.

Assuming that disparity in articular surface profile across the metacarpal heads is indicative of weight bearing, and that gorillas, having more equal ray lengths, distribute body weight more evenly across the hand, it can be hypothesized that the ratio of ventral to dorsal curvature should be higher across all lateral metacarpals in gorillas as compared to chimps or bonobos. Results from this study do not support this hypothesis. Gorillas are very similar to chimps in overall joint surface geometry from MII - MV, and depart only slightly from that of bonobos. The ratio of ventral to dorsal curvature of MII and MV in African apes does not differ significantly from many other taxa. It is MIII and MIV, however, that do distinguish knuckle-walkers from all others. Gorillas, chimps and bonobos share a pattern of metacarpal head curvature wherein MIII has a greater disparity than MII. Gorillas share with chimps an MIV that has even more disparity across the profile than MIII. MV in all African apes has a morphology reminiscent of MII in having more equal ventral and dorsal curvatures.

Based on interspecific studies of ray lengths, it has been suggested that gorillas and chimps engage in kinematically distinct modes of knuckle-walking (Inouye 1989,1992,1994; Tuttle, 1967, 1969a,b, Tuttle and Basmajian,1978). Gorillas tend to use highly pronated hand positions and hyperextended elbows, while chimps utilize a more flexed elbow stance and variable hand positions (Inouye 1989,1992,1994; Tuttle, 1967, 1969a,b, Tuttle and Basmajian,1978). Observations of preferred digit use during knuckle-walking reveal that the second, third and forth digits are used for support with equal frequency in all knuckle-walkers, but that the fifth digit is used much less frequently in both chimps and bonobos than in gorillas (Inouye, 1994). In gorillas, the fifth digit is used with equal frequency for support as the second, third and forth digits (Inouye, 1994). Furthermore, these interspecific differences in preferred digit use are present throughout ontogeny and into adulthood, which has led Inouye (1994) to conclude that use of the fifth digit in knuckle-walking is not influenced by size or sex and is, therefore, nonallometric. In other words, interspecific differences in ray lengths and digit use are not size-dependent and are not the result of *frequencies* of knuckle-walking behaviours, in that juveniles utilize hand postures that are stereotypic of their adult counterparts despite higher frequencies of arboreal activity (Doran, 1992; Inouye, 1992,1994; Tuttle 1967,1969a,b; Tuttle and Basmajian, 1972). Rather, these differences are likely a consequence of kinematically distinct modes of knuckle-walking in *Gorilla* and *Pan* (Inouye, 1992,1994).

The present study yields information regarding the pattern of loading and weight distribrution across all four lateral metacarpal heads. As described above, no interspecific differences exist in the frequency of second, third and fourth metacarpal use for support among knuckle-walkers, and gorillas are distinctive only in their habitual use of MV in knuckle-walking stance. Examination of joint surface morphology however, reveals that the disparity in curvature across the head of MV is *less* than that of MII in *all* African apes, including gorillas, implying that this digit does not play a significant role in support of body weight. The contrast in ventral to dorsal curvature across the profiles of MIII and MIV suggest that these rays are the primary weight bearing rays in all knuckle-walkers, despite the more equal metacarpal lengths of gorillas. These results support Susman's (1979) earlier findings that many of the "classic" knuckle-walking characters of African apes are typically found on MIII and MIV.

The functional significance of greater dorsal head curvature in MIII and MIV may have to do with the requirement for increased hyperextension capabilities in knuckle-walkers. Extreme hyperextension of the proximal phalanx accords greater mechanical efficiency to the forelimb acting as a prop by allowing the metacarpal to align with the longitudinal axis of the radius during stance phase. This permits even weight distribution across the proximal metacarpal surfaces at the carpometacarpal joints and prevents shearing. Extreme ranges of hyperextension at the metacarpophalangeal joint are also conducive to optimizing propulsion by effectively increasing the stride length of the forelimb as the weight of the body is brought foreward over the supporting hand. This may be particularly important to gorillas who use highly pronated postures and place their hands perpendicular to the line of forward progression, rather than obliquely as in chimps and bonobos.

The final question to be addressed is whether the shape of the proximal articular surface of the proximal phalanx is more oval in African apes as compared to Asian apes, indicating reduced axial rotation at the metacarpophalangeal joint and increased stability in close packed positioning. The results presented here show that gorillas and chimps are most similar to humans and arboreal monkeys in having more oval proximal articular surfaces than

Asian apes. Of particular interest is the close relationship of bonobos to orangs and gibbons in proximal phalangeal articular morphology. Bonobos share with Asian apes a much more rounded articular shape, which permits greater ranges of axial rotation about the metacarpophalangeal joint and is important to arboreal animals engaging in high frequencies of suspensory and climbing behaviours. This accords well with Susman's (1979) and Inouye's (1992) findings that bonobos are intermediate between chimps and orangs in having a more "arboreal" finger morphology overall. Specifically, they note the thicker metacarpal shaft cortices, the less well-defined knuckle-walking characters such as large epicondyles and dorsal ridges on the metacarpal heads, the reduced metacarpal and phalangeal midshaft diameters, and the more curved proximal phalanges of bonobos as compared to other African apes. This analysis has shown that bonobo MIII joint surface morphology closely resembles that of other African apes and possesses a high degree of disparity in ventral to dorsal curvature of the head. At the same time, the third proximal phalanx does not exhibit the morphology typical of other knuckle-walkers, in that its proximal articular surface is much more rounded. This suggests that bonobo morphology reflects a compromise between terrestrial knuckle-walking behaviours and the need for increased mobility of the metacarpophalangeal joint neccessary for arboreal activity.

The fact that gorillas, chimps, humans and arboreal monkeys are not significantly different in the shape of the articular surface of the proximal phalanx implies that an oval shape is not a knuckle-walking character *per se*, but may represent a retained primitive character and bonobos have secondarily acquired a more rounded shape adaptive to higher frequencies of arboreal activities. Conversely, it is more likely that bonobos have retained a primitive hominoid condition of rounded morphology characteristic of Asian apes, and gorillas, chimps and humans are derived in having oval proximal articular surfaces. An oval surface acccomodates the mediolaterally expanded dorsal aspect of the metacarpal heads typical of gorillas and chimps, but expressed to a lesser degree in bonobos. In addition, an elongated surface will inhibit axial rotation with the proximal phalanx in close packed, hyperextended position. Maximum contact between the proximal phalanx and metacarpal head is not only neccessary to reduce compressive joint stress, but accords greater stability to the metacarpophalangeal joint in knuckle-walking stance.

That humans share with gorillas and chimps a more oval shaped proximal articular surface may be the result of shared phylogenetic history. However, despite the fact that there are some similarities in gross morphological pattern of joint surface geometry across metacarpals, human metacarpal heads overall do not share a close resemblence to those of African apes. Human metacarpals are highly derived in terms of assymetry of the articular surfaces, and reflect secondarily derived adaptations to the requirements of manipulatory capabilities. Perhaps, rather than modifying the morphology of the proximal phalanx articular surface to accomodate increased ranges of motion about the metacarpophalangeal joint, humans have opted to redefine the morphology of the metacarpal heads.

Conclusions

This study of metacarpophalangeal morphology has attempted to define discreet characters of joint surface geometry that reflect knuckle-walking characters in African apes.

The results presented here have demonstrated that knuckle-walkers have a high disparity in ventral to dorsal curvature of the third and fourth metacarpal heads, and these represent the primary weight bearing rays of the hand. Highly curved dorsal aspects of MIII and MIV articular surfaces permit sliding translation of the proximal phalanx and extreme ranges of hyperextension at the metacarpophalangeal joint of African apes. The functional significance of hyperextension to knuckle-walkers is that it increases the mechanical efficiency of the forelimb acting as a supporting prop, and serves to increase stride length during the propulsive phase. Previous research has established that gorillas are distinguished among hominoids by having rays of more equal length. Observational studies have also shown that gorillas, to the exclusion of other knuckle-walkers, typically use the fifth digit for support in knuckle-walking stance. The hypothesis that body weight is evenly distributed across metacarpals II - V in gorillas is not supported by the present study however, since gorillas do not differ from chimps in the pattern of joint surface curvature across all metacarpals. Inouye (1994) has alluded to the fact that gorillas may, in some way, be more energetically efficient knuckle-walkers than either chimps or bonobos. Perhaps joint surface geometry, in the form of *more* highly curved dorsal aspects of MIII and MIV, is one such mechanism according gorillas greater efficiency in knuckle-walking and making them, in some small way, kinematically distinct from other African apes.

Table 4.1: Descriptive Statistics For Metacarpal Curvature and Arc lengths

Taxon (n)	Vent arc	Dors arc	Varc/mc	D arc/mc	V NRC	D NRC	VD NRC	V IA	D IA	VD IA
Gor MII(30)										
x	15.43	16.04	1.24	1.28	.5767	.5210	1.12	98.35	109.82	.9069
sd	2.15	2.24	.1427	.1387	.052	.056	.1662	8.92	11.64	.1369
cv	13.94	13.97	11.51	10.75	9.02	11.32	14.84	9.07	10.60	15.06
Gor MIII(30)										
x	16.23	17.24	1.28	1.35	.6150	.4653	1.34	92.10	123.13	.7548
sd	2.18	2.44	.1002	.1088	.053	.039	.2024	8.00	10.41	.1014
cv	13.43	14.16	7.83	8.06	8.62	8.38	15.10	8.68	8.45	13.43
Gor MIV(30)										
x	14.67	16.07	1.16	1.27	.6577	.4577	1.45	85.88	124.29	.6983
sd	1.98	2.16	.099	.1151	.073	.037	.2288	9.22	10.70	.1131
cv	13.50	13.44	8.55	9.06	11.10	8.08	15.78	10.74	8.61	16.20
Gor MV(30)										
x	13.71	14.33	1.08	1.13	.5427	.5510	.9973	104.14	103.35	1.022
sd	2.03	2.31	.075	.086	.037	.063	.1306	7.02	11.21	.1515
cv	14.81	16.12	6.94	7.61	6.82	11.43	13.09	6.74	10.85	15.12
Chimp										
MII(25)	13.22	13.95	1.36	1.44	.6012	.5184	1.18	93.74	110.10	.8651
x	1.11	1.23	.1177	.1437	.042	.067	.1586	6.27	14.16	.1274
sd	8.40	8.82	8.65	10.05	6.99	13.12	13.56	6.69	12.85	14.73
cv										

Taxon (n)	Vent arc	Dors arc	Varc/mc	D arc/mc	V NRC	D NRC	VD NRC	V IA	D IA	VD IA
Chimp										
MIII(25)	13.99	14.93	1.43	1.53	.6360	.4828	1.33	88.57	118.24	.7583
x	1.37	1.44	.1487	.1629	.050	.051	.1329	6.51	12.30	.0860
sd	9.79	9.58	10.40	10.65	7.86	10.56	9.99	7.35	10.40	11.34
cv										
Chimp										
MIV(22)	12.92	14.07	1.45	1.58	.6500	.4836	1.36	86.78	117.60	.7558
x	1.07	1.49	.3892	.4427	.057	.052	.1991	7.39	13.24	.1112
sd	8.28	10.59	26.84	28.02	8.77	10.75	14.64	8.52	11.26	14.71
cv										
Chimp										
MV(20)	10.89	11.43	1.22	1.28	.5820	.5295	1.12	97.33	107.21	.9315
x	1.21	1.38	.4284	.4411	.066	.057	.2206	10.06	12.55	.1631
sd	11.11	12.07	35.11	34.46	11.34	10.76	19.70	10.34	11.71	17.51
cv										
Bono										
MII(13)	13.56	14.34	1.44	1.50	.5500	.4985	1.11	101.65	114.92	.8953
x	1.86	2.02	.1453	.1625	.035	.058	.1297	5.41	14.14	.1031
sd	13.72	14.09	10.09	10.83	6.36	11.63	11.68	5.32	12.30	11.52
cv										
Bono										
MIII(13)	13.19	14.07	1.57	1.67	.5938	.4538	1.31	95.05	125.26	.7608
x	1.04	1.29	.1518	.1505	.066	.039	.1394	11.25	9.62	.088
sd	7.88	7.88	9.67	9.01	11.12	8.59	10.56	11.82	7.68	11.57
cv										

Taxon (n)	Vent arc	Dors arc	Varc/mc	D arc/mc	V NRC	D NRC	VD NRC	V IA	D IA	VD IA
Bono MIV(13) x sd cv	12.48 1.19 9.53	13.31 1.04 7.81	1.48 .1214 8.20	1.58 .1330 8.42	.5808 .042 7.23	.4654 .033 7.09	1.25 .1195 9.56	95.97 7.79 8.12	120.70 8.00 6.63	.7984 .083 10.39
Bono MV(12) x sd cv	10.22 .8169 7.99	10.83 1.26 11.63	1.22 .075 6.15	1.30 .1151 8.85	.5433 .029 5.15	.5100 .055 10.78	1.08 .1504 13.94	102.67 5.60 5.45	110.27 12.25 11.11	.9436 .1319 13.98
Pongo MII(11) x sd cv	13.56 1.86 13.72	14.34 2.02 14.09	1.34 .1250 9.33	1.42 .1423 10.02	.5682 .051 8.80	.5227 .065 12.43	1.10 .1467 13.34	99.48 9.03 9.08	109.15 13.23 12.11	.9221 .1305 14.15
Pongo MIII(12) x sd cv	13.17 1.83 13.9	13.76 1.86 13.52	1.32 .1297 9.83	1.38 .1469 10.57	.6017 .056 9.31	.5658 .074 13.08	1.08 .1407 13.15	94.62 9.64 10.18	102.23 13.60 13.30	.9369 .1233 13.16
Pong MIV(8) x sd cv	12.38 1.45 11.71	13.08 1.49 11.39	1.28 .1051 8.21	1.35 .1054 7.81	.6325 .058 9.17	.5725 .038 6.64	1.11 .1183 10.66	88.70 9.61 10.83	99.20 7.26 7.32	.8968 .099 11.02

Taxon (n)	Vent arc	Dors arc	Varc/mc	D arc/mc	V NRC	D NRC	VD NRC	V IA	D IA	VD IA
Pong MV(8)										
x	11.83	12.54	1.22	1.29	.6025	.5475	1.11	93.28	103.34	.9096
sd	1.28	1.55	.1132	.1205	.076	.043	.1514	10.37	8.83	.1391
cv	10.82	12.36	9.28	9.34	12.61	7.85	13.64	11.11	8.54	15.29
Hum MII(10)	11.13	11.67	1.05	1.10	.6690	.6530	1.05	85.94	88.20	1.00
x	1.21	1.16	.044	.047	.041	.1021	.1936	5.26	13.6	.1971
sd	10.87	9.40	4.19	4.27	6.13	15.63	18.44	6.12	15.42	19.71
cv										
Hum MIII(10)	11.27	11.73	1.06	1.11	.7090	.6090	1.17	80.90	93.27	.8735
x	1.50	1.63	8.00	.086	.089	.053	.1703	10.07	8.52	.1347
sd	13.31	13.89	7.55	7.75	12.55	8.70	14.56	12.45	9.14	15.42
cv										
Hum MIV(10)	10.01	10.67	.9477	1.01	.7320	.6210	1.19	76.74	89.99	.8575
x	.9564	1.07	.063	.052	.072	.052	.1436	7.38	7.28	.1056
sd	9.55	10.03	6.65	5.25	9.84	8.21	12.07	9.62	8.09	12.32
cv										
Hum MV(10)										
x	9.09	9.41	.8614	.8907	.6300	.7170	.9003	90.00	79.63	1.16
sd	.8269	.9968	.060	.072	.078	.1273	.1760	12.32	15.48	.2443
cv	9.10	10.59	6.96	8.08	12.38	17.75	19.55	13.69	19.44	21.06

Taxon (n)	Vent arc	Dors arc	Varc/mc	D arc/mc	V NRC	D NRC	VD NRC	V IA	D IA	VD IA
Gibb MII(13)										
x	6.19	6.27	1.40	1.42	.5900	.7038	.8718	94.97	81.71	1.21
sd	.7891	.6855	.1441	.099	.061	.1330	.2228	11.46	17.14	.2620
cv	12.75	10.95	10.29	6.97	10.34	18.90	25.56	12.08	20.97	21.65
Gibb MIII(11)										
x	5.99	6.08	1.36	1.38	.5809	.6773	.9052	96.50	85.09	1..21
sd	.6393	.5814	.1319	.1328	.065	.1705	.2335	11.59	20.05	.3800
cv	10.67	9.56	9.70	9.62	11.19	25.17	25.79	12.00	23.56	31.41
Gibb MIV(12)										
x	5.51	5.66	1.25	1.29	.5917	.6492	.9474	93.74	87.29	1.12
sd	.5254	.4773	.1210	.070	.056	.1367	.2137	10.18	16.51	.2863
cv	9.54	8.43	9.68	5.43	9.46	21.06	22.56	10.86	18.91	25.56
Gibb MV(12)										
x	4.74	4.96	1.07	1.12	.5617	.6217	.9188	99.98	89.41	1.14
sd	.5049	.6028	.1026	.1407	.071	.088	.1615	10.52	12.88	.2134
cv	10.65	12.15	9.59	11.53	12.64	14.15	17.58	10.52	14.41	18.72
Siam MII(3)										
x	7.25	7.11	1.46	1.42	.5800	.6500	.9031	99.28	87.14	1.16
sd	.9016	1.38	.1058	.1339	.1015	.098	.1918	17.67	13.34	.2647
cv	12.44	19.41	7.25	9.43	17.50	15.08	21.24	17.80	15.31	22.82

Taxon (n)	Vent arc	Dors arc	Varc/mc	D arc/mc	V NRC	D NRC	VD NRC	V IA	D IA	VD IA
Siam MIII(3)										
x	7.64	7.70	1.51	1.52	.5800	.5933	.9933	100.88	92.73	1.10
sd	1.94	1.92	.097	.098	.1114	.071	.2513	21.59	7.72	.3100
cv	25.39	24.93	6.42	6.38	19.21	11.97	25.30	21.40	8.31	28.18
Siam MIV(3)										
x	6.78	6.59	1.35	1.31	.6100	.5800	1.06	90.88	97.55	.9418
sd	1.36	1.28	.050	.028	.066	.046	.1933	9.42	8.45	.1769
cv	20.06	19.42	3.70	2.13	10.82	7.93	18.24	10.38	8.66	18.78
Siam MV(3)										
x	5.68	5.10	1.14	1.02	.6033	.6667	.9334	96.27	82.93	1.18
sd	1.27	.6755	.1927	.086	.1620	.080	.3716	22.20	8.26	.3617
cv	22.36	13.25	16.90	8.43	26.72	12.15	34.03	23.07	9.96	30.65
AQ MII(5)										
x	6.25	6.32	1.18	1.20	.5200	.5040	1.03	106.37	110.75	.9605
sd	.4625	.1076	.1136	.1130	.069	.046	.067	9.80	9.11	.049
cv	7.40	1.70	9.63	9.42	13.27	9.13	6.51	9.21	8.23	5.10
AQ MIII(6)										
x	6.59	6.85	1.24	1.29	.5667	.4883	1.56	100.47	115.65	.8684
sd	.3869	.5224	.1640	.1870	.1154	.067	.1168	17.57	15.03	.1047
cv	5.87	7.63	13.23	14.50	20.36	13.72	10.07	17.49	13.00	12.06
AQ MIV(5)										
x	6.63	6.87	1.26	1.31	.5180	.4760	1.09	107.43	116.31	.9269
sd	.3006	.3817	.1581	.1619	.047	.053	.063	8.53	13.10	.046
cv	4.53	5.57	12.55	12.56	9.07	11.28	5.78	7.94	11.26	4.96

Taxon (n)	Vent arc	Dors arc	Varc/mc	D arc/mc	V NRC	D NRC	VD NRC	V IA	D IA	VD IA
AQ MV(4)										
x	6.08	6.17	1.14	1.16	.4925	.5050	.9815	112.71	111.32	1.02
sd	.4934	.3999	.1689	.1630	.069	.073	.1215	14.94	17.21	.1245
cv	8.12	6.48	14.82	14.05	14.01	14.46	12.37	13.26	15.47	12.21
TQ MII(11)										
x	6.83	7.01	1.13	1.16	.5536	.4982	1.12	101.88	113.13	.9076
sd	.8449	.9165	.063	.093	.067	.038	.1604	12.01	9.54	.1437
cv	12.37	13.09	5.58	8.02	12.10	7.63	14.45	11.79	8.43	15.83
TQ MIII(10)										
x	6.92	7.19	1.14	1.18	.6070	.5120	1.19	94.65	110.09	.8659
sd	.7327	.7728	.095	.093	.1060	.048	.1914	14.14	10.38	.1536
cv	10.59	10.75	8.33	7.88	17.46	9.57	16.08	14.94	9.43	17.74
TQ MIV(11)										
x	6.84	7.20	1.13	1.19	.5555	.4918	1.13	101.54	113.51	.8964
sd	.8508	.9286	.079	.087	.059	.026	.1261	9.93	5.06	.099
cv	12.44	12.90	6.99	7.31	10.62	5.29	11.16	9.78	4.46	11.04
TQ MV(11)										
x	6.47	6.54	1.07	1.08	.5491	.5191	1.07	105.03	107.20	.9920
sd	.9025	.8133	.070	.064	.1144	.032	.2527	20.63	8.32	.2468
cv	13.95	12.43	6.54	5.93	20.83	6.16	23.62	19.64	7.68	24.88

n = number; arc length measured in mm; mc = metacarpal composite; NRC = normalized radius of curvature; IA = included angle, measured in degrees;
V= ventral; D= dorsal; VD = ratio of ventral/dorsal; x = mean; sd = standard deviation; cv = coefficient of variation, expressed as a percent

Table 4.2: Descriptive Statistics For the Proximal Phalanx

Taxon(n)	PAS Area	PAS / mc	PAS Area/msb	PAS BW	PAS Shape
Gorilla(29)					
x	212.09	16.34	11.68	1.32	.8576
sd	64.38	3.19	2.31	.1775	.02
cv	30.34	19.52	19.78	13.45	2.33
Chimp(13)					
x	119.65	12.95	9.92	1.26	.8692
sd	18.48	1.77	1.77	.073	.01
cv	15.45	13.67	17.84	5.79	1.59
Bonobo(12)					
x	108.84	12.76	10.69	1.07	.8817
sd	13.34	1.18	1.39	.081	.014
cv	12.26	9.25	13.00	7.58	1.59
Pongo(7)					
x	138.25	14.38	12.49	1.02	.8857
sd	33.73	2.43	2.11	.059	.011
cv	24.40	16.90	16.89	5.87	1.24
Human(10)					
x	109.81	10.30	10.65	1.36	.8630
sd	23.96	1.44	1.51	.1735	.012
cv	21.82	13.89	14.08	12.76	1.39
Gibbon(13)					
x	31.70	7.13	5.95	1.08	.8869
sd	5.06	.6316	.9772	.062	.075
cv	16.96	8.86	16.42	5.73	8.46
Siamang(3)					
x	45.59	8.80	6.83	.9533	.8900
sd	21.45	2.41	1.5	.061	.010
cv	47.05	29.39	21.96	6.30	1.12
AQ(6)					
x	32.46	5.96	5.84	1.35	.8500
sd	8.86	1.00	1.21	.1115	.054
cv	27.29	16.78	20.72	8.26	6.35
TQ(10)					
x	36.13	5.85	6.34	1.51	.8300
sd	9.56	.9255	1.59	.1104	.025
cv	26.46	15.82	25.24	7.31	3.01

(n) = number; PAS = proximal articular surface; msb = midshaft breadth; BW = breadth/width ratio; shape = shape variable calculated by *Mocha* from perimeter measures, value of 1.0 represents a circle, lower values are increasingly oval.

TABLE 4.3: Summary of Spearman Rank Order Correlations

MEASURE	MII	MIII	MIV	MV
Mcall * Ventral Arclength	***	***	***	***
Mcall * Dorsal Arc length	***	***	***	***
Mcall * Ventral NRC	ns	**	***	ns
Mcall * Dorsal NRC	*	***	***	ns
Ventral Arc * Ventral NRC	ns	ns	**	ns
Dorsal Arc * Dorsal NRC	***	***	***	***
Ventral NRC * Dorsal NRC	*	ns	ns	ns

Mcall = metacarpal composite body size surrogate, * p <= 0.05, ** p <= 0.01, *** p <= 0.001

NRC = Normalized Radius of Curvature

Table 4.4: Summary of Mann-Whitney U-test Pairwise Comparisons For MIII and MIV Arc Length Z-scores and Arc Length/Metacarpal Size Ratio (* $p<=0.05$; ** $p<=.01$; *** $p<=.001$)

Taxa	MIII z-score ventral arc	MIII z-score dorsal arc	MIII vent arc/mc	MIII dors arc/mc	MIV z-score ventral arc	MIV z-score dorsal arc	MIV vent arc/mc	MIV dors arc/mc
Gor-Chimp	***	**	***	***	**	**	***	***
Gor-Bono	***	***	***	***	***	***	***	***
Gor-Pongo	***	***	ns	ns	**	**	**	*
Gor-Human	***	***	***	***	***	***	***	***
Gor-Gibb	***	***	*	ns	***	***	*	ns
Gor-AQ	***	***	ns	ns	***	***	ns	ns
Gor-TQ	***	***	***	***	***	***	ns	ns
Chimp-Bono	ns	*	*	**	ns	ns	*	ns
Chimp-Pongo	ns	ns	ns	*	ns	ns	ns	**
Chimp-Human	***	***	***	***	***	***	***	***
Chimp-Gibb	***	***	***	*	***	***	**	***
Chimp-AQ	***	***	***	*	***	***	ns	*
Chimp-TQ	***	***	***	***	***	***	***	**
Bono-Pongo	ns	ns	***	***	ns	ns	**	***
Bono-Human	**	**	***	***	***	***	***	***
Bono-Gibb	***	***	**	***	***	***	***	***
Bono-AQ	***	***	***	***	***	***	*	**
Bono-TQ	***	***	***	***	***	***	***	***
Pongo-Human	*	*	***	***	**	**	***	***
Pongo-Gibb	***	***	ns	ns	***	***	ns	ns
Pongo-AQ	***	***	ns	ns	**	**	ns	ns
Pongo-TQ	***	***	**	**	***	***	**	**
Human-Gibb	***	***	***	***	***	***	***	***
Human-AQ	***	***	*	ns	**	**	**	**
Human-TQ	***	***	ns	ns	***	***	***	***

Taxa	MIII z-score ventral arc	MIII z-score dorsal arc	MIII vent arc/mc	MIII dors arc/mc	MIV z-score ventral arc	MIV z-score dorsal arc	MIV vent arc/mc	MIV dors arc/mc
Gibb-AQ	*	**	ns	ns	**	***	ns	ns
Gibb-TQ	**	***	***	**	***	***	**	**
AQ-TQ	ns	ns	ns	ns	ns	ns	ns	*

Table 4.5: Summary of Mann-Whitney U-test Pairwise Comparisons for MIII and MIV Head Curvatures

Taxa	MIII vent nrc	MIII dors nrc	MIII v/d nrc	MIV vent nrc	MIV dors nrc	MIV v/d nrc
Gor-Chimp	*	ns	ns	ns	*	ns
Gor-Bonobo	ns	ns	ns	***	ns	ns
Gor-Pongo	ns	***	***	ns	***	***
Gor-Human	***	***	●	**	***	***
Gor-Gibb	*	***	***	***	***	***
Gor-AQ	ns	ns	●	***	ns	***
Gor-TQ	ns	*	ns	**	**	***
Chimp-Bono	ns	*	ns	***	ns	ns
Chimp-Pongo	ns	**	**	ns	***	**
Chimp-Human	**	***	*	**	***	*
Chimp-Gibb	**	***	***	*	***	***
Chimp-AQ	ns	ns	**	***	ns	**
Chimp-TQ	ns	ns	ns	***	ns	***
Bono-Pongo	ns	***	***	*	***	*
Bono-Human	**	***	**	***	***	ns
Bono-Gibb	ns	***	***	ns	***	***
Bono-AQ	ns	ns	*	*	ns	*
Bono-TQ	ns	**	ns	ns	*	*
Pongo-Human	**	*	ns	**	ns	ns
Pongo-Gibb	ns	*	*	ns	ns	ns
Pongo-AQ	ns	*	ns	**	*	ns
Pongo-TQ	ns	*	ns	*	**	ns
Human-Gibb	***	ns	ns	***	ns	*
Human-AQ	*	**	**	**	**	ns
Human-TQ	*	**	**	***	***	ns
Gibb-AQ	ns	**	*	*	**	ns
Gibb-TQ	ns	**	**	ns	***	*
AQ-TQ	ns	ns	ns	ns	ns	ns

* p<= 0.05; ** p<=0.01; *** p<=.001

Table 4.6: Summary of Mann-Whitney U-test Pairwise Comparisons of Proximal Phalanx Measures

Taxa	Z-score PAS	PAS/MC	PASBW	PAS shape	Area/msb
Gor-Chimp	***	***	ns	ns	*
Gor-Bono	***	***	***	***	ns
Gor-Pongo	**	ns	***	***	ns
Gor-Human	***	***	ns	ns	ns
Gor-Gibb	***	***	***	***	***
Gor-AQ	***	***	ns	ns	***
Gor-TQ	***	***	***	**	***
Chimp-Bono	ns	ns	***	*	ns
Chimp-Pongo	ns	ns	***	**	*
Chimp-Human	ns	**	ns	ns	ns
Chimp-Gibb	***	***	***	***	***
Chimp-AQ	***	***	ns	ns	***
Chimp-TQ	***	***	***	***	***
Bono-Pongo	*	ns	ns	ns	*
Bono-Human	ns	**	***	**	ns
Bono-Gibb	***	***	ns	ns	***
Bono-AQ	***	***	***	ns	***
Bono-TQ	***	***	***	***	***
Pongo-Human	*	**	***	**	ns
Pongo-Gibb	***	***	ns	ns	***
Pongo-AQ	**	**	**	ns	**
Pongo-TQ	***	***	***	***	***
Human-Gibb	***	***	***	***	***
Human-AQ	***	***	ns	ns	***
Human-TQ	***	***	*	***	***
Gibb-AQ	ns	*	***	*	ns
Gibb-TQ	ns	**	***	***	ns
AQ-TQ	ns	ns	*	ns	ns

PAS= proximal phalanx proximal articular surface; PASBW= proximal articular surface breadth/width ratio; PAS shape= shape variable calculated by *Mocha* whereby a value of 1.0 represents a perfect circle; Area/msb= proximal articular surface area divided by midshaft breadth of phalanx shaft.

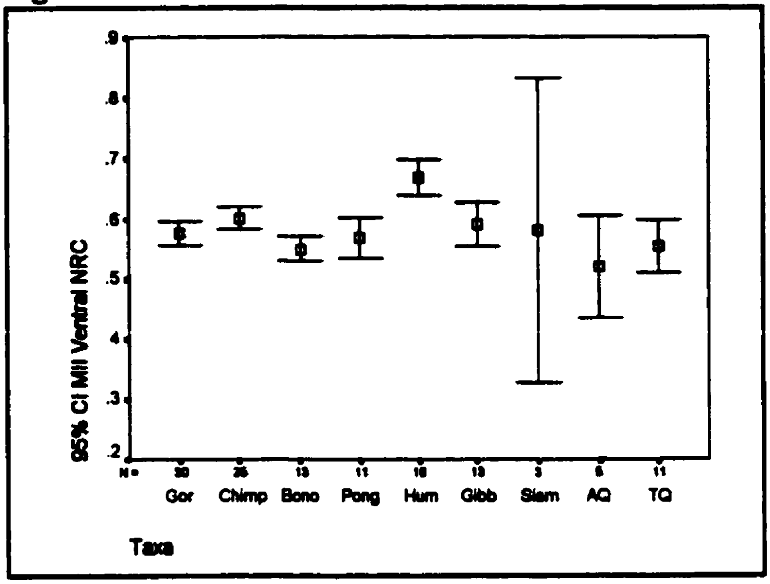
Table 4.7: Regression Results of Metacarpal and Proximal phalanx against Metacarpal Composite Size

bone	measure	*r*	*slope	95% CI	y-intercept	95% CI
MII	vent arc	.930	.908	.843 - .973	.195	.133 - .265
			(.978)	(.911 - 1.044)	(.129)	(.066 - .192)
	dors arc	.931	.939	.872 - 1.006	.181	.118 - .245
			(1.010)	(.942 - 1.078)	(.116)	(.051 - .180)
MIII	vent arc	.879	.885	.798 - .972	.229	.147 - .312
			(1.008)	(.919 - 1.097)	(.114)	(.029 - .198)
	dors arc	.878	.922	.831 - 1.012	.216	.130 - .302
			(1.047)	.955 - 1.140)	(.098)	(.010 - .186)
MIV	vent arc	.898	.868	.788 - .947	.216	.141 - .291
			(.995)	(.925 - 1.064)	(.100)	(.036 - .164)
	dors arc	.901	.923	.841 - 1.006	.193	.115 - .271
			(1.034)	(.961 - 1.106)	(.093)	(.027 - .159)
MV	vent arc	.917	.914	.838 - .990	.121	.048 - .193
			(1.000)	(.922 - 1.078)	(.041)	(-.033 - 114)
	dors arc	.912	.942	.861 - 1.023	.111	.035 - .188
			(1.032)	(.949 - 1.116)	(.027	(-.052 - .106)
PP	PAS	.955	.929	.872 - .986	.121	.067 - .174
			(.976)	(.918 - 1.034)	(.078)	(.023 - .132)

*** RMA results in brackets below OLS results**

PP = Proximal phalanx, PAS = proximal articular surface

Figure 4.1: MII Ventral NRC



*Center = Mean; bars represent 95% confidence interval (a range of values based on the sample mean that, with a 95% liklihood, include the population mean

Figure 4.2: MII Dorsal NRC

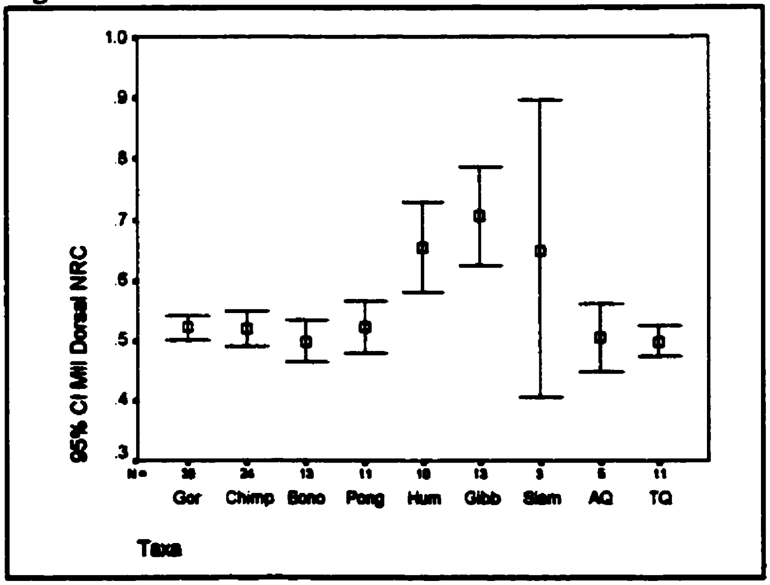
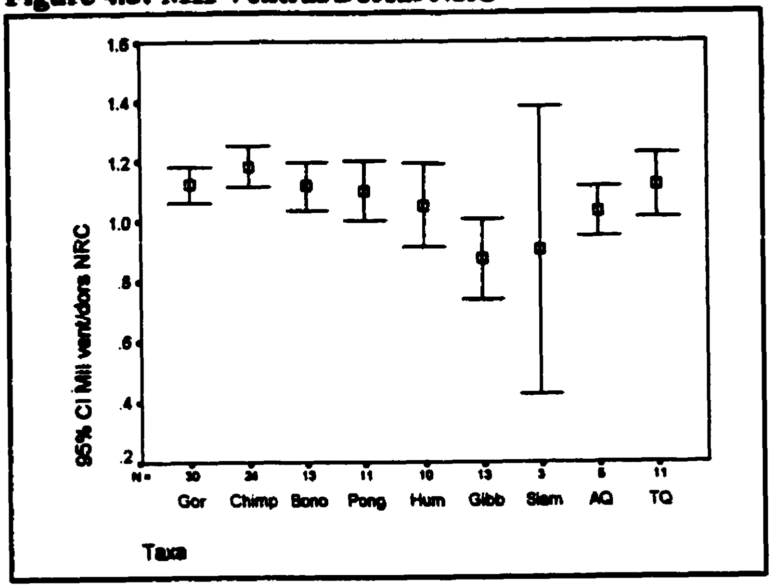


Figure 4.3: MII Ventral/Dorsal NRC



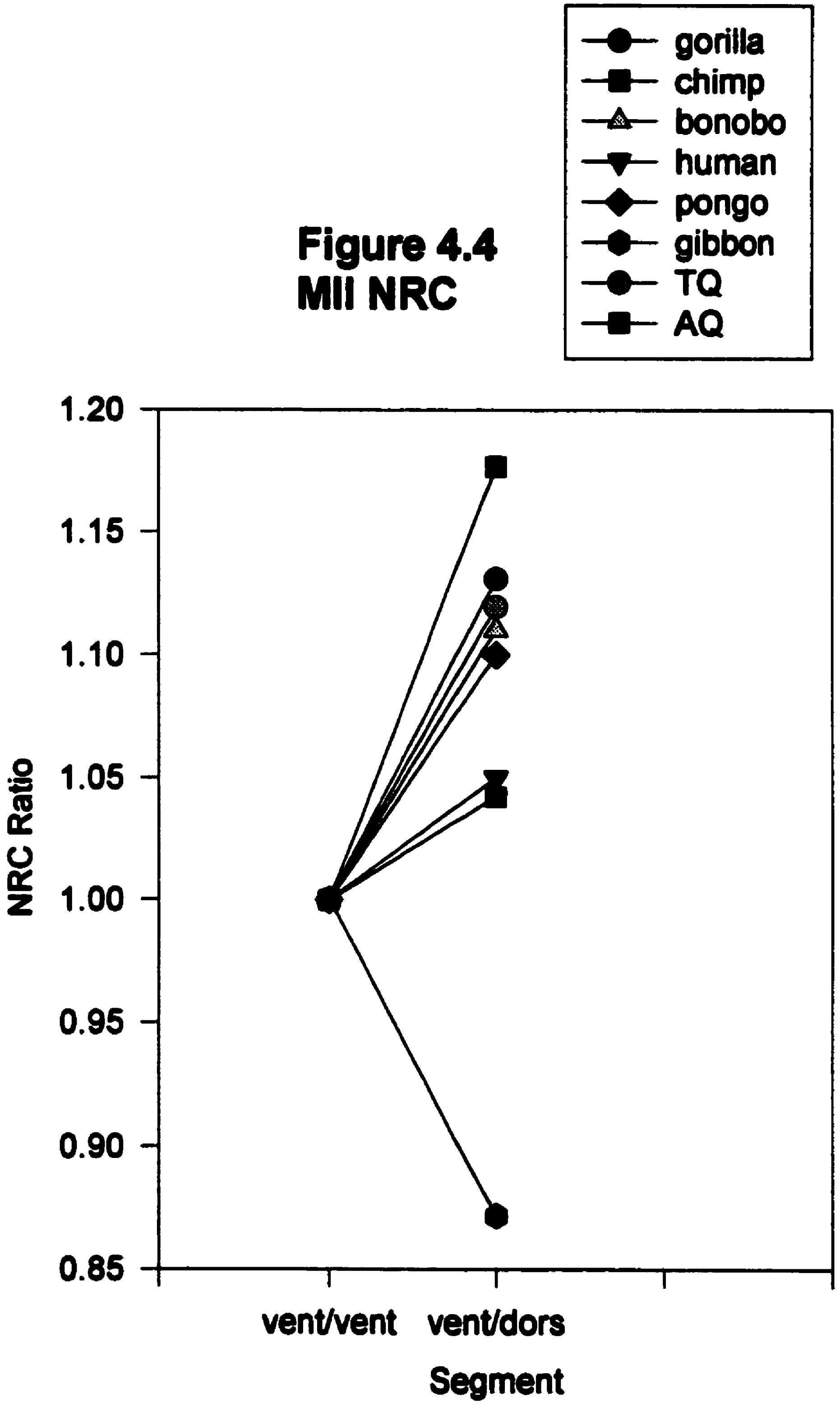


Figure 4.4
MII NRC

Figure 4.5: MII Z-scores for Dorsal Arc Length

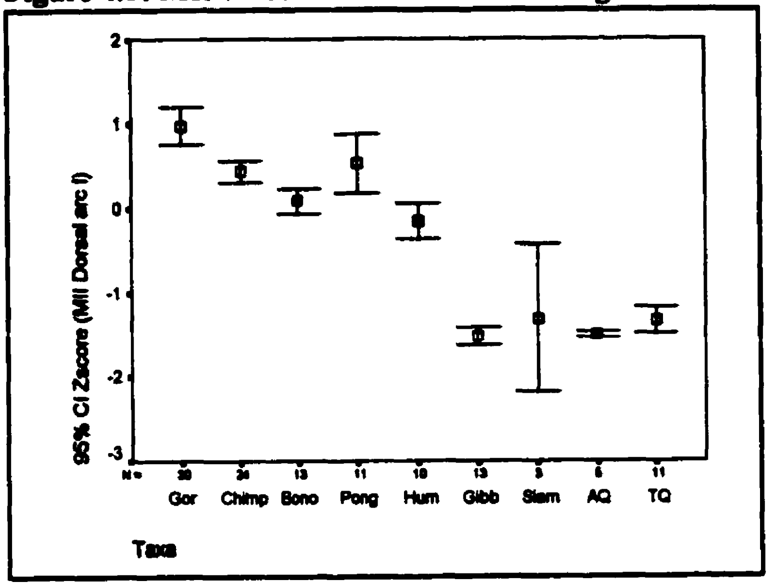


Figure 4.6: MII Dorsal Arc/Metacarpal Composite

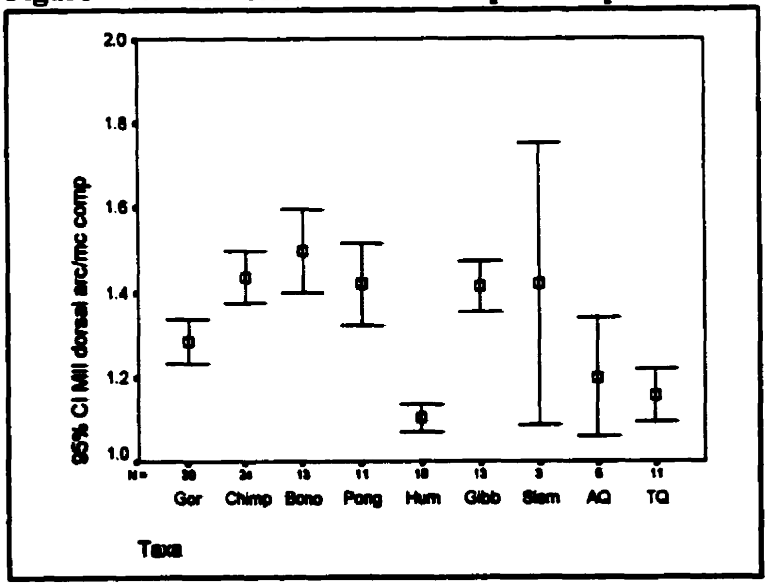


Figure 4.7: Regression of MII Dorsal Arc Length versus Metacarpal Composite

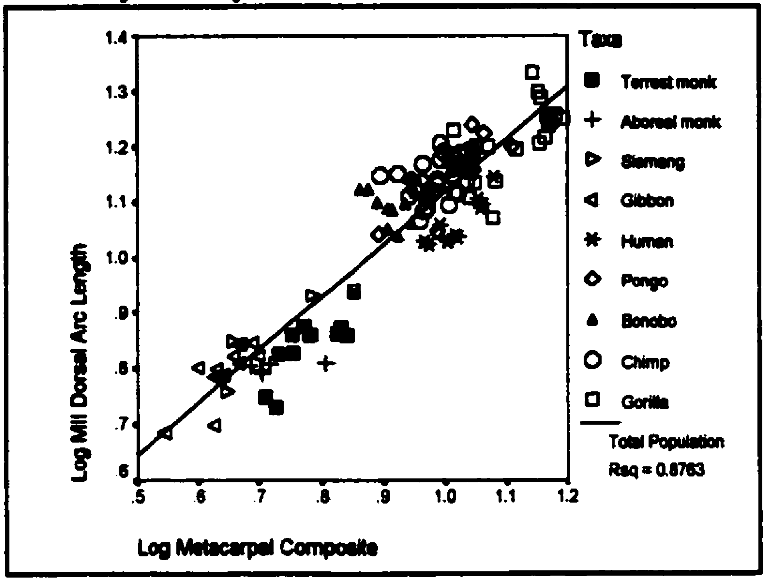


Figure 4.8: MIII Ventral NRC

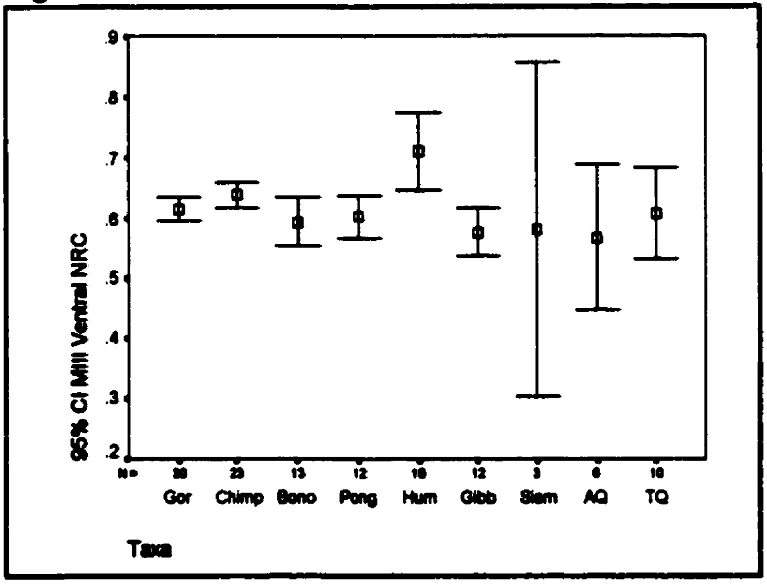


Figure 4.9: MIII Dorsal NRC

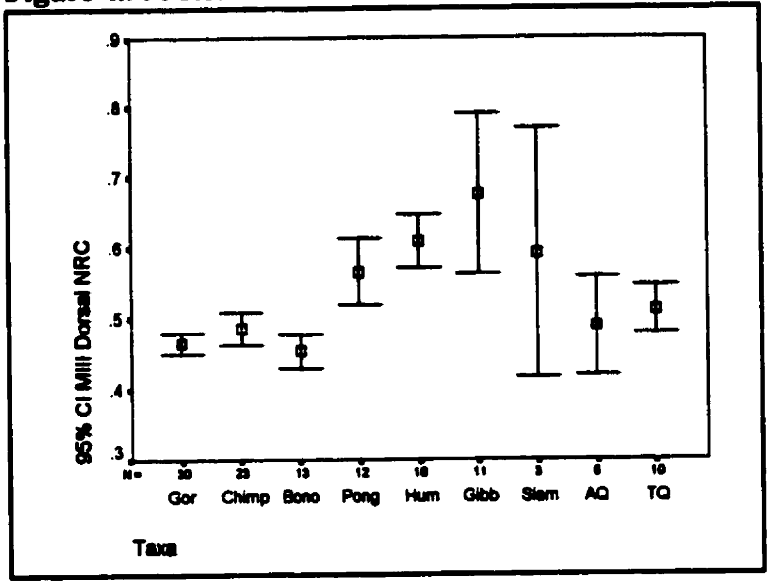


Figure 4.10: MIII Ventral to Dorsal NRC

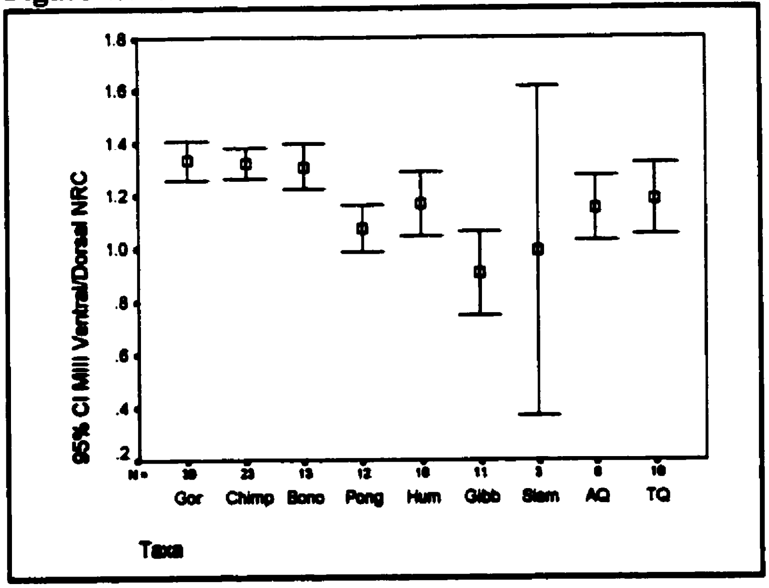


Figure 4.11
MIII NRC

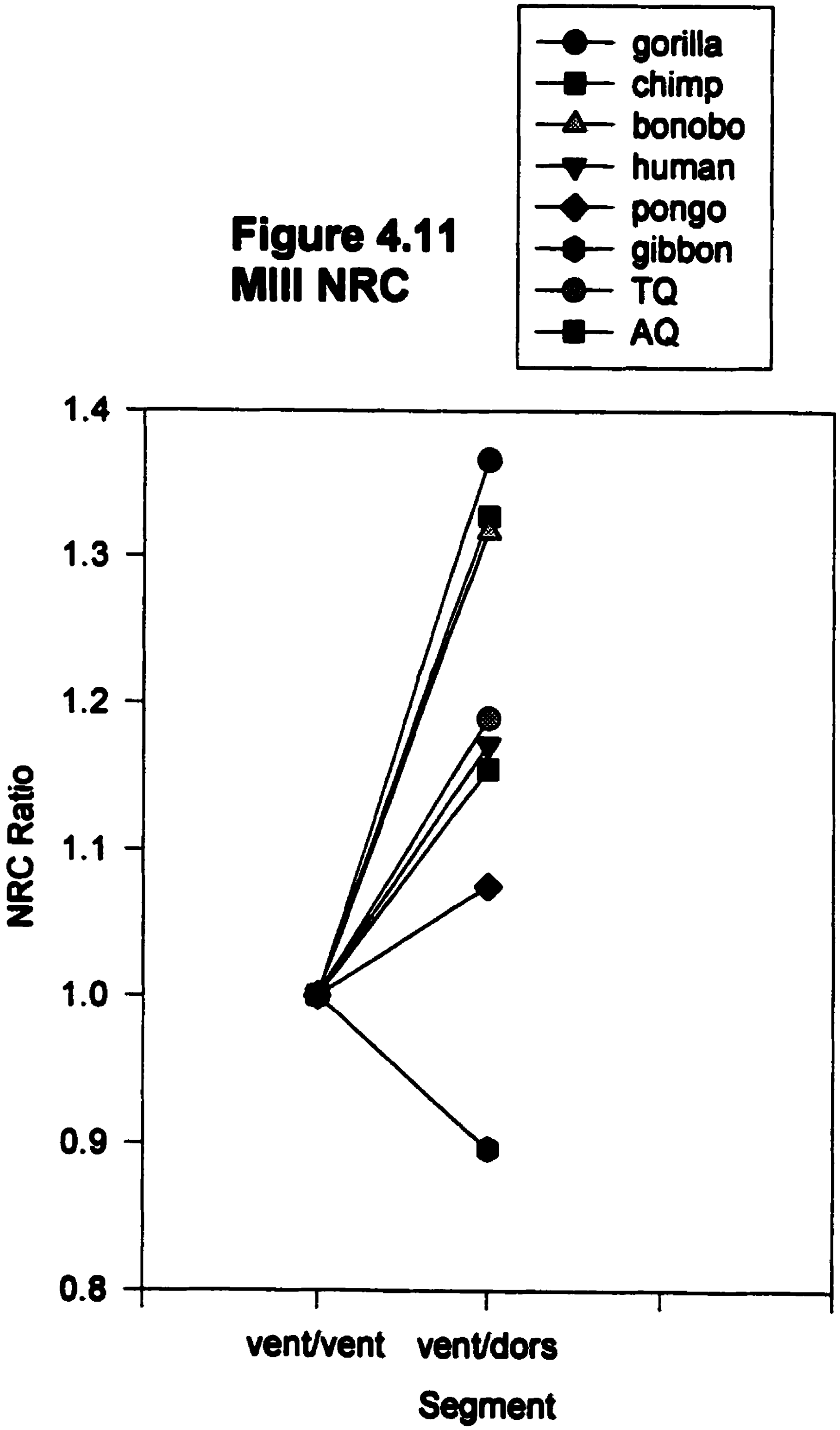


Figure 4.12: MIII Z-scores for Dorsal Arc Length

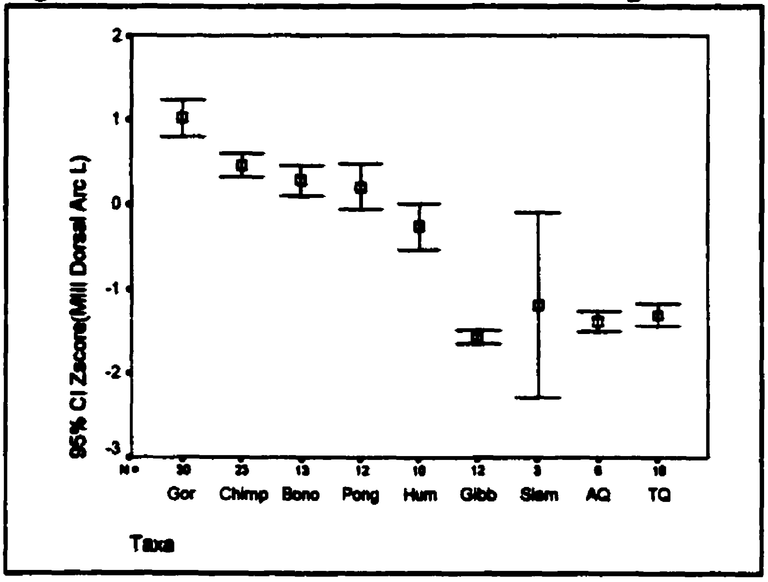


Figure 4.13: MIII Dorsal Arc/Metacarpal Composite

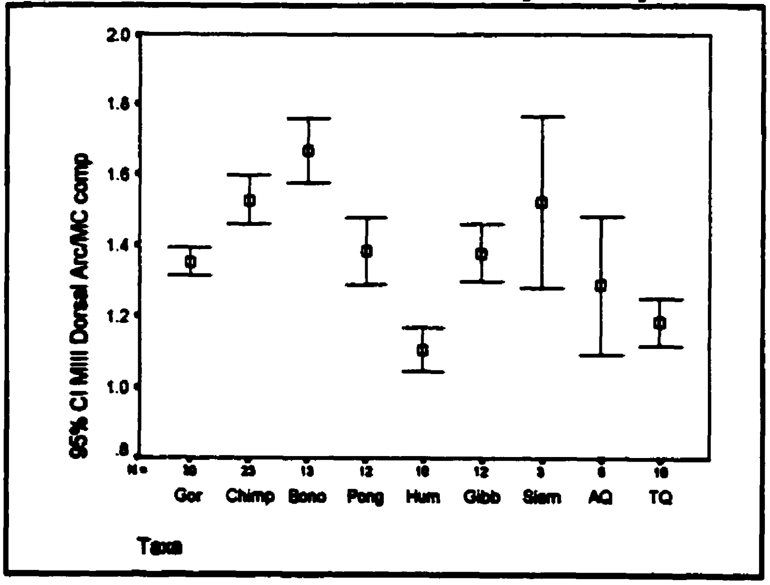


Figure 4.14: Regression of MIII Dorsal Arc Length versus Metacarpal Composite

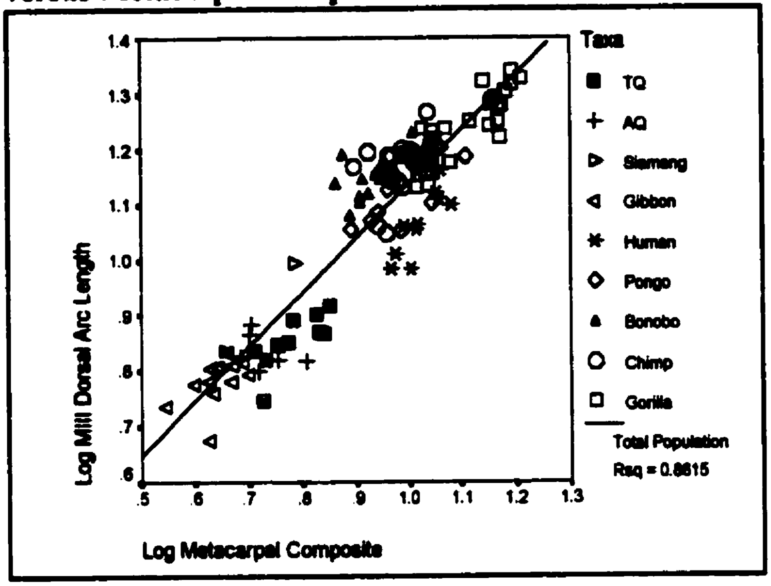


Figure 4.15: MIV Ventral NRC

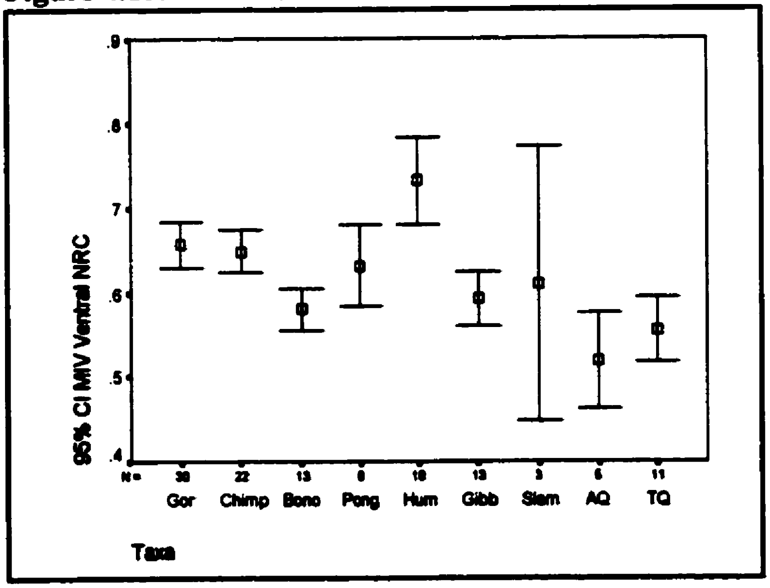


Figure 4.16: MIV Dorsal NRC

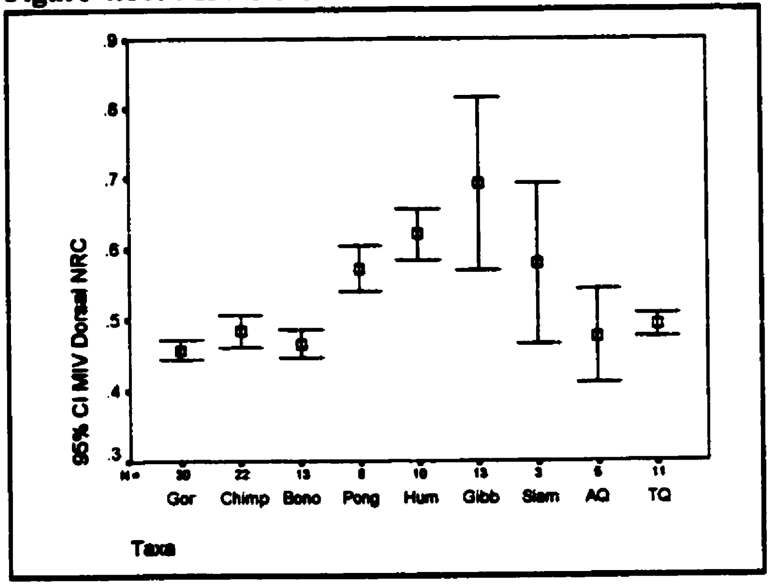
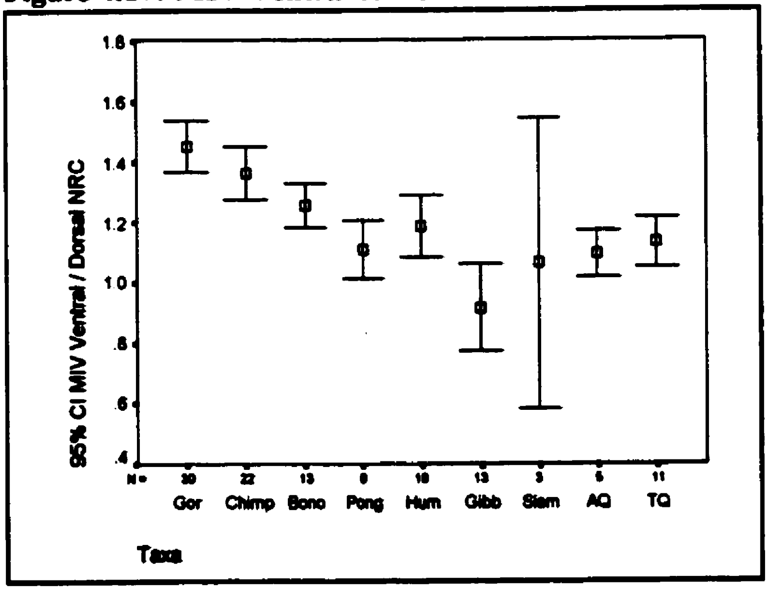


Figure 4.17: MIV Ventral to Dorsal NRC



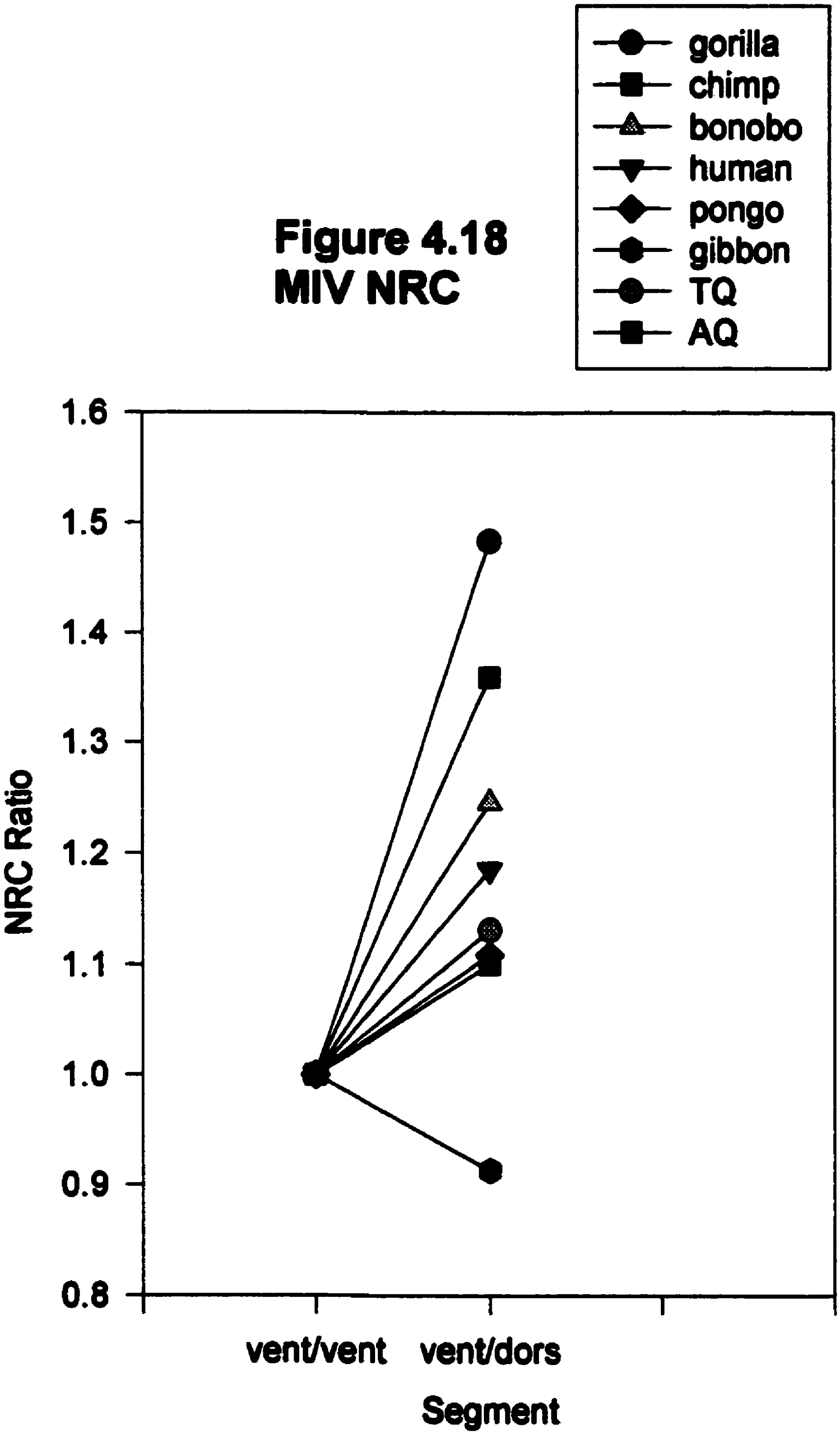


Figure 4.18
MIV NRC

Figure 4.19: MIV Z-scores for Dorsal Arc Length

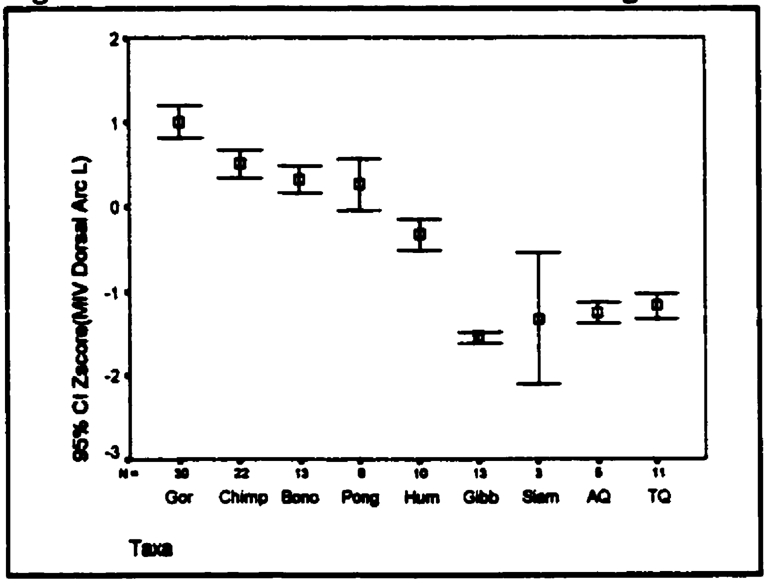


Figure 4.20: MIV Ventral Arc/Metacarpal Composite

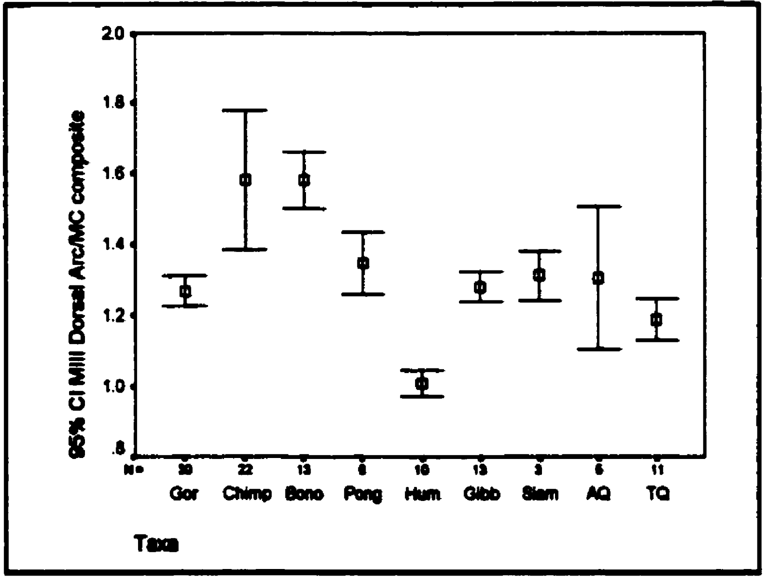


Figure 4.21: MIV Regression of Dorsal Arc Length versus Metacarpal Composite

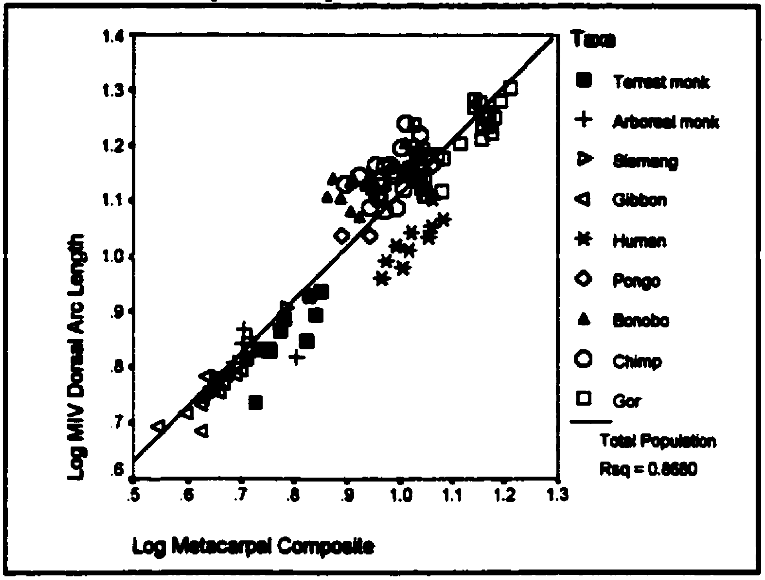


Figure 4.22: MV Ventral NRC

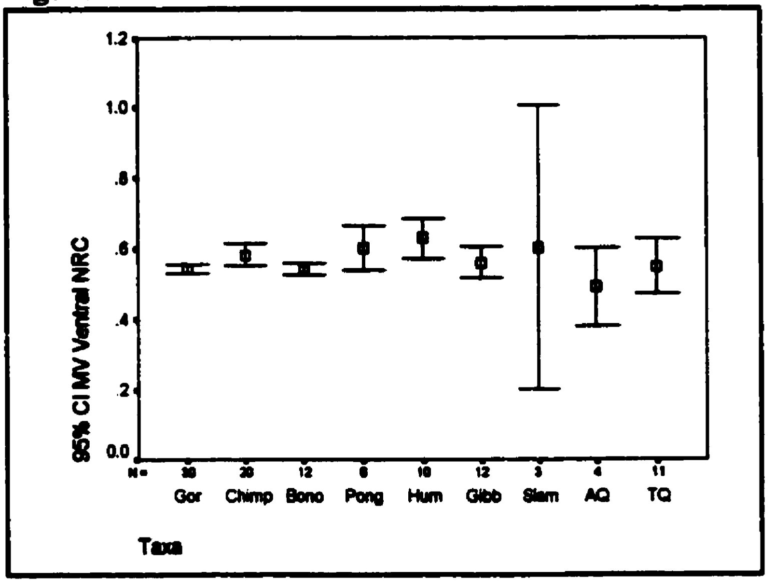


Figure 4.23: MV Dorsal NRC

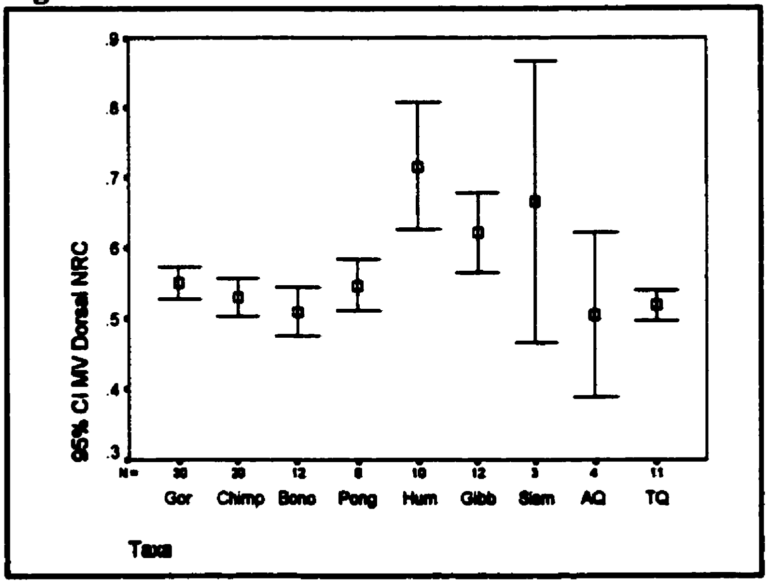


Figure 4.24: MV Ventral to Dorsal NRC

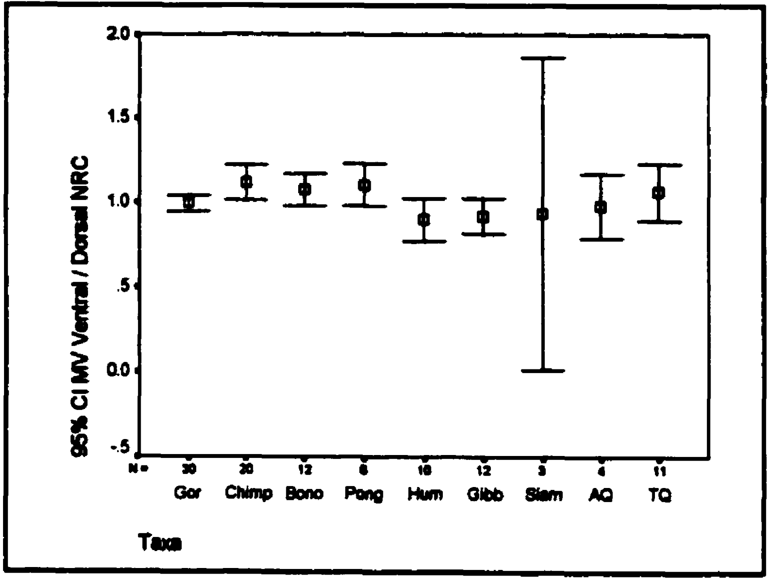


Figure 4.25
MV NRC

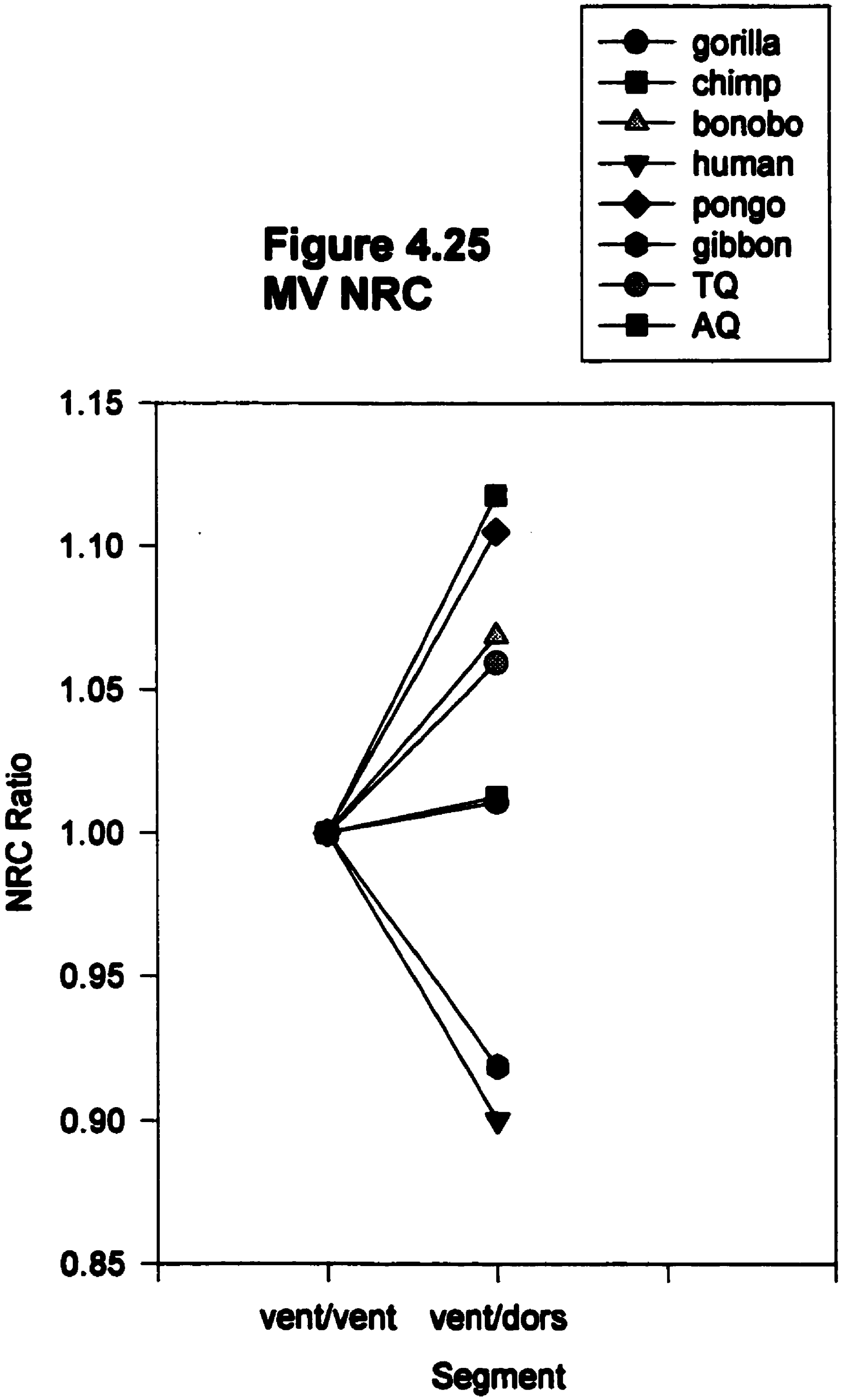


Figure 4.26: MV Z-scores for Dorsal Arc Length

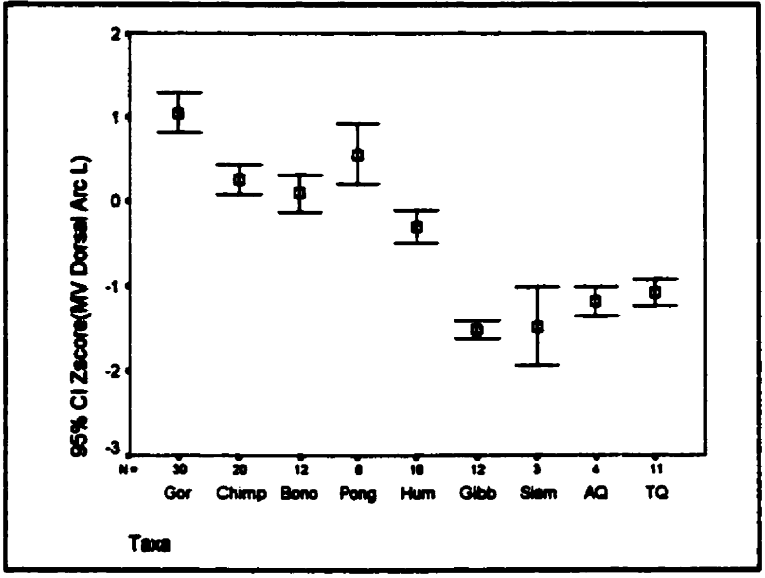


Figure 4.27: MV Dorsal Arc Length / Metacarpal Composite

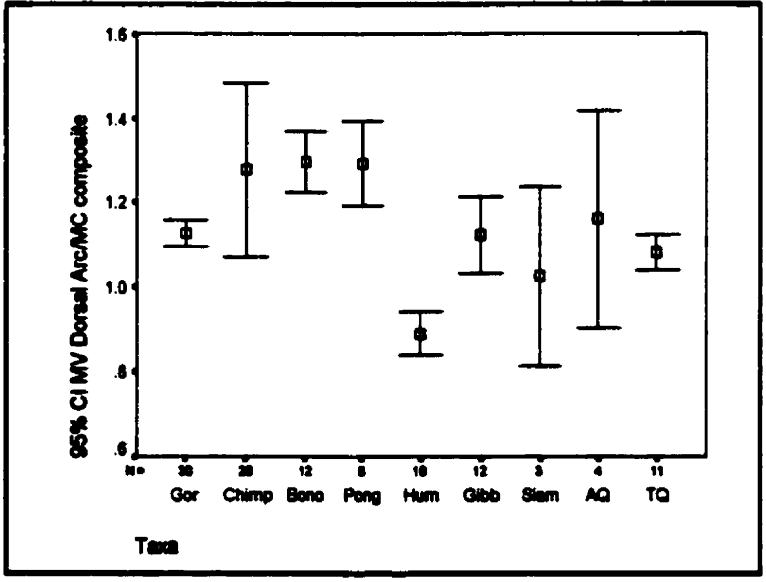


Figure 4.28: MV Regression of Dorsal Arc length versus Metacarpal Composite

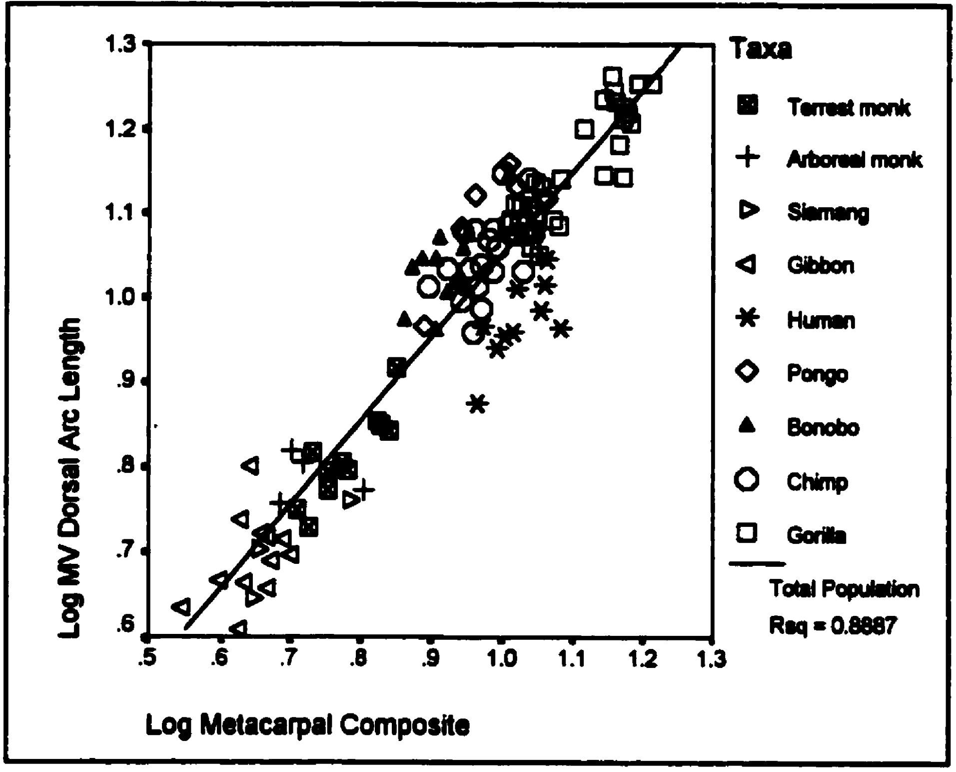


Figure 4.29
Ventral Curvature
MII-MV

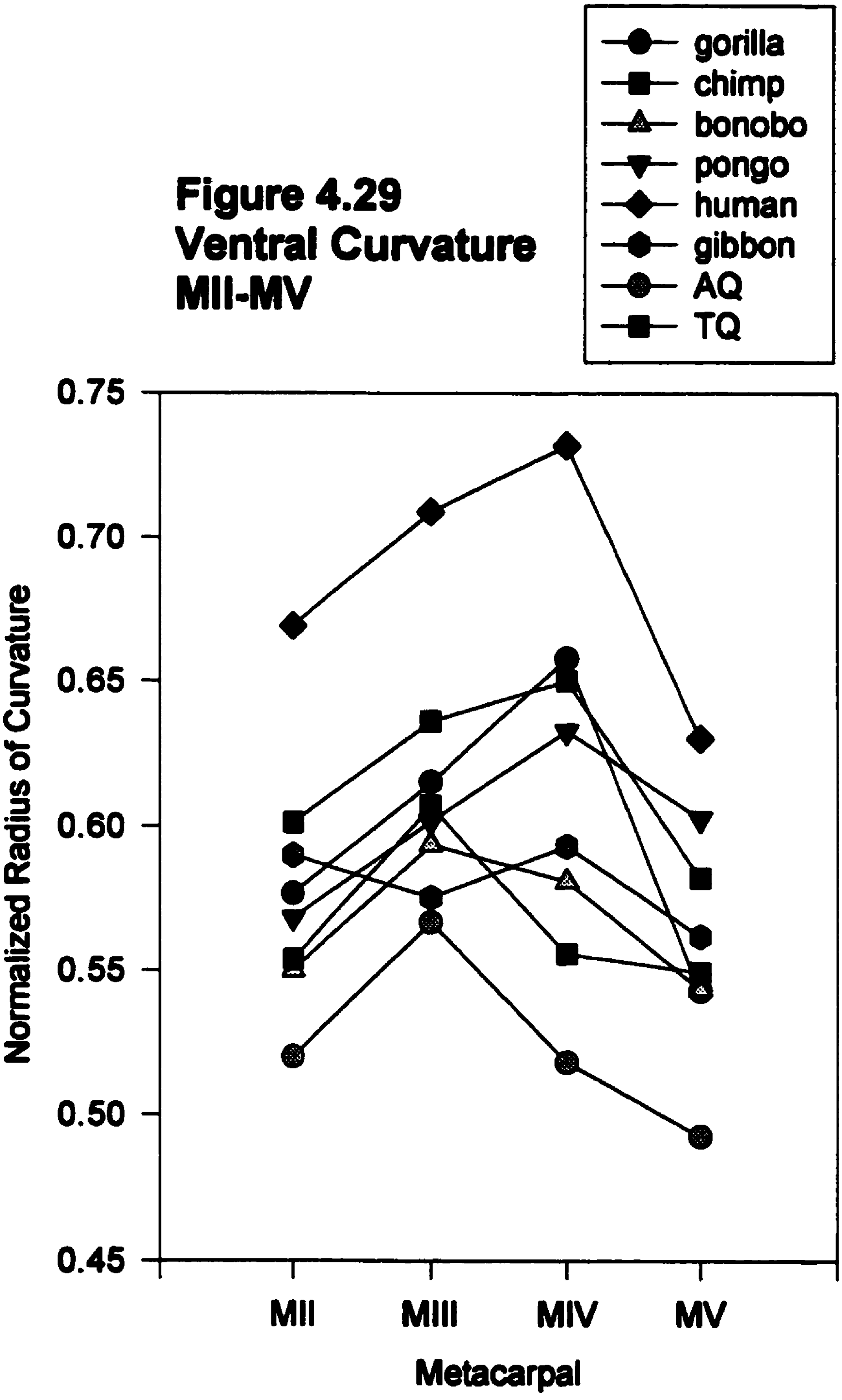


Figure 4.30
Dorsal Curvature
MII-MV

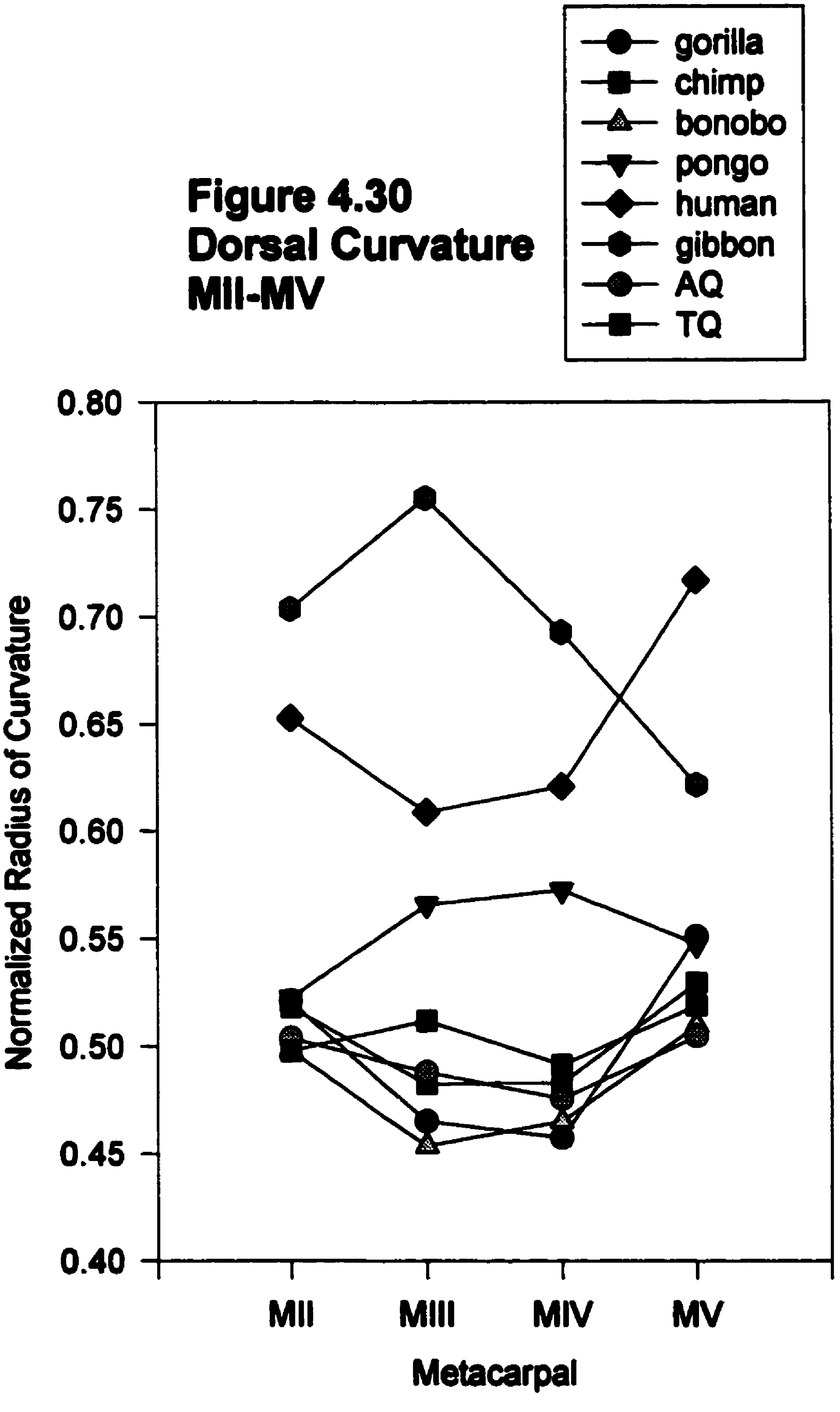


Figure 4.31
Ratio of Ventral-Dorsal Curvature For MII-MV

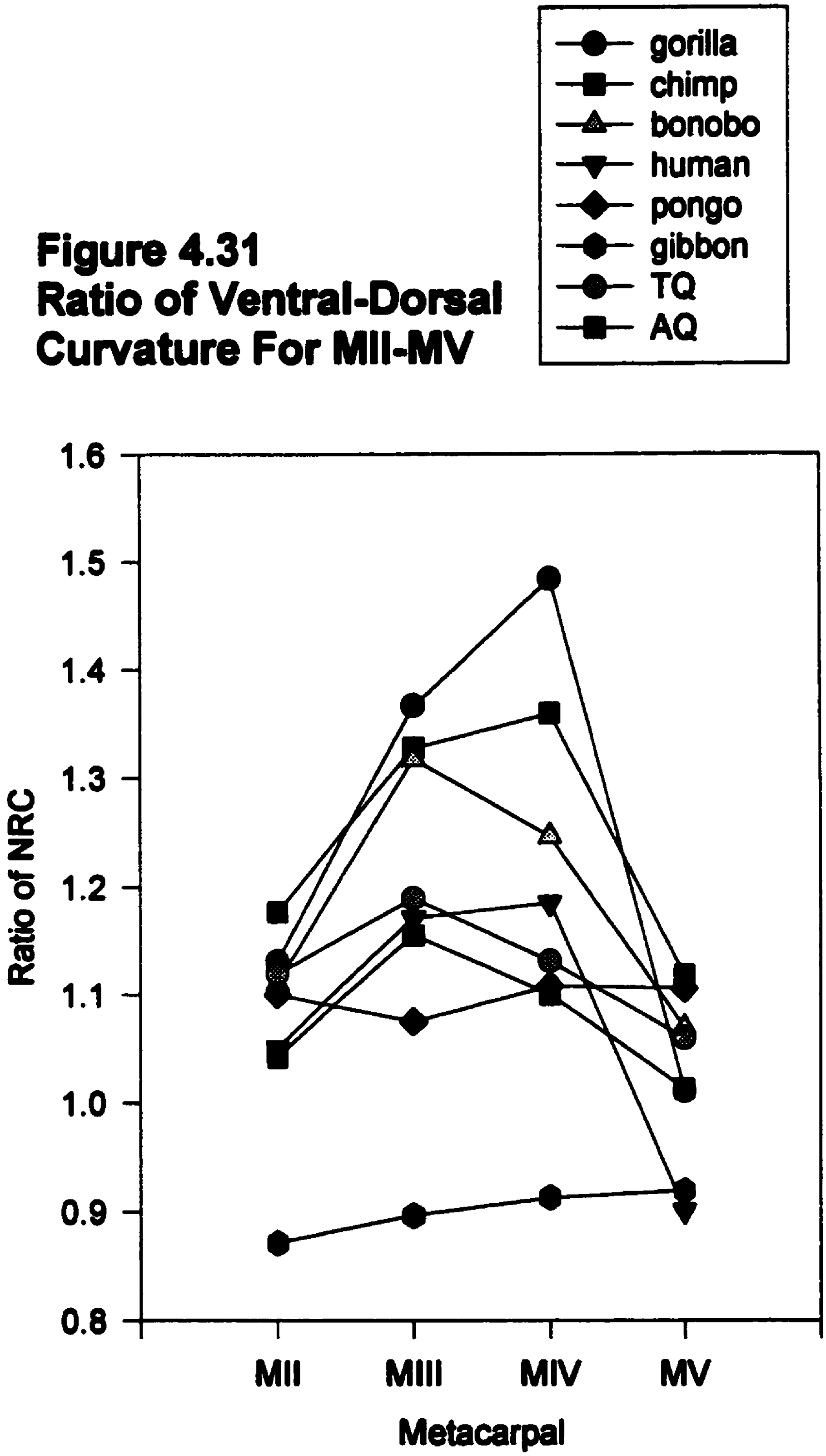


Figure 4.32: Proximal Phalanx Proximal Articular Surface Area Z-scores

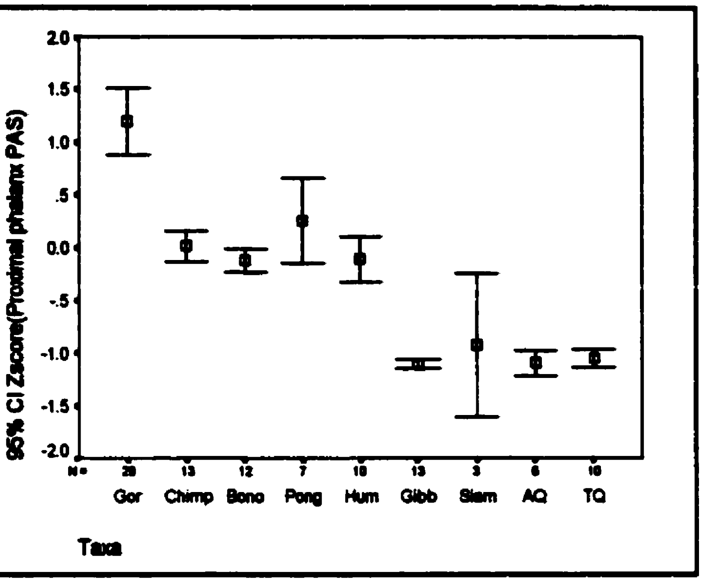


Figure 4.33: Proximal Phalanx Proximal Articular Surface Area / Metacarpal Composite

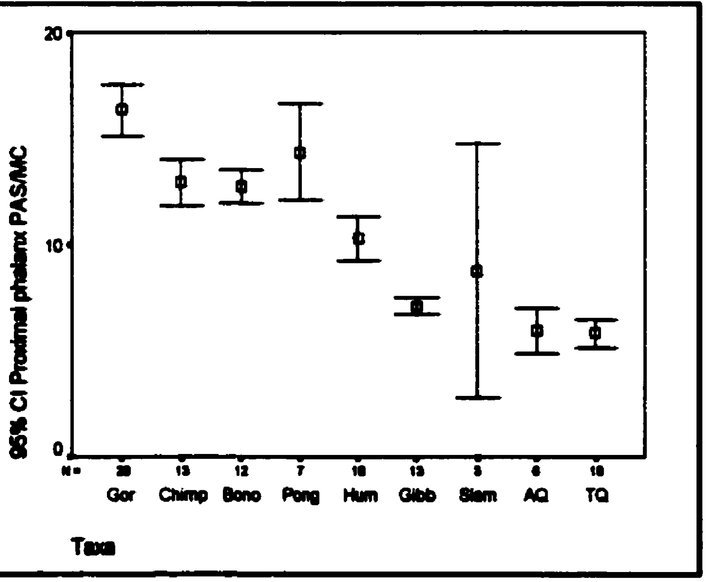


Figure 4.34: Proximal Phalanx Proximal Articular Surface Area / midshaft breadth

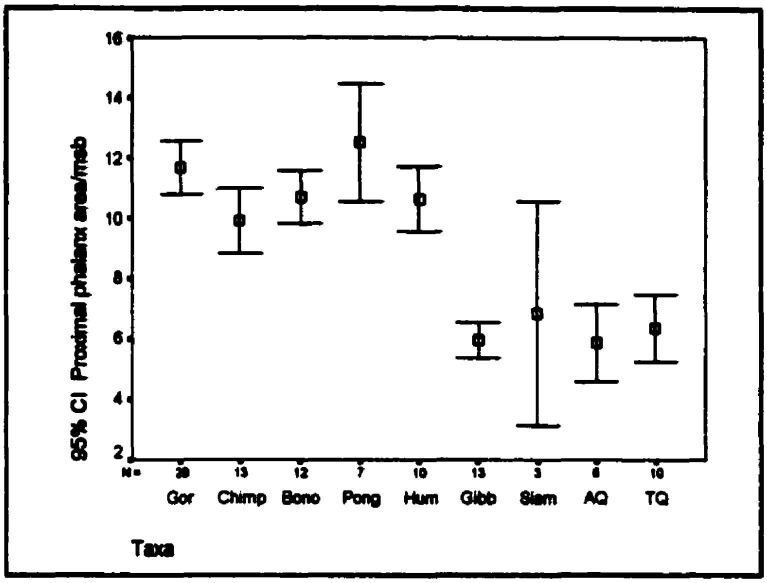


Figure 4.35: Proximal Phalanx Proximal Articular Surface Area Breadth / Width

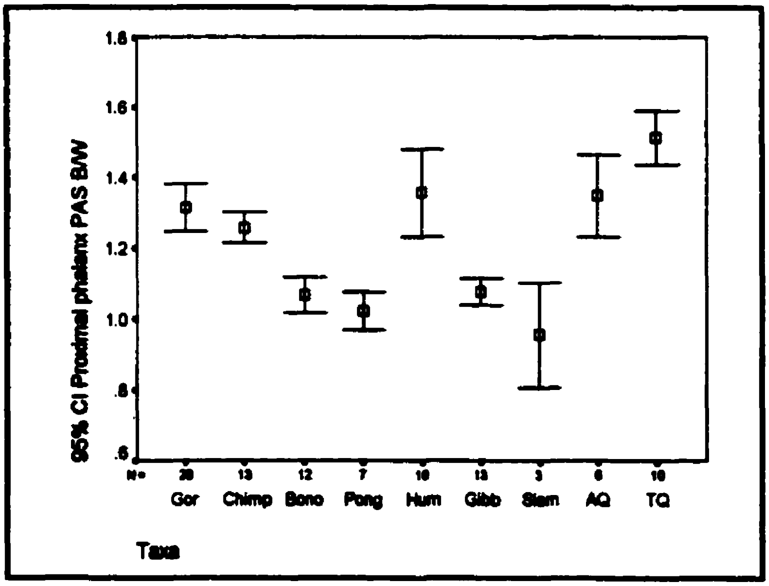


Figure 4.36: Proximal Phalanx Proximal Articular Surface Shape

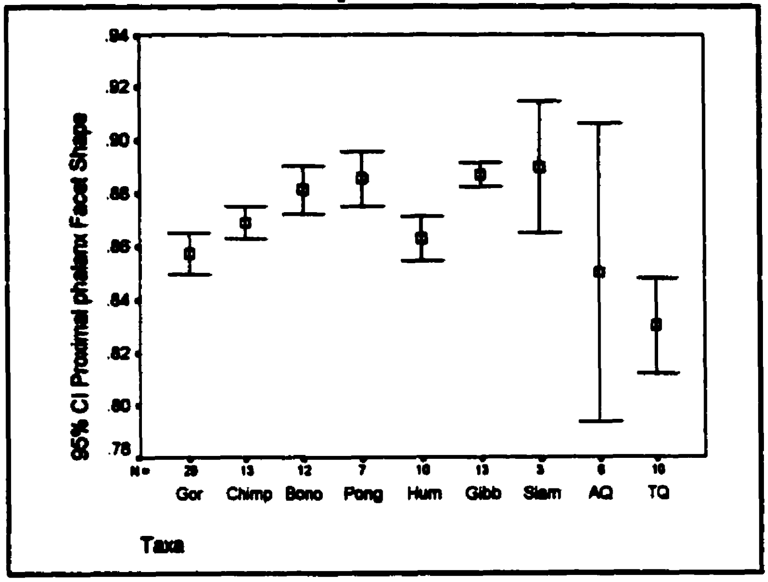
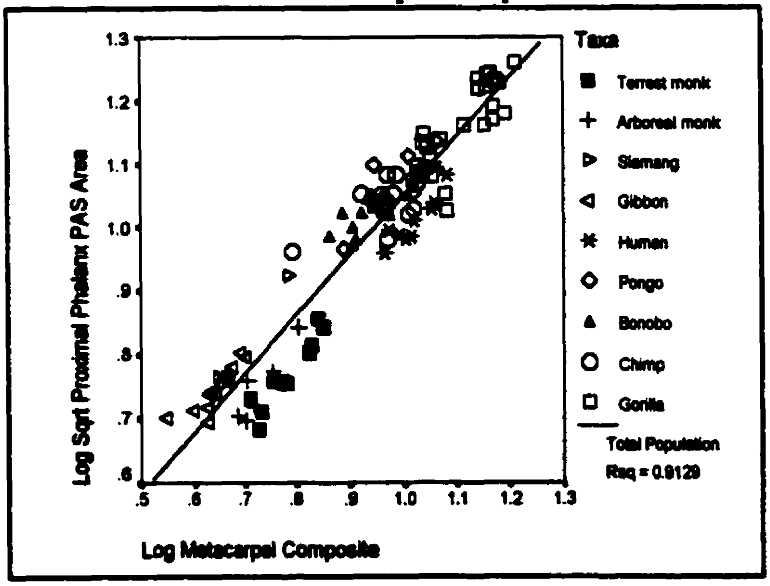


Figure 4.37: Regression of Proximal Phalanx Articular Surface Area versus Metacarpal composite



CHAPTER 5

Conclusion

One of the goals of this study has been to quantify hominoid forelimb joint surface proportions and geometry that heretofore has only been accomplished through linear measurement of discreet characters. The purpose has been to elucidate, using new measurement techniques, characters known to differ among hominoids, as well as identify novel traits and patterns of variation that may be functionally linked to alternative loading regimes across the forelimb. Specifically, the primary thrust has been to tease out subtle differences in great ape forelimb morphology that reflect knuckle-walking as an habitual mode of locomotion in African apes.

Swartz (1989) has stated that species specific locomotor specializations may not differ significantly enough to result in profound modifications of joint surface design, and that only certain types of locomotor patterns may be reflected in joint morphology. In light of the evidence presented in this study, I would have to agree with this statement. Living hominoids, by virtue of their *shared* positional repertoire (such as hanging and vertical climbing), must also share certain traits that will functionally allow them to engage in similar behaviours. However, it is also true that gross disparities in overall body mass exist within the *Hominoidea*, and these have resulted in unique locomotor adaptations and forelimb loading patterns. Hence, differences in joint surface morphology may be subtle, but they are sufficient to distinguish apes from other non-hominoid anthropoids. In addition, a small number of features can be added to the list of known traits characterizing knuckle-walking African apes.

The second goal of this project is to clarify the relationship of fossil taxa to extant hominoids and their locomotor patterns. To this end, Table 5.1 (**page xx**) summarizes a number of characters shared among great apes, African apes, humans and selected fossil taxa. The traits listed in Table 5.1 refer only to those features analyzed in this study, with the understanding that numerous other characters reviewed in the published literature exist to discriminate among anthropoids. Bivariate plots (figures 5.1 -5.5) of selected variables illustrate the relationship of fossil taxa to extant primates. Individual fossil species are discussed separately.

Summary of Great Ape and African Ape Characters

Elbow

Results from this study have shown that structural modifications of the distal humerus and proximal ulna in extant hominoids are directly linked to maximally stabilizing the elbow during all positions of flexion - extension and/or pronation - supination. These varied forearm positions are typical components of daily activity of large apes in an arboreal milieu, and are also integral to maintaining joint stability in knuckle-walking postures adopted by African apes. Godfrey *et al* (1991) have stated that there is a tendency among hominoids towards a medial shift in the transmission of force through the elbow. Hominoids, therefore, have larger humeral trochlear surfaces relative to capitulum surfaces, such that much of the load is borne through the humero-ulnar joint. The opposite is true of cercopithecoids, wherein the capitulum area is enlarged and load bearing is shared more evenly between the humero-ulnar

Table 5.1: Summary of Great Ape and African ape Shared Characters

Taxon	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*
Human	A	A	P	P	P	P	A	P	P	P	P	A	A	P	A
AL 288-1	P	A	P	A	A	-	A	A	-	A	P	-	A	#	-
AL 333	-	-	-	-	-	-	P	-	P	-	-	-	A	-	-
**A.afarensis*	-	-	-	-	-	-	A	-	-	-	-	-	A	-	-
A.anamensis	P	P	P	-	-	-	-	-	-	-	-	-	-	-	-
A.robustus	P	P	P	-	-	-	-	-	-	-	-	-	-	-	-
A.boisei	-	P	A	-	-	-	-	-	-	-	-	-	-	-	-
Sivapithecus	-	-	-	-	-	-	P	P	P	A	-	-	P	P	-
Lufengpithecus	-	-	-	-	-	-	-	-	-	P	-	-	-	P	-
Dryopithecus	A	A	P	-	-	P	A	A	A	-	-	-	-	P	-
Afropithecus	-	-	-	-	-	P	-	-	-	A	-	A	A	P	-
Kenyapithecus	A	A	P	-	-	-	-	-	-	-	-	-	-	-	-
Proconsul	A	A	P	A	A	P	A	A	A	-	-	A	A	-	P

P = character present; A = character absent; - = character / element not available for measurement
* *A.afarensis* = AL 288-1 and AL 333 together; # = intermediate status between bonobos and other African apes, bonobos have rounded proximal surface, unlike other African apes and similar to Asian apes:

Great Ape Characters

1. Small trochlear angle ventrally
2. Small trochlear angle distally
3. Large trochlear area relative to capitulum area
4. High ulnar notch angle
5. Enlarged radius distal articular area
6. Enlarged lunate area relative to scaphoid area*
7. Enlarged capitate distal articular area
8. Enlarged capitate area on hamate
9. Enlarged hamate distal articular area
10. Enlarged proximal phalanx proximal articular area relative to midshaft breadth

African Ape Characters

11. Scaphoid area > lunate area on distal radius
12. Enlarged scaphoid proximal articular surface
13. Enlarged scaphoid facet area on the capitate
14. Elongated proximal articular facet on proximal phalanx*
15. MIII and MIV metacarpal heads highly curved dorsally *

* Characters similar to terrestrial quadrupeds

and humero-radial joints.

This analysis has demonstrated the following characters of the elbow:

1. Increase in trochlea and capitulum areas is correlated with increasing body size, but trochlea area increases at a faster rate than capitulum area.
2. The "trochleiform" nature of the humeral trochlea, represented as the angle between the medial and lateral keels, is not strictly a function of increasing body size. It is best expressed in those species engaging in climbing and suspensory behaviours, suggesting a greater need for stability at the humero-ulnar joint.
3. Reorientation of the trochlear notch of the ulna in a more cranial direction is functionally related to the need for increased flexion/extension capabilities in large arboreal species, rather than strictly a function of increasing body size.

Radius

All great apes possess an enlarged distal articular surface of the radius. However, interspecific scaling patterns reveal that gorillas, humans and terrestrial quadrupeds scale closest to isometry of radius distal area. Chimps, bonobos and orangs have much lower slope values for this feature. Hence, there is a distinction between terrestrial and arboreal species. The faster rate of increase in surface area acts to reduce joint stress in those taxa habitually loading the forelimb in compression. The lower slopes of more arboreal species is indicative of a greater mobility requirements neccessary for vertical climbing, and suspensory activities.

Proximal Carpal Row

For the entire sample representing a broad array of catarrhines differing greatly in body size and locomotor patterns, the scaphoid proximal articular surface area increases at a lower rate than that of the lunate. Lunate surface area is isometric with body size for a wide range of species, which supports Godfrey *et al*'s (1991) statement regarding emphasis on ulnar loading in larger animals in general and hominoids in particular. However, evaluation of intertaxonal comparisons of scaling patterns across the proximal carpal row reveals that scaphoid area increases at a faster rate than lunate area in gorillas, chimps and humans.

All African apes have relatively and absolutely larger scaphoid proximal articular surface areas than Asian apes, and scaphoid area is larger than lunate area. In the ratio of scaphoid to lunate area the pattern is as follows: Bonobo > chimp/gor > human > orang ; within cercopithecines arboreal quadrupeds > terrestrial quadrupeds. Thus, there is a progressive increase in size of the lunate with increasing body size. This concurs with Godfrey *et al* (1991) with respect to ulnar loading patterns. A large lunate, in conjunction with a reduced ulnar styloid and developement of the interarticular meniscus, enhances mobility of the wrist by enabling a greater range of ulnar deviation. Wrist mobility and a stable humero-ulnar joint are neccessary adaptations for large primates engaging in vertical climbing and suspensory behaviours. At the same time, a relatively larger lunate in terrestrial digitigrade quadrupeds acts in concert with the extensive ulno-carpal articulation to maximize joint stability and dissipate forces, thus reducing joint stress.

Departing from this general trend, a shift occurs in the enlarged size of the scaphoid proximal articular surface in African apes. Hence, emphasis on loading on the radial side of the forelimb is indicated not only by fusion of the os centrale, but also by overall scaphoid proximal surface size increase and a change in the pattern of scaling whereby scaphoid area increases at a faster rate than lunate area. Observations of chimp knuckle-walking kinematics have demonstrated that as the body moves over the supporting limb, transmission of weight is shifted from between digits three and four toward the radial side. Bonobos do not conform to this pattern of scaphoid relative to lunate scaling exhibited by other African apes and humans. However the low slope values of bonobo scaphoid areas merely indicate that at all sizes, they have enlarged surface areas.

Distal Carpal Row

All great apes typically have enlarged distal articular surfaces of the capitate and hamate. Clearly, this serves as a joint stress reduction mechanism, but does not distinguish between knuckle-walkers and slow climbers. Humans share with large hominoids an expanded distal hamate surface, but capitate distal area does not show the same degree of enlargement. Human hands are designed for maximum manipulatory capability and possess a number of unique anatomical characters. The morphology of the distal hamate has a convex contour rather than one that is concave as in apes. A broad convex surface accords the fourth and fifth digits the ablility to oppose the thumb. Articulating with the distal capitate, the base of the third metacarpal has a proximally projecting dorsal styloid process which likely acts to stabilize the capitate - MIII joint without increasing the conjoining joint surface areas.

African apes have relatively larger scaphoid facet areas on the capitate compared to humans and other hominoids. The scaphoid, situated laterally and extending dorsoventrally in an oblique manner, articulates with both the lunate and the capitate. By virtue of its lateral position between the center of rotation of the capitate and lunate and in conjunction with numerous ligamentous connections, the scaphoid acts as a radial strut stabilizing the midcarpal joint. Increased surface area contact between the scaphoid and capitate not only enhances midcarpal stability, but also enables more effective transmission of forces directed through these two bones. This feature, in conjunction with those described above, reflects a greater emphasis on loading across the radial aspect of the forelimb typical of knuckle-walkers.

All great apes have enlarged articular surfaces joining the capitate with the hamate. An expanded joint surface between these two bones likely serves to stabilize the midcarpal joint and reduce frictional stress. Soft tissue structures may act as shock absorbers to either tensile or compressive loads placed on the ulnar aspect of the forelimb, transmitting forces to the more stable capitate via the well developed hamatocapitate ligaments. It is possible that a large, flat articulation between the capitate and hamate, in addition to strongly developed ligaments, may enable these two bones to function as a single bone, linking the proximal carpal row to the metacarpals. Humans are similar to great apes in having an expanded capitate - hamate articulation, likely as a response to extensive forces generated through the human hand from various manipulatory activities such as tool-making.

Metacarpal Heads and Proximal Phalanges

Large hominoids and humans all have expanded proximal articular surfaces of the proximal phalanges relative to midshaft breadth. These larger facets accomodate the much larger metacarpal heads of great apes as compared to lesser apes and monkeys, and maximizes joint mobility at the metacarpophalangeal joint. All large apes, gorillas included, are adept climbers and require powerful grasping ability as well as enhanced joint excursion in order to manouver efficiently in an arboreal setting. Having said that, gorillas and chimps possess proximal facets that are much more elongated or oval in shape than those of orangs. African apes (chimps and gorillas especially) are unique in having metacarpal heads that are widest along the dorsal aspect, as opposed to broader ventral surfaces typical of all other taxa. In knuckle-walking stance, the metacarpophalangeal joint reaches close-packed positioning when the proximal phalanx is hyperextended and the dorsum of the metacarpal head achieves maximum congruency with the facet. The large size of the proximal surface of the phalanx reduces stresses incurred during habitual compressive loading, and its oval shape aids in preventing axial rotation of the phalanx during weight bearing, thereby stabilizing the joint. Its oval shape reflects movement that is *principally* hinge-like in nature. Humans share this type of morphology with gorillas and chimps, as do monkeys. Terrestrial quadrupeds in particular have extremely elongated facets, however cercopithecine proximal surfaces are of a wholly different nature than that of hominoids. For example, the facet in monkeys is dorsally deflected whereas in apes the surface faces directly proximally. Bonobos, on the other hand, resemble orangs, gibbons and siamangs in having more rounded proximal articular surfaces.

This indicates greater rotational capabilities at the metacarpophalangeal joint, neccessary in a large, slow climbing and/or suspensory primate grasping branches of varying sizes and moving in a variety of directions.

Finally, the joint surface topography of African ape third and fourth metacarpal heads is unique among hominoids. It is demonstrated that knuckle-walkers have a high disparity in ventral to dorsal curvature of the third and fourth metacarpal heads, and these represent the primary weight bearing rays of the hand. Highly curved dorsal aspects of MIII and MIV articular surfaces permit sliding translation of the proximal phalanx and extreme ranges of hyperextension at the metacarpophalangeal joint of African apes. The functional significance of hyperextension to knuckle-walkers is that it increases the mechanical efficiency of the forelimb acting as a supporting prop, and serves to increase stride length during the propulsive phase. Cercopithecines exhibit a pattern of dorsal curvature that is somewhat similar to that of African apes, reflecting habitual loading of the metacarpal head in hyperextension that is typical particularly of digitigrade terrestrial quadrupeds.

Fossils

Proconsul

The three species of *Proconsul* included in this analysis (*P.africanus*, *P.heseloni*, and *P.nyanzae*) are morphologically similar and will be referred to simply by genus name. There has been some debate in the literature as to the actual nature of *Proconsul* locomotion. Most researchers argue that it is a generalized palmigrade arboreal quadruped (Clark and Leakey, 1951; Clark, 1948a,b, 1949a,b; Corruccini et al, 1975,1976; McHenry and Corruccini, 1983; Morbeck, 1975,1977; Napier and Davis, 1959; Napier, 1967; O'Connor, 1975,1976; Preuschoft, 1973; Rose, 1983,1988,1993,1994,1997; Schon and Ziemer, 1973; Straus, 1949; Washburn, 1968; Ward, 1993; Walker *et al*, 1993). Others suggest it most closely resembles a terrestrial quadruped and may even have been an incipient knuckle-walker (Conroy and Fleagle, 1972; Zwell and Conroy, 1973). Lewis (1971,1972, 1989) believes that *Proconsul* is a brachiator. This taxon does present a mosaic of features in the forelimb, however it does not share any anatomical affinities with hylobatids indicative of brachiation, nor does it possess any knuckle-walking characteristics.

Despite numerous primitive, monkey-like characters of the *Proconsul* forelimb, the distal humerus is said to have some hominoid-like traits (Rose, 1983,1988,1993,1994,1997; Walker, 1997). As illustrated in Table 5.1, *Proconsul* shares very few traits with extant large hominoids. The conformation of the humeral trochlea is most similar to monkeys in its degree of constriction (fig. 5.6- 5.7), however in the ratio of trochlea area to capitulum area *Proconsul* does resemble living apes (fig. 5.8- 5.9). *Proconsul* also has an enlarged lunate. In standardized z-scores for scaphoid and lunate surface areas, as well as ratio of scaphoid to lunate area, *Proconsul* most closely resembles terrestrial monkeys (figs 5.10-5.12). As discussed earlier, lunate area scales isometrically with body size, and ulnar loading is emphasized as animals get bigger. *Proconsul* departs greatly from the pattern seen in lesser apes and arboreal monkeys. Other characters of the of the forelimb and wrist in particular attest to the fact that this fossil taxon was not a modern hominoid (see Rose, 1983 and *seq.*). In addition, Begun *et al* (1994) note that *Proconsul* had powerful grasping hands, however on large supports the hand position may have been slightly hyperextended at the metacarpophalangeal joint. Morphological characters of the proximal phalangeal base suggest the presence of strong flexors and possible weight bearing at the metacarpophalangeal joint (Begun *et al*, 1994). This analysis shows that the metacarpal heads of *Proconsul* are quite curved dorsally and very similar to living digitigrade terrestrial quadrupeds (fig 5.13-5.14).

Several features point to increased loading across the ulnar aspect of the *Proconsul* forelimb. The greater size of the humeral trochlea relative to the size of the capitulum, as well as an enlarged lunate proximal surface relative to the scaphoid. According to Rose (1983 and *seq.*), the olecranon fossa is deep, suggesting extensive forelimb extension, however the olecranon process of the ulna projects proximoposteriorly as in terrestrial quadrupeds. He claims that this may also be associated with overhead use of the forelimb during arboreal activities (Rose, 1993, 1997). Indeed, trochlear notch angle of the proximal ulna is not cranially oriented as in great apes (fig 5.15), however neither is that of hylobatids.

These traits combined seem to indicate that *Proconsul* was a large bodied primate with powerful grasping ability (Begun *et al*, 1994), but with closer affinities to living terrestrial digitigrade quadrupeds.

Afropithecus

Postcranial remains of *Afropithecus* are scant, however available forelimb elements indicate very similar size and morphology to *Proconsul*, particularly *P.nyanzae* from Rusinga Island (Andrews *et al*, 1997). The trochlea of the distal humerus is thought to resemble that of small apes (Rose, 1997 and *seq.*), but Begun *et al* (1997; and Begun, 1992) consider *Afropithecus* to be much more primitive than hylobatids. Evidence presented here consists of a scaphoid, lunate, capitate and proximal phalanx. Scaphoid proximal surface area is slightly larger than *Proconsul*, and lunate area is within the 50% range of bonobo values. So, *Afropithecus* has an extremely enlarged lunate relative to the scaphoid, and fig 5.12 clearly illustrates that for this feature it approaches the ratio of orangs. Other aspects of the available carpals do not resemble hominoids in any way, nor does the proximal articular area of the proximal phalanx. In relative phalangeal surface area and shape, *Afropithecus* is most similar to terrestrial quadrupeds.

The available data for *Afropithecus* shows no affinities with living hominoids. The enlarged lunate surface area is consistent with a pattern of increased ulnar loading in larger animals, particularly terrestrial quadrupeds. Proximal phalangeal morphology suggests weight bearing and a stereotypic pattern of loading consistant with digitigrady. In light of these factors and *Afropithecus*' relatively large size, it is likely that this taxon engaged in higher frequencies of terrestrial rather than arboreal behaviours, and likely used less palmigrade hand postures.

Kenyapithecus

Kenyapithecus wickeri from Fort Ternan is similar to *Proconsul* and *Afropithecus* in retaining many primitive characters of the elbow (Rose, 1983 and *seq.*), and it shares with semiterrestrial and terrestrial cercopithecines several features associated with digitigrade hand postures (McCrossin and Benefit, 1997). Only the distal humerus was available for analysis in this study, and details of its anatomy reveal that like large hominoids, *Kenyapithecus* does have a large trochlea relative to capitulum area. However, *contra* McCrossin and Benefit (1997), it does not resemble large hominoids in having a well developed lateral keel. The morphology of the trochlea in *Kenyapithecus* is essentially the same as in a terrestrial quadruped.

Dryopithecus

Dryopithecus is a Late Miocene form from Europe possessing a number of characters of the elbow, forearm and hand that are ape-like, but without the locomotor specializations seen in living brachiators, slow climbers and knuckle-walkers (Begun,1988, 1992a,b, 1993, 1994, 1995; Begun and Kordos, 1997; Morbeck, 1975, 1983; Rose 1983,1988, 1993a, 1993b, 1994, 1997). Great ape features characterizing *Dryopithecus* include a spool shaped humeral trochlea with well developed medial and lateral keels, large and deep coronoid fossa, broad trochlea, certain aspects of the lunate and hamate (Begun, 1992; Morbeck, 1975,1983; Rose, 1983 and *seq.*). The proximal phalanges are strongly curved and more similar in overall morphology to large bodied arboreal monkeys (Begun, 1993; Rose, 1997).

Results from this study indicate that trochlear morphology of the distal humerus is not great ape like in most respects, but closely resembles gibbons in degree of constriction of the joint, particularly distally. Trochlear angle ventrally is somewhat less constrained, suggesting that stabilization of the elbow in extended positions was of greater importance. The ratio of trochlear width relative to capitulum width is similar to living great apes. Lunate proximal area is expanded, which follows a pattern typical of most large bodied primates studied so far, and falls intermediate between the slightly smaller *Pronconsul* and minimally larger *Afropithecus* specimens. In *Dryopithecus*, the relative area of the capitate distal articular surface does not resemble living great apes. Measurements of the hamate distal area and capitate facet on the hamate demonstrate that *Dryopithecus* is intermediate between large cercopithecines and great apes. Z-scores for proximal articular surface area of the proximal phalanx indicate that *Dryopithecus* values fall within the range of gibbons rather than monkeys. The shape of the phalangeal proximal facet is oval, and falls within the range of arboreal monkeys, African apes (excluding bonobos) and humans in degree of elongation.

These results support the conclusions of Begun (1992, 1993; Begun and Kordos, 1997; Rose, 1983 and *seq.*) that *Dryopithecus* was likely an arboreal quadruped, but also engaging in generalized orthograde suspensory behaviours. The degree of stabilization of the humero-ulnar joint, and expansion of the trochlea relative to the capitulum (among other characters) suggest that below branch suspensory postures with fully extended elbow were indeed possible in *Dryopithecus*. Furthermore, the size and shape of the proximal phalanx articular surface are indicative of a large, arboreal quadruped rather than a highly derived suspensory ape or an habitually terrestrial digitigrade monkey.

Lufengpithecus

The proximal phalanx of *Lufengpithecus* is similar to *Sivapithecus* according to Begun *et al* (1997) and Rose (1997). These two taxa share well developed basal tubercles as well as an oval shaped proximal articular surface (Rukang *et* al, 1986). Results from this study indicate that *Lufengpithecus* falls within the 50% range of chimps in proximal articular size, and is similar to gorillas, humans and arboreal monkeys in overall articular shape. It also closely resembles *Dryopithecus* in breadth/width dimensions of the proximal surface, but not *Sivapithecus*.

The shaft of the *Lufengpithecus* proximal phalanx is quite long and curved, with well developed fibrous sheath ridges (Rukang *et* al, 1986). The morphology of the shaft and proximal articular surface suggests that this taxon was a large arboreal primate likely engaging in some below branch suspensory behaviours, but without the specializations seen in extant hylobatids or *Pongo*.

Sivapithecus

Sivapithecus presents a mosaic of primitive, monkey-like features as well as some hominoid characters (Pilbeam et al, 1980, 1990; Rose, 1984,1986,1989,1997; Spoor *et al* 1991; Ward, 1997). Traits such as a somewhat elongated humeral head, a proximal humeral shaft that is retroflexed, and a flat anterolaterally facing deltoid plane are cercopithecine- like in nature. The distal humerus is said to be more similar to hominoids and its overall morphology suggests a stable humeroulnar articulation. The distal capitate resembles that of great apes in having an irregular surface, and the head is moderately inflated, suggesting considerable movement at the midcarpal joint. The hamate is broad mediolaterally, the hamulus is small, the triquetral facet faces more proximally than medially and is truncated, and the distal articular surface is irregular in shape. The conformation of the hamate in total is similar to that of monkeys and gorillas, and is suggestive of stability rather than mobility, reflecting considerable load transfer through the ulnar aspect of the wrist. The *Sivapithecus* proximal phalanges are relatively long with well developed secondary features. The proximal articular surface faces proximodorsally, and is mediolaterally broad as in cercopithecine monkeys. Generally, it is considered that *Sivapithecus* was a quadruped and lacks anatomical traits associated with suspensory behaviours (Rose, 1986; Pilbeam *et* al, 1990; Spoor *et al*, 1991; Gebo, 1996; Walker, 1997).

This study shows that *Sivapithecus* does share with great apes enlarged capitate distal area, scaphoid facet on the capitate, hamate distal area, and capitate-hamate articulation. All these features act as joint stress reduction mechanisms and are indicative of high levels of weight transmission through the carpus. It is interesting to note that the capitate was recovered from the Chinji Formation of Pakistan and is somewhat older (11.55-11.73 mya) than the hamate and proximal phalanges recovered from the Seth Nagri Formation (~ 8.8 mya) (Kappelman *et* al, 1991). The latter have been attributed to *S.parvada* (Pilbeam *et* al, 1990; Spoor *et* al, 1991). The proximal articular surface area of the phalanx is unlike that of great apes in being relatively much smaller, and its extremely elongated shape most closely resembles that of terrestrial cercopithecines. These findings support conclusions that

Sivapithecus was a quadruped, likely semi-terrestrial, and lacking any anatomical traits associated high frequencies of arborealism (Rose, 1986; Pilbeam *et* al, 1990; Spoor *et al*, 1991; Gebo, 1996; Walker, 1997).

Early Hominids

There is some debate in the literature as to whether Plio-Pleistocene hominids were not habitual bipeds and engaged in high frequencies of arboreal activity (Berger and Tobias, 1996; Clarke and Tobias, 1995; Day, 1978; Kay, 1973; Leakey, 1971; McHenry and Temerin, 1979; McHenry and Berger, 1996; Robinson, 1972; Senut, 1981a,b; Senut and Tardieu, 1985; Jungers, 1982; Jungers and Stern, 1983; Stern and Susman, 1983; Susman and Stern, 1984; Lague and Jungers, 1996), or whether early hominids were fully adapted and committed to bipedalism utilizing an upright gait that was kinematically indistinct from that of modern humans (Dart, 1958; Latimer *et al*, 1987, 1989,1990a,b; Latimer, 1991; Lovejoy *et al*, 1973; Lovejoy 1974,1975,1978; White, 1980, 1981). A comprehensive review of early hominid locomotor functional anatomy is beyond the scope of this paper, and discussion is limited to upper limb comparative morphology as it pertains to affinities with living great apes and inferred functional capacities for climbing, suspensory activities, and knuckle-walking.

Distal humeri available for analysis here include *A.robustus* (TM 1517), *A.boisei* (KNM-ER 1504 and 739)- but see Lague and Jungers, 1996 for an alternate view of the taxonomic status of these specimens, *A.afarensis* ("Lucy"), and the specimen from Kanapoi .

(KNM KP 271) attributed to *A.anamensis* (Leakey et al., 1995). Some researchers consider the *A.anamensis* humerus to be very human-like (Aiello and Dean, 1990; Day, 1978; McHenry and Corruccini, 1975; McHenry, 1975,1976,1984; Senut, 1980,1981a,b; Senut and Tardieu, 1985), while others (Hill and Ward, 1988; Patterson and Howells, 1967; Lague and Jungers, 1996) believe it has closer affinities with other known species of australopithecines.

Figure 5.7 demonstrates that *A.robustus*, *A.boisei* and *A.anamensis* all fall well within the range of African apes in the degree of constriction of the distal trochlea. These three fossil taxa do not overlap with modern humans who have wider trochlear angles and, therefore, less constrained humero-ulnar joints. Ventrally, measurements for *A.boisei* are unavailable, however the position of *A.robustus* does not change. Kanapoi exhibits a somewhat larger angle ventrally, however it still falls within the upper 50% range of African apes.

The contention by Senut (1981a,b) and Senut and Tardieu (1985) that robust australopithecines (*A.boisei* specifically) are *Homo/Pongo*- like is difficult to address, since human trochlear morphology is wholly unlike that of orangs. These authors state that shared affinities with great apes, to the exclusion of humans, include greater robusticity, more pronounced medial and lateral epicondyles, and larger muscle insertions. They also assert that *A.boisei* lacks the steep lateral margin of the olecranon fossa typical of African apes, but conclude that overall distal humeral morphology reflects some use of the forelimb in locomotion. Analysis of trochlear constriction presented here reveals that robust australopithecines are virtually indistinguishable from great apes, however it is unlikely that the forelimb was used in locomotion in the same manner as extant great apes. Small trochlear angles indicate that a high degree of humeroulnar joint stability was of some importance, and it is possible that robust australopithecines were using the forelimb for some degree of climbing and/or hoisting behaviours (see also Lague and Jungers, 1996). Unlike the conclusions of McHenry (1975,1976), Senut (1981a,b) and Senut and Tardieu (1985), *A.anamensis* is not more human-like and is not distinct from robust australopithecines in aspects of trochlear morphology considered here.

Many believe that *A.afarensis* engaged in considerable arboreal climbing activity (see references above). Examination of distal humerus trochlear morphology however, reveals that "Lucy" shares no affinities with great apes in distal trochlear angle and is very similar to modern humans in having a less constrained humero-ulnar joint. Even in comparison to bonobos, the smallest of great apes, *A.afarensis* is quite distinct. The trochlear angle ventrally does fall within the range of great apes and is similar to Kanapoi, but unlike humans. This implies greater humero-ulnar joint stability with flexed arm positions. This pattern is not consistent with that of great apes wherein maximum stability is required with extended forelimbs either for suspensory behaviours or knuckle-walking.

Great apes are also characterized by having cranially oriented trochlear notches of the proximal ulna. This is an effective mechanism for increasing the range of flexion and hyperextension of the forelimb neccessary for a large primate engaging in slow climbing and suspensory activities, or knuckle-walking. *A.afarensis* does not share this trait with great apes (fig. 5.15). Other great ape characters not shared with *A.afarensis* include enlarged: radius distal articular surface area; capitate distal area; capitate area on the hamate; proximal .

phalanx proximal articular surface area. *A.afarensis* also lacks African ape characters such as an enlarged scaphoid facet on the capitate. AL 333 is a considerably larger individual than AL 288-1 (for example see Jungers and Stern, 1983 among others). The former is similar to great apes in the relative size of the distal capitate and distal hamate areas. When taken together, however, the average for these two specimens is more similar to humans than great apes. Only the hamate of the larger individual is available, hence it is unclear what the pattern is for this bone.

Of the characters mentioned above, *A.afarensis* differs from humans in cranial orientation of the ulnar trochlear notch, and capitate-hamate articular surface. Modern human forelimbs are not used in locomotion and are not adapted for any kind of arboreal activity. Cranial orientation of the ulnar trochlear notch may be convergent on great apes and adaptive for increased ranges of flexion-extension requirements neccessary for enhanced manipulatory capacities. Similarly, the capitate-hamate articulation likely serves as a midcarpal stabilizing mechanism. Humans do have expanded distal hamate surfaces, but the facet has a different conformation than that of great apes, in being convex instead of concave. A convex hamate distal surface permits opposition of the fifth digit with the thumb, critical in precision and power grips (for example, see Marzke, 1983). Any object gripped firmly and manipulated in some way (as in tool making, or digging) would generate considerable stresses across the ulnar aspect of the wrist and from the hamate to the capitate. Since *A.afarensis* does not have an expanded capitate-hamate articulation, it is possible that modern humans are convergent on great apes for this character, and that it may have arisen out of the need to reduce joint stress resulting from manipulatory functions.

Canonical discriminant function analysis including a subset of variables from the elbow, wrist and proximal phalanx was undertaken to assess the relationship of *A.afarensis* (AL 288-1) to extant species. Homogeneity of variance tests indicate that equal variance can be assumed for trochlear angle ventrally, the ratio of trochlea to capitulum area ventrally, ulnar notch angle, the ratio of scaphoid to lunate of the distal radius, and proximal articular breadth to width ratio of the proximal phalanx. All variables considered are not highly correlated. The discriminant function analysis using all the available forelimb elements of "Lucy" clearly demonstates the intermediate position of this taxon between lesser apes and chimps/humans (Fig 5.16). AL 288-1 is transitional between these two groups based on function 1 (radius distal area, capitate distal area/total length, ulnar notch angle, accounting for 61.7% of total variation), however it is not distinguished from these groups on the basis of function 2 (trochlear angle distally and ventrally, proximal phalanx proximal articular surface shape, accounting for 21.8% of total variation).

Traits described here for *A.afarensis* show very few affinities with great apes that can be associated with vertical climbing, suspension, or knuckle-walking. Granted, characters under consideration in this study are limited in nature and any accurate assessment of locomotor behaviour in fossil taxa must be based on morphologic and metric analyses of a variety of fore and hindlimb elements. The wealth of published information of such analyses clearly indicates that *A.afarensis* was a predominantly, if not completely, bipedal hominid. Results from this study add to our knowledge of this taxon, and favours the view that it was not engaging in behaviours similar to great apes and that is was not an adept climber.

Possibilities For Future Research

Anatomical descriptions based on observations, linear measurements and 2-D image analysis are rather limited in their ability to assess movement capabilities within the wrist. Research into human wrist dysfunction has been successful in visually reproducing the dynamic kinematics of individual carpal bones (Nicodemus *et al*, 1994; Viegas *et al*, 1993). Using a process of CT scan imaging and optoelectronic stereo cinephotogrammetry, it is possible to reconstruct carpal elements 3-dimensionally and determine intra and intercarpal movements within the context of global wrist motion. Analysis of extant primate forelimbs using this methodology would greatly enhance our understanding of wrist joint kinematics and associated limb usage. We already know that living anthropoids differ considerably in forelimb size, proportions and gross anatomical details. Using this new method of comparative analysis would aid immensely in our ability to evaluate the relationship between morphology and function.

Figure 5.1: Capitate Distal Area Relative to CapitateTotal Length

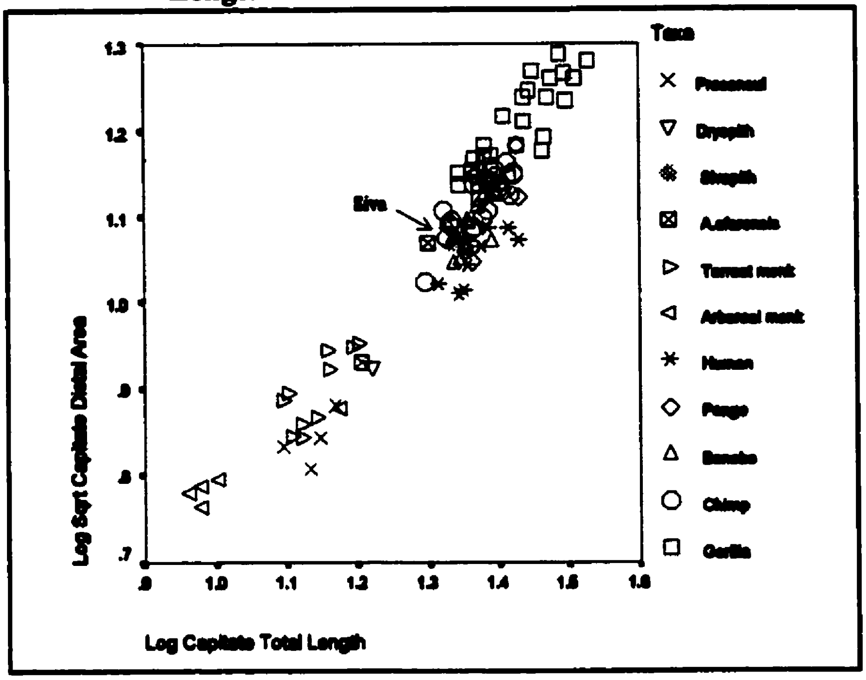


Figure 5.2: Scaphoid Facet Area on Capitate

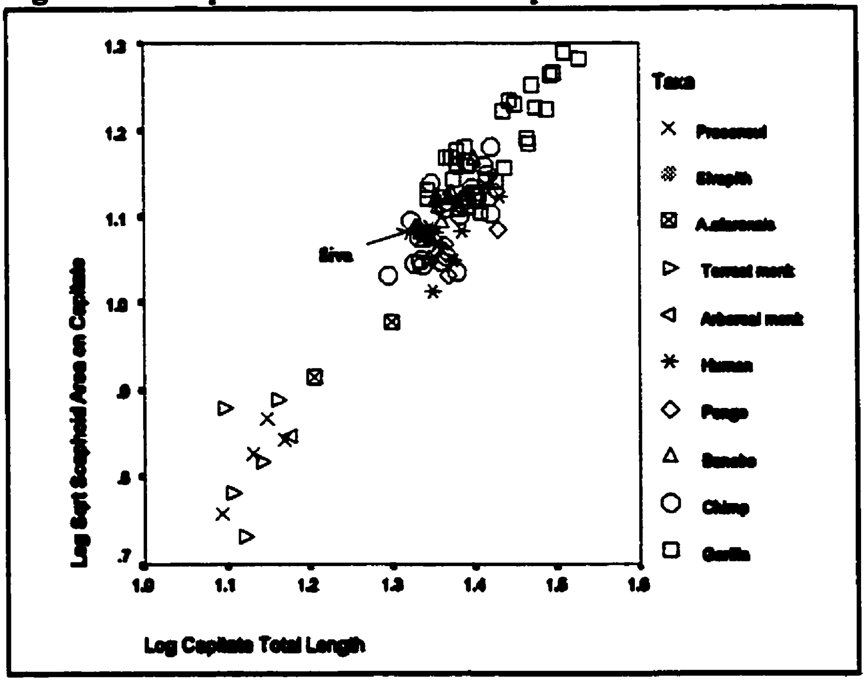


Figure 5.3: Hamate Distal Area Relative to Total Length

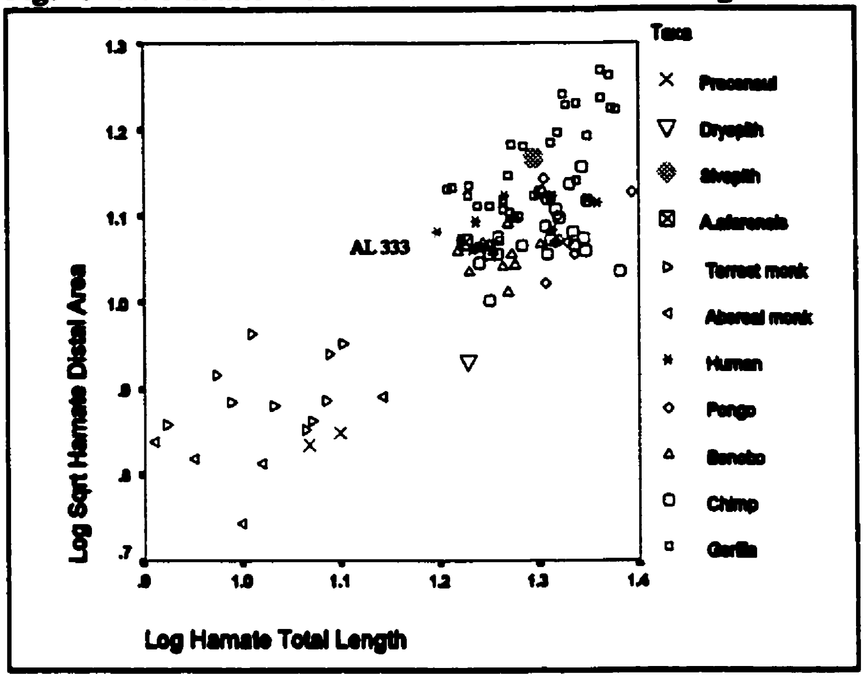


Figure 5.4: Capitate Facet on Hamate

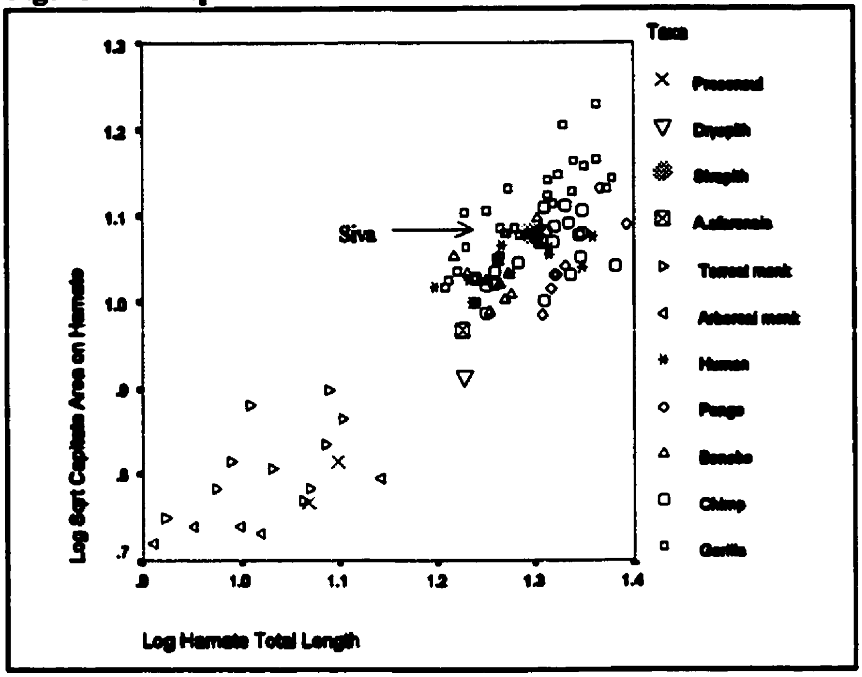


Figure 5.5: Proximal Phalanx Articular Surface to Midshaft Breadth

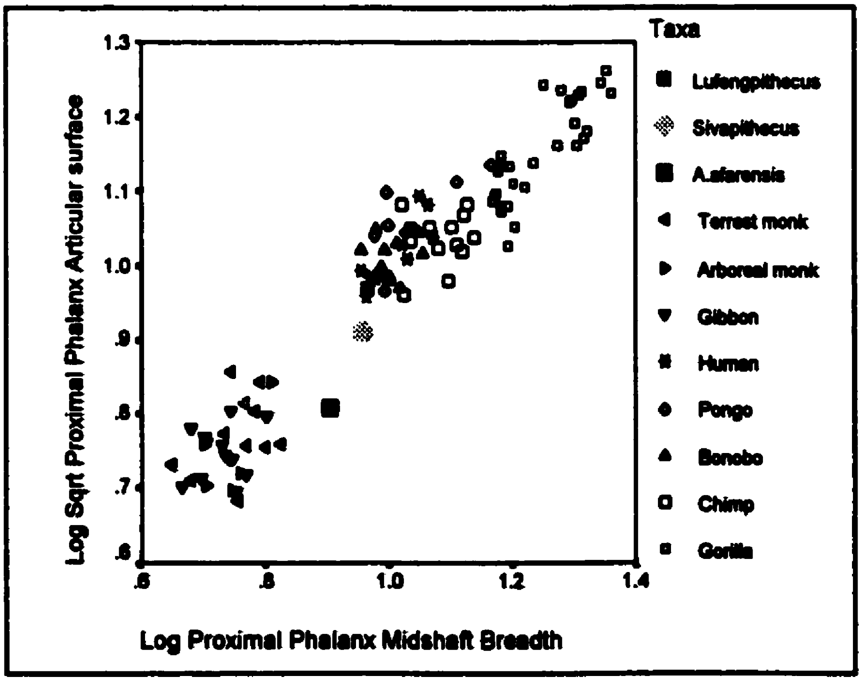
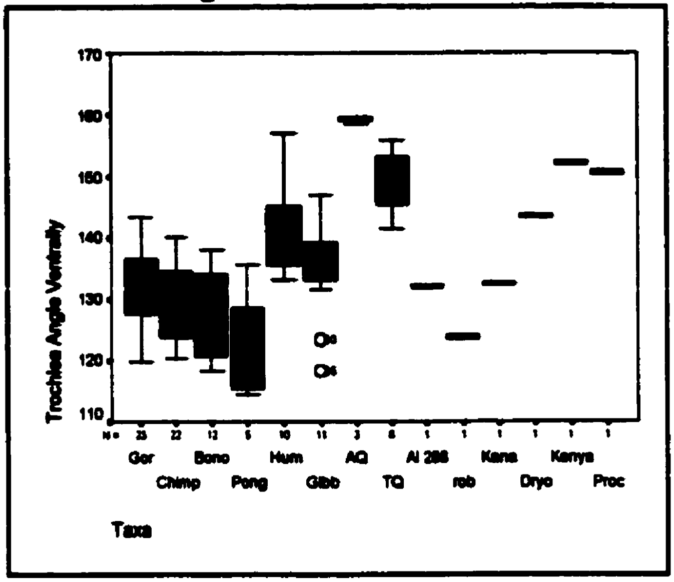


Figure 5.6: Boxplot of Ventral Trochlea Angle



*Box represents interquartile range which contains 50% of total values.

Figure 5.7: Boxplot of Distal Trochlea Angle

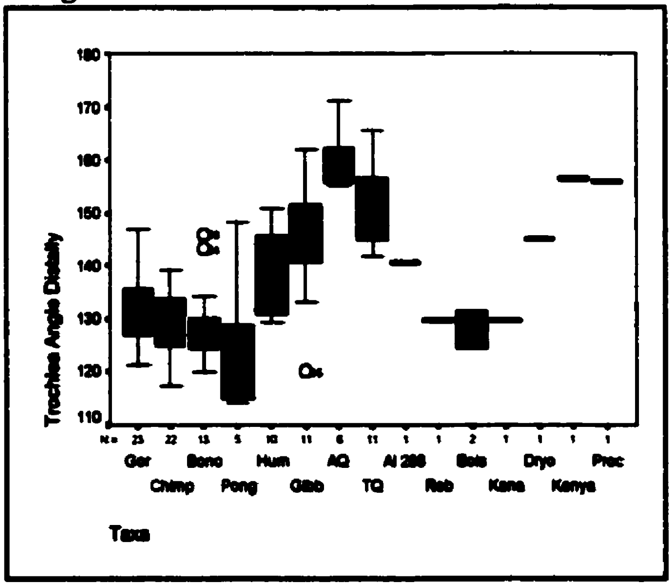


Figure 5.8: Boxplot of Ventral Trochlea to Capitulum Area

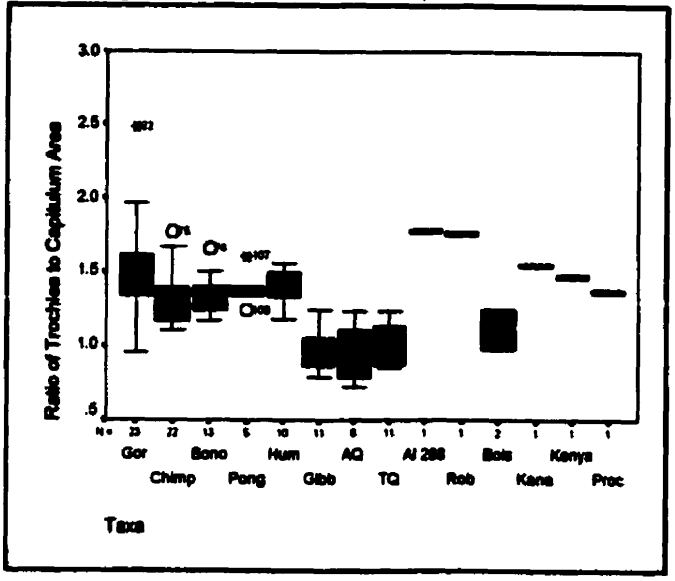


Figure 5.9: Boxplot of Trochlea to Capitulum Area Distally

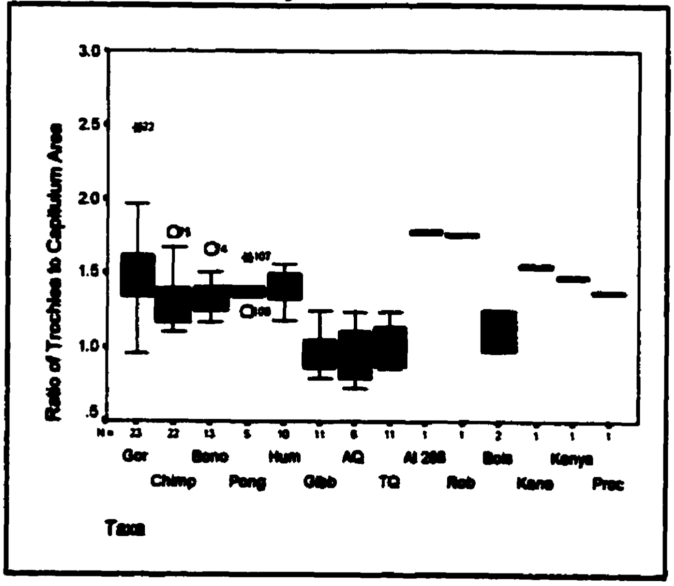


Figure 5.10: Z-scores for Scaphoid Proximal Area

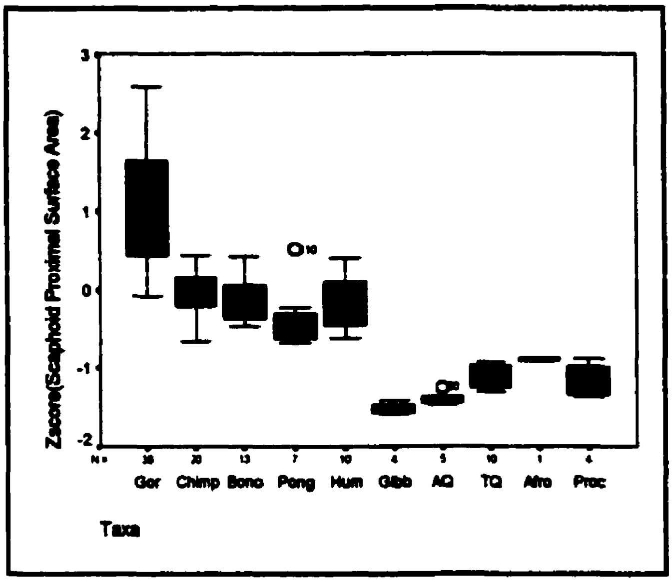


Figure 5.11: Z-scores for Lunate Proximal Area

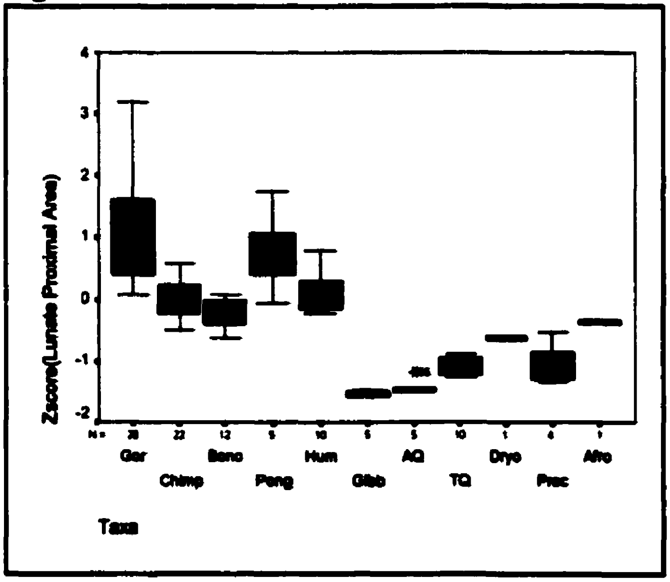


Figure 5.12: Ratio of Scaphoid to Lunate Area

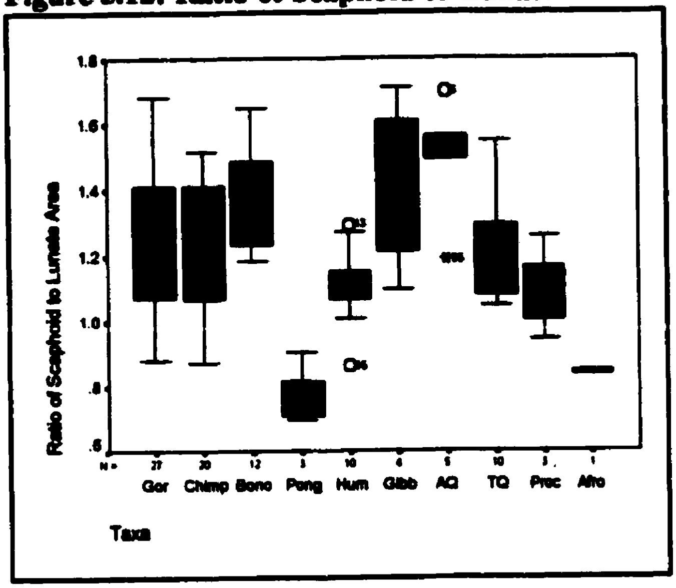


Figure 5.13: Error Plot of MIII Head Curvature Ratio

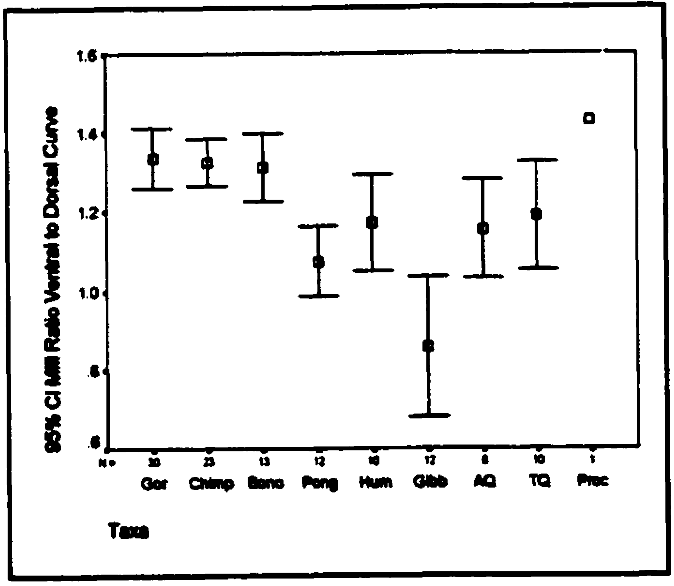


Figure 5.14: Error Plot of MIV Head Curvature Ratio

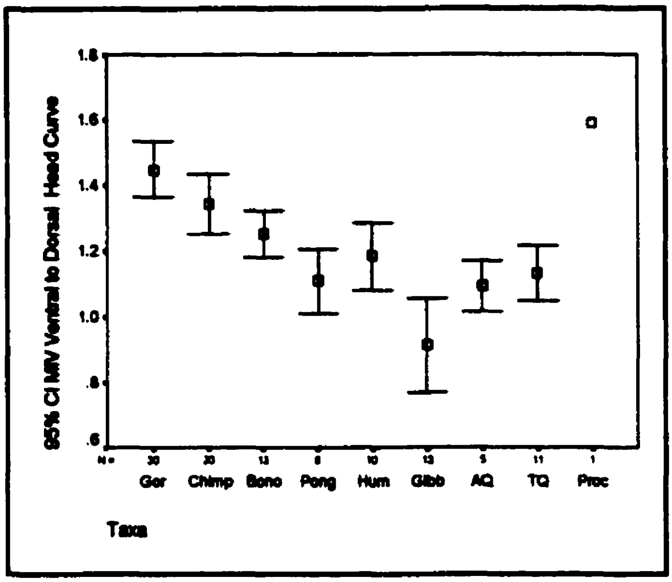


Figure 5.15: Boxplot of Ulnar Trochlear Notch Angle

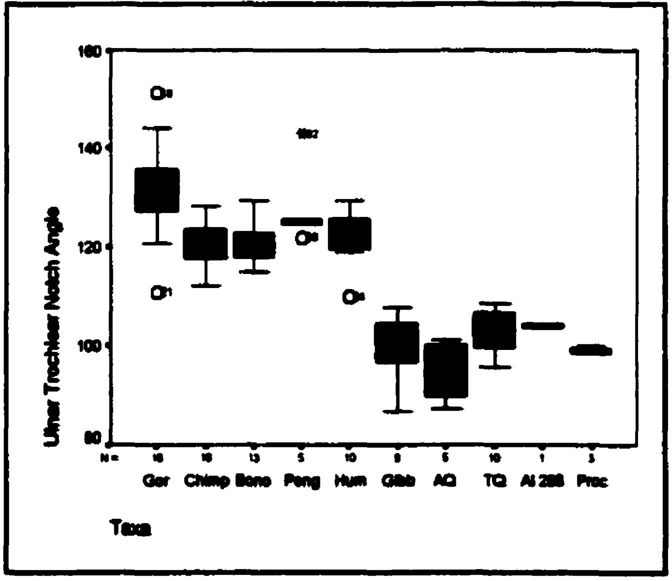
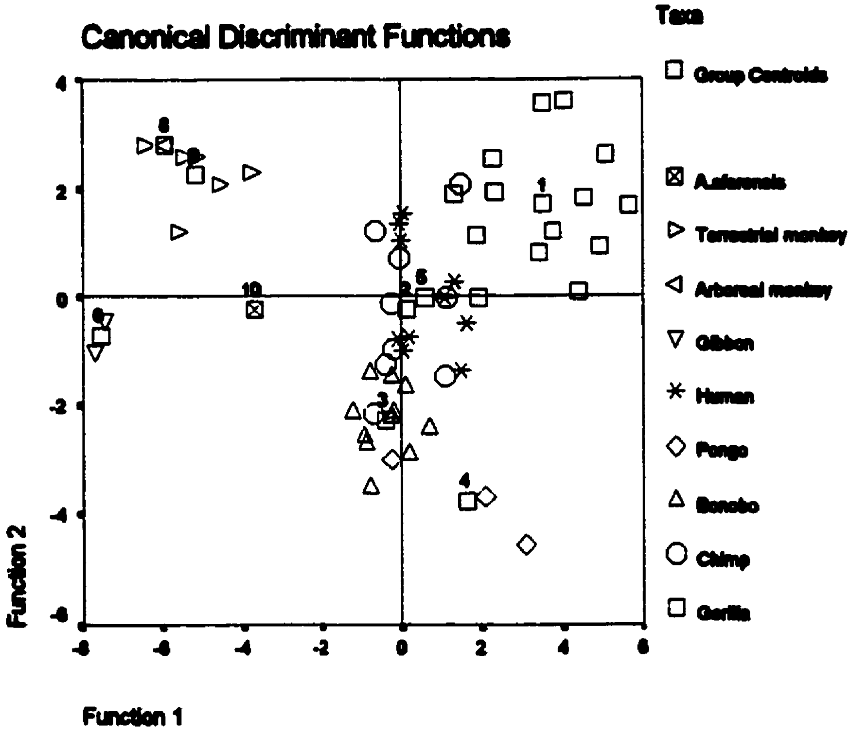


Figure 5.16: **Canonical Discriminant Function Analysis of elbow, wrist, and proximal phalanx variables for extant taxa and *A.afarensis* (AL 288-1)**



APPENDIX I

MODERN AND FOSSIL SPECIMENS ANALYZED

Abbreviations:
AMNH: American Museum of Natural History
CMNH: Cleveland Musuem of Natural History
GRANT: University of Toronto Grant Collection
KNM: Kenya National Musuems
MRAC: Musee Royal de l'Afrique Centrale
NMNH: National Museum of Natural History (Smithsonian Institute)
PC: Powell-Cotton Museum
ROM: Royal Ontario Musuem
UT: Primate Collections at the University of Toronto
DRB: Casts provided by David R. Begun, University of Toronto

Taxon	Specimen	Sex	Institute
Gorilla gorilla berengei	2263	F	MRAC
	8607	F	MRAC
Gorilla gorilla gorilla	17202	F	MRAC
	B1408	M	CMNH
	B1710	F	CMNH
	B1712	M	CMNH
	B1754	M	CMNH
	B1756	F	CMNH
	B1797	M	CMNH
	B1801	F	CMNH
	B1806	F	CMNH
	B1846	F	CMNH
	B1991	M	CMNH
	CamI 105	M	PC
	M135	M	PC

Taxon	Specimen	Sex	Institute
	M139	F	PC
	M150	F	PC
	M204	M	PC
	M372	M	PC
	M470	F	PC
	M729	F	PC
	MII 2	F	PC
	ZIII 31	M	PC
Gorilla gorilla graueri	1000	M	MRAC
	1001	M	MRAC
Gorilla gorilla graueri	18739	M	MRAC
	27755	F	MRAC
	27839	F	MRAC
	8187	M	MRAC
	995	F	MRAC
Pan troglodytes schweinfurtii	51376	M	AMNH
	51379	M	AMNH
	51392	F	AMNH
	51393	F	AMNH
Pan troglodytes troglodytes	B1056	M	CMNH
	B1708	M	CMNH
	B1722	M	CMNH
	B1723	F	CMNH
	B1726	M	CMNH
	B1748	F	CMNH
	B1749	F	CMNH
	B1855	F	CMNH
	B1758	F	CMNH
	B1759	M	CMNH

Taxon	Specimen	Sex	Institute
	B1761	F	CMNH
	B1766	F	CMNH
	CamI 147	M	PC
	CamI 207	M	PC
	CamIII 301	F	PC
	FC 116	M	PC
Pan troglodytes troglodytes	M424	F	PC
	M440	M	PC
	M712	F	PC
	M724	M	PC
Pan paniscus	15294	M	MRAC
	15295	F	MRAC
	27696	M	MRAC
	29404	F	MRAC
	29042	F	MRAC
	29044	M	MRAC
	29045	F	MRAC
	29047	M	MRAC
	29051	M	MRAC
	29052	M	MRAC
	29053	M	MRAC
	29054	M	MRAC
	29060	F	MRAC
Pongo pygmeaus abelli	145305	M	NMNH
Pongo pygmeaus pygmeaus	140426	M	AMNH
	145309	F	NMNH
	153823	M	NMNH
	239847	F	AMNH
	28252	M	AMNH

Taxon	Specimen	Sex	Institute
	28253	M	AMNH
Pongo pygmeaus ?	2170	F?	UT
	5645	M?	UT
	7120	M?	UT
	7122	F?	UT
	27807	F	NMNH
	B1444	M	CMNH
	B623	M	CMNH
Hylobates concolor	87251	M	AMNH
Hylobates concolor gabriellae	87253	F	AMNH
Hylobates hoolock hoolock	11092	F	AMNH
	112676	F	AMNH
	112721	F	AMNH
	80068	F	AMNH
	83425	F	AMNH
	99340	F	AMNH
	112720	F	AMNH
Hylobates klossi	103347	F	AMNH
Hylobates lar estelloides	208985	F	AMNH
Hylobates lar ?	402	?	UT
Hylobates pileatus	140230	M	AMNH
Hylobates syndactylus	106851	M	AMNH
	35613	F	AMNH
	90337	F	AMNH
Colobus guereza	OM3058	M	KNM
	OM3067	M	KNM
	OM3075	M	KNM
	OM3091	F	KNM

Taxon	Specimen	Sex	Institute
	OM3126	F	KNM
Nasalis larvatus	01-12-1-26	M?	ROM
Macaca fascicularis	FA 431-2	M	UT
Papio cynocephalus	70110	F	ROM
Papio hamadryas	91308	M	ROM
	91309	F	ROM
Papio anubis	OM5056	M	KNM
	OM5061	M	KNM
	OM5068	M	KNM
	OM6615	F	KNM
	OM314	F	KNM
Mandrillus sphynx	FA 432-2	F	UT
Erythrocebus patas	FA 435-1	M	UT
Homo sapiens sapiens	189	F	GRANT
	227	F	GRANT
	298	F	GRANT
	409	F	GRANT
	522	F	GRANT
	653	M	GRANT
	683	M	GRANT
	694	M	GRANT
	780	M	GRANT
	830	M	GRANT
Proconsul heseloni	KNM-RU 2036	?	KNM
	KPS III	?	KNM
	KPS VIII	?	KNM
Proconsul africanus	KNM CA 409	?	KNM
	KNM SO 999	?	KNM
	KNM SO 1002	?	KNM

Taxon	Specimen	Sex	Institute
	KNM LG 6	?	KNM
Proconsul nyanzae	KNM RU 15100	?	KNM
	KNM RU 1786	?	KNM
Afropithecus turkanensis	KNM WK 18372	?	KNM
	KNM WK 18121	?	KNM
Kenyapithecus wickeri	KNM FT 2751	?	KNM
Australopithecus boisei	KNM ER 739	?	KNM
	KNM ER 1504	?	KNM
Australopithecus anamensis	KNM KP 271	?	KNM
Lufengpithecus lufengensis (cast)	PA 1057	?	DRB
Sivapithecus sp. (cast)	GSP 17119	?	DRB
Sivapithecus parvada (cast)	GSP 19833	?	DRB
	NG 940	?	DRB
Dryopithecus laetanus (cast)	IPS 4340	?	DRB
	IPS 4344	?	DRB
Dryopithecus brancoi (cast)	RUD 53	?	DRB
	RUD 167	?	DRB
	RUD 166	?	DRB
Australopithecus afarensis (cast)	AL 288-1	F	DRB
	AL 333-40,50	M?	DRB
Australopithecus robustus (cast)	TM 1517	?	DRB

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