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Morphological Correlates of Primate Hallucal Grasping

A Thesis Presented

by

Katherine Elizabeth Goodenberger

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Master of Arts

in

Anthropology

(Physical Anthropology)

Stony Brook University

August 2012

Stony Brook University

The Graduate School

Katherine Elizabeth Goodenberger

We, the thesis committee for the above candidate for the

Master of Arts degree, hereby recommend

acceptance of this thesis.

James B. Rossie – Thesis Advisor
Associate Professor, Department of Anthropology

Karen L. Baab – Second Reader
Assistant Professor, Department of Anthropology

Biren A. Patel – Outside Committee Member
Research Instructor, Department of Anatomical Sciences

Caley M. Orr – Outside Committee Member
Research Instructor, Department of Anatomical Sciences

This thesis is accepted by the Graduate School

Charles Taber

Interim Dean of the Graduate School

Abstract of the Thesis

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Primates are unusual among mammals in having a well-developed hallucal grasping mechanism. Hallucal grasping has been featured in many adaptive scenarios of primate evolution. Some authors have suggested that primates possess more powerful hallucal grasping than non-primate euarchontans and that there are variations in hallucal grasping power and grasping type among primates. In these scenarios, powerful grasping is associated with the use of different substrate size and orientation and some authors have argued that these differences should be reflected in the morphology of the hallucal metatarsal (Mt1). Using data taken from the primate behavior literature, this thesis examines the morphology of the first metatarsal to establish what features are associated with differential substrate size and orientation use. This thesis further examines differences in first metatarsal morphology as it relates to grasping type and taxonomic group. The results of this study suggest that isolated features of the Mt1 are not good at distinguishing taxa with different substrate preferences or grasp type, but that taxonomic groups may be distinguished in this way. Among substrate groups, vertical clingers and leapers may be distinguishable on the basis of isolated curvatures of the proximal articular surface and peroneal process length and non-grasping taxa are significantly different from all other graspers in having lower torsion. Multivariate analyses of Mt1 shape do not successfully discriminate between substrate preference groups However, multivariate analyses of Mt1 shape across taxa that have different grasp types and belong to different taxonomic groups have high percentages of correctly classified cases. The results of this study suggest that Mt1 morphology may be useful in determining grasp type and taxonomic affinities of isolated fossil specimens, but that caution should be taken in interpreting substrate preference.

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INTRODUCTION

Primates are unusual among eutherian mammals in possessing grasping hands and feet (Smith, 1924; Cartmill, 1972, 1974, 1992). This feature is considered ecologically important because the extremities are involved in resource procurement and they are in direct contact with the substrate during locomotion in a complex three-dimensional environment. Accordingly, the ability to grasp has been invoked in adaptive scenarios of primate origins and intraordinal relationships (Smith, 1924; Cartmill, 1974, 1992; Szalay and Delson, 1979; Szalay and Dagosto, 1980, 1988; Sussman, 1991; Rollinson and Martin, 1981; Gebo, 1986, Bloch and Boyer, 2002; Bloch et al, 2007; Patel et al, 2012a). For example, three prominent models of primate origins proposed by Cartmill (1974, 1992), Sussman (1974, 1991), and Rasmussen (1990) suggest that well-developed pedal grasping ability allowed the earliest primates to access resources on small diameter branches in the understory or forest canopy (see also Bloch and Boyer, 2002, Bloch et al, 2007). Moreover, some scenarios for anthropoid origins suggest that a decrease in pedal grasping ability in this group led to the transition from habitually using vertical clinging and leaping behaviors to habitually using quadrupedal locomotion on relatively large diameter substrates (e.g., Rollinson and Martin, 1981; Gebo, 1986; Patel et al, 2012a).

Because there is significant variation in pedal grasping type and ability in living primates, several hypotheses have been proposed to account for the evolution of pedal grasping behaviors in primates and their closest living and fossil relatives (Figure 1). Some authors have suggested that the basal euarchontan possessed a rudimentary pedal grasping mechanism much like that of the extant, plesiomorphic tree shrew *Ptilocercus lowii* (Sargis, 2002; Sargis et al, 2007). A more powerful pedal grasping mechanism that facilitated fine branch locomotion is suggested to have appeared along the stem primate lineage at the common ancestor of Plesioadapoidea and crown

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primates ('Euprimateforms' of Bloch et al, 2007; Sargis et al, 2007; but see Gebo, 2004, 2009), culminating in a characteristically powerful pedal grasp that appeared at the base of euprimates. The more primitive form of the powerful pedal grasp is found in lorisiforms, cheirogalids and daubentoniids who all posses what Gebo (1985) described as a I-V pedal grasping mechanism in which the first ray grasps by opposing the other four lateral rays. This contrasts the typical, but likely more derived lemuriform condition of having a I-II pedal grasp in which the first ray opposes the second ray. Some authors have argued that pedal grasping in anthropoids is less powerful, and likely related to habitually using an above-branch quadrupedal locomotor repertoire, thus constituting a possible evolutionary reversal in hallucal grasping ability (Rollinson and Martin, 1981; Gebo, 1986; Patel et al, 2012a).

Because pedal grasping is both adaptively and ecologically important, paleoprimatologists and functional morphologists have tried to identify skeletal traits that reflect the type and potential power of grasping in order to reconstruct this behavior in fossil taxa, as well as to shed light on its evolution. Specifically, several features of the hallucal metatarsal (Mt1) have been associated with differences in grasping ability. Among these, a long and/or robust peroneal process, a high physiological abduction angle, a high degree of torsion, and a saddle-shaped, rather than ovoid, proximal articular surface are believed to reflect more powerful grasping ability (Figure 2).

A long and robust peroneal process has traditionally been considered an indicator of enhanced grasping ability in strepsirrhine primates because it is believed that this feature increases the mechanical advantage for *m. peroneus longus*, a muscle thought to be an important adductor of the hallux during powerful grasping (Walker, 1974; Conroy 1976; Szalay and Dagosto, 1988; Gebo 1986, 1987, 2004; Gebo et al, 2008). Recent electromyography (EMG)

research indicates that this muscle is recruited similarly in static behaviors and in grasping locomotion in both lemurs (Boyer et al, 2007) or lorises (Kingston et al, 2010), suggesting that *m. peroneus longus* may not play an important role in grasping. Accordingly, the peroneal process may not be a good indicator of pedal grasping abilities.

A longer peroneal process is correlated with a larger physiologic abduction angle (*sensu* Boyer et al, 2007, Jacobs et al, 2009, Patel et al, 2012a). This angle is between the long axis of the Mt1 diaphysis and its proximal articular surface, and may facilitate greater hallucal abduction (Jacobs et al, 2009) and thereby orient the Mt1 into a more favorable position to oppose the other digits. Taken together with a longer peroneal process, the physiologic abduction angle could serve as an indicator of a greater range of hallucal abduction. While both physiologic abduction angle and peroneal process size have been quantitatively examined in the context of leaping behaviors (Jacobs et al, 2009), neither has been examined as it relates to differences in grasping.

Metatarsal torsion is the rotation of the distal articular surface (i.e., its head) relative to the proximal articular surface (Largey et al, 2007) and it effectively realigns the axis of rotation around which flexion takes place at the first metatarsophalangeal and tarsometatarsal joints. Hence, the former joint is moved into a position that is more favorable for opposition of the first ray toward the lateral rays and this feature is thought to facilitate flexion of the joints around a curved surface such as a branch (Gebo, 1993). The enhanced ability to flex the first pedal ray around a curved surface has led some to infer that the presence of high Mt1 torsion is associated with more powerful grasping and an ability to utilize substrates that are small relative to body size (Bloch and Boyer, 2002; Patel et al, 2012a). Unlike peroneal process size and physiological abduction angle, Mt1 torsion has yet to be rigorously quantified in most primates other than hominoids (Pontzer et al, 2010; but see Moriyama, 1981). Rather, the amount of Mt1 torsion in

both living primates and fossils has typically been described qualitatively (e.g., "high torsion" or "little torsion") (Conroy, 1976, Bloch and Boyer, 2002, Bloch et al, 2007; Patel et al, 2012a). Furthermore, how Mt1 torsion relates to pedal grasping capabilities is unclear.

The relationship between articular surface curvature and both stability and range of excursion in joints is relatively well established (MacConaill, 1946; Godfrey 1991; Hamrick, 1996a,b). The proximal articular surface of the Mt1 is generally classified as either saddle-shaped, in which there is a concavity in the dorsovolar aspect and a convexity in the tibioperoneal direction, or ovoid, in which the tibioperoneal curvature is not convex, and the concavity of the dorsovolar aspect is decreased (Szalay and Dagosto, 1988). An ovoid proximal articular facet presumably facilitates a greater range of motion when compared to the more restrictive sellar articular facet (MacConaill, 1946; Szalay and Dagosto, 1988). Some authors have suggested that a more sellar-shaped proximal facet on the hallucal metatarsal may be associated with more effective grasping because the concave and convex surfaces allow for efficient rotation of the Mt1 toward the lateral digits, a condition necessary for opposable pedal grasping (MacConaill, 1946; Szalay and Dagosto, 1988). Like Mt1 torsion, the shape of the proximal articular surface, its curvature in particular, has yet to be quantitatively compared in most primate taxa other than hominoids (Proctor et al, 2008). Moreover, the functional relationship with this morphology and pedal grasping abilities is unknown.

Grasping 'power' has never been quantified or compared experimentally across primates. Rather, grasping ability has regularly been associated with relative substrate size preference. Specifically, relatively smaller (and thus more unstable) substrates are assumed to require a powerful grasp, relatively larger are assumed to require a less powerful grasp, and with vertical postures possibly requiring a more powerful grasp than horizontal postures require (Gebo, 1993).

Some recent experimental data do indicate higher digital flexor recruitment during grasping of small-sized, simulated arboreal substrates when compared with those of larger size (Boyer et al, 2007). Given the presumed relationship between powerful pedal grasping and substrate size and orientation, the current study examines the relationship between Mt1 morphology and substrate preference. It was predicted that primates that use relatively smaller horizontal or vertical arboreal substrates, when compared to those that use relatively large horizontal arboreal or terrestrial substrates, would have an Mt1 with a longer and more robust peroneal process, a greater angle of physiological abduction, a higher degree of torsion, and a more saddle-shaped proximal articular surface (e.g. higher curvature in the dorsovolar aspect and lower curvature in the tibioperoneal direction). After evaluating the functional morphology of the Mt1 in living primates, the Mt1s from fossil primates, including a stem primate, several stem strespsirrhines, a stem haplorrhine, several basal crown anthropoids, and a putative stem ape, were examined to understand how and when transitions in pedal grasping may have taken place.

In addition to examining hallucal morphology in the context of differences in substrate preferences, this study builds on a previous study (Patel et al, 2012a) in evaluating the differences of several variables that have never been previously quantified as they relate to grasping type (e.g., I-II, I-V, and DLG) and their relationship to taxonomic group (e.g., non-primate, prosimian, or anthropoid).

MATERIALS AND METHODS

Institutional Abbreviations

AMNH, American Museum of Natural History, New York; **DPC**, Duke Lemur Center Division of Fossil Primates, Durham, North Carolina; **MCZ**, Museum of Comparative Zoology –

Harvard University, Cambridge, Massachusetts; **NHMB**, Naturhistorisches Museum Basel, Basel, Switzerland; **SBU**, Stony Brook University, Stony Brook, New York; **USNM,** United States National Museum, Smithsonian, Washington D.C.; **UM**, University of Michigan, Ann Arbor, Michigan; **YPM**, Yale Peabody Museum, New Haven, Connecticut

Comparative sample

First metatarsals of 79 extant primate taxa with representatives from all major clades (n=208), one tupaiid species (n=6) and one dermopteran species (n=1) housed in the collections of the AMNH, DPC, MCZ, SBU, and USNM were included in this study (Table 1). Nine fossil taxa (n=14), including one stem primate (*Carpolestes simpsoni*), four adapids (*Notharctus osborni, Leptadapis magnus, Adapis parisiensis,* and *Adapoides troglodytes*), one omomyid, (*Hemiacodon gracilis*), three stem catarrhines (*Aegyptopithecus zeuxis, Catopithecus browni*, and *Epipliopithecus vindobonensis*), and one stem hominoid, (*Proconsul africanus*) were also studied.

Substrate preference and grasp type

Taxa were divided into groups based on 1) substrate preference and by 2) grasping type as defined by Gebo (1985) and modified by Patel et al (2012a) (Table 1).

Substrate categories that are meant to reflect the power of pedal grasping were based on substrate size and orientation data gathered from the primate behavior literature. Taxa were divided into six groups: non-grasping (NG), terrestrial (T), semiterrestrial (S), large branch quadrupeds (LQ), small branch quadrupeds (SQ), and vertical clingers and leapers (VCL). Non-graspers were those taxa that lack a primate-like grasping hallux (*Tupaia* and *Cynocephalus*),

and *Homo*, which represents a reversal from the grasping hallux of other extant primates. Terrestrial taxa were those that spend >75% of their time on the ground whereas semiterrestrial taxa were those that spend between 30-75% of their time on the ground. Vertical clingers were those arboreal taxa that are traditionally described as vertical clingers and leapers (*sensu* Napier and Walker, 1967) and routinely use orthograde progression and postures in the trees. Large branch quadrupeds and small branch quadrupeds are those that predominantly use above-branch quadrupedal locomotion.

Small branch quadrupeds (SQ) and large branch quadrupeds (LQ) were divided into their respective groups based on the frequency of small branch use. In order to correct for the influence of body size, relative branch size was defined as a function of body mass following Stevens (2008). Using average body mass taken from Smith and Jungers (1997) the diameter that defined relatively small branches was calculated as:

$$\text{Diameter} = \sqrt[3]{Mass} \text{ x 2.5cm.}$$

Stevens (2008) observed that taxa using small branches defined in this way were able to almost entirely encircle by the grasping foot.

Taxa that spend ≥25% of their time on branches at or below this size were included in the PA group while those that spend <25% of their time on these branches were included in the NA group.

Definitions of positional behavior and substrate preference and the resulting data vary substantially between studies. For example, some studies only report substrate size and orientation in locomotion, whereas others present it as a part of overall time. In most of the behavioral literature, branch diameter used by primate taxa is grouped into bins (e.g. 0-5 cm, 5-10 cm), and substrate size bins vary widely across studies even of the same taxa (e.g., Gebo and

Chapman, 1996, 1996 vs. McGraw, 1996, 1998). When relatively small branch size as calculated from the above equation did not match the upper limit of a bin (e.g., when relatively small branches are 6.5cm but substrate size bins from the literature are 0-5cm, and 5-10cm), percentage of time spent in small branches was taken as the time spent on the proportion of time in the bin rounded to the nearest value. In only one case, *Pan troglodytes* (Hunt, 1992) was it necessary to round up to the next highest bin. In cases in which more than one study was available for a given species, proportion of time spent on relatively small branches was obtained from the study that had bins that had an upper limit closest to the branch size defined as relatively small. For example, there are several studies of the positional behavior *Piliocolobus badius* including those by Gebo and Chapman (1996; 1996) and McGraw (1996; 1998). Relatively small branches for *Piliocolobus badius*, based on its average body mass, are those branches with diameters at or below 4.99 cm. Gebo and Chapman's (1996; 1996) studies have substrate size bins which include a category "0-5 cm" whereas McGraw's (1996; 1998) studies have substrate diameter bins, divided into "twig" which is 0-2cm, and "branch" which is 2-10cm. In this case, because Gebo and Chapman's (1995; 1996) studies have bins that match more closely with relatively small branches, only data from their studies were used. When more than one study had bins that were directly comparable, proportion of time on small branches was calculated as an average. For example, in their studies of *Alouatta seniuculus* positional behavior, Fleagle and Mittermeier (1980), Schon-Ybarra and Ybarra (1987), and Youlatos (2001) all use the same substrate diameter bins, and as such, proportion of time spent on small branches is based on the average of all three studies. Additionally, in some taxa, e.g. *Ateles* (Cant et al, 2001), many postures such as forelimb-dominated or tail-assisted suspension do not involve

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pedal grasping. In those cases, time spent in postures that do not involve contact between the foot and substrate was not included in proportion of time spent in relatively small branches.

When available, precise proportion of time spent on small branches was taken from the literature; however, when data were not available for precise percentage of time spent on different substrate sizes qualitative data on substrate size preference (e.g., "*[Microcebus murinus] is generally active in what can be called the fine branch niche" (Martin, 1973 p. 15)* was used for classification.

Grasping types included: primitive non-grasping (PNG) for the two non-primate taxa, *Tupaia* and *Cynocephalus*; I-V grasping (I-V) for cheirogaleids, *Daubentonia*, *Lepilemur*, lorisiforms, and *Tarsius*; I-II grasping (I-II) for all other lemuriforms; and derived limited grasping (DLG) for all anthropoids. Modern humans were also classified in DLG even though they do not habitually grasp with their highly specialized, adducted hallux.

Measurements

Thirteen measurements on each metatarsal were obtained including the same seven linear and angular measurements described in Jacobs et al (2009) and Patel et al (2012a), two new linear measurements on the distal end of the Mt1, proximal articular surface area, two curvatures from the proximal articular surface, and Mt1 torsion.

Linear and angular measurements of peroneal process length, peroneal process thickness, proximodistal maximum length, proximodistal interarticular length, mid-diaphyseal dorsoplantar diamter, proximal articular surface dorsoplantar height, and physiologic abduction angle were taken in AxioVision Rel 4.4 or SigmaScan Pro on photographs or digital reconstructions

following Jacobs et al (2009) and Patel et al (2012a). In addition, distal articular width and distal articular height, both taken at the location of widest epicondylar breadth of the distal articular facet were taken on digitally reconstructed models. Proximal articular surface area was calculated in Geomagic (Studio v. 10).

Proximal articular surfaces were segmented from three-dimensional models in Geomagic Studio (v. 10) software. Some taxa (e.g. ceboids and hylobatids) have an entocuneiform first metatarsal joint that includes a prehallux (Lewis, 1972; Wikander et al, 1986) and this feature is often reflected by an additional facet on the proximal metatarsal. For the purposes of this study, the prehallux facet was not included in the segmented mesh. Each proximal articular surface was then modeled with a least-squares fit quadric function following the methodology of Marzke et al (2010) (Figure 3). The two principal curvatures (approximating the dorsoplantar and tibioperoneal axes) were extracted as the first and second coefficients of that quadric function. Each coefficient was then scaled to joint size by multiplying the curvature by the square root of the surface area, such that a higher scaled coefficient indicated greater curvature.

In one previous attempt to quantify torsion of the first metatarsal, Pontzer et al (2010) estimated the major axis of the proximal articular surface from the longest diameter of the surface and calculated the angle between that and the major axis of the distal end, which was calculated as a line oriented dorsovolarly and parallel to the midline keel. In this study, the tarsometatarsal axis was calculated using the curvatures fit to the proximal articular surface. The eigenvector orthogonal to the principal curvature of the quadric fit to the proximal surface was calculated to approximate the flexion of the tarsometatarsal joint (i.e., the orientation of motion between the Mt1 and entocuneiform during adduction and abduction) (see Ogihara et al, 2009). In contrast to previous studies, the orientation of the distal axis of rotation was calculated as a

vector of two points connecting the deepest points of the grooves on the volar surface of the distal metatarsal. The impressions house the sesamoid bones of the *m. flexor hallucis brevis*, a flexor of the tarsometatarsal joint, and these sesamoids project volarly to form a canal through which the long flexor (*m. flexor hallucis longus* of human anatomy, or *m. flexor digitorum fibularis* and *m. flexor digitorum tibialis* of non-human primate anatomy) passes. Experimental evidence suggests that *m. flexor tibialis* is an important muscle in 'powerful' pedal grasping as it is recruited to a greater extent during narrow-pole locomotion than during static behaviors or large-pole locomotion (Boyer et al, 2007; Kingston et al, 2010). The sesamoid grooves represent a good approximation of the location of the important flexor muscles and so a vector connecting the deepest location of the sesamoid grooves may be a more adequate estimation of the orientation of the axis of flexion of the metatarsophalangeal joint.

To estimate the orientation of the axis of flexion, specimens were oriented in dorsal view and the distal-most aspect of the bone was removed using the line boundary tool at the location of the widest epicondylar breadth (Figure 4A). Three landmarks were placed on the cut surface, one in the deepest location within sesamoid groove as defined by the greatest perpendicular distance between the points connecting the epicondyle on the ipsilateral side and the midline keel, and one point on the dorsal surface midway between the epicondyles (Figure 4B).

Torsion was calculated as the angle between the eigenvector from the proximal articular surface and the vector between the two points in the sesamoid grooves (Figure 5). Using this redefined distal axis, specimens with what is usually described as high torsion will actually have a lower angle. In order to conform to previous terminology the resulting angle was subtracted from 90 degrees.

Analyses

The non-independence of data due to shared evolutionary history requires that species' relatedness be accounted for in order to reduce type I and type II error in comparative analyses (Felsenstein, 1985; Harvey and Pagel, 1991). The phylogenetic position and branch lengths of the taxa included in this study were taken from a consensus tree from the 10k Trees website (Arnold et al, 2010). In analyses that included *Tupaia* and *Cynocephalus*, the primate consensus tree was modified based on the tree topology and branch lengths of these outgroup taxa from Janecka et al (2007). All phylogenetic analyses used species means for each variable.

In order to test for differences in each variable as it relates to grasping, phylogenetic ANOVAs were calculated between groups (e.g., substrate preference and grasp type) as described above. Analyses were conducted using the R package Geiger (Harmon et al, 2007) that follows Garland et al's (1993) method that simulates evolution of a trait along a phylogenetic tree under a Brownian motion model and then generates a simulated F-statistic. Post-hoc tests using the Bonferroni method were conducted in the R package phytools (Revell, 2012). For comparison, each variable was examined among substrate preference and grasp type groups using standard ANOVAs. All variables were examined to determine whether or not taxonomic groups (e.g. non-primates, prosimians, and anthropoids) differ using a standard ANOVA with Bonferroni and Games-Howell post-hoc comparison calculated in SPSS 16.0.

Phylogenetic generalized least squares (PGLS) accounts for the impact of species' relatedness in a linear regression model. In order to test for a linear relationship between increased small branch use (i.e., proportion of time spent on the narrow branch category) and each variable, PGLS regressions were conducted using Pagel's lambda optimization in the Caper package of R (Orme et al, in press) on a subset of the taxa for which precise proportion of time

on small branches could be calculated. Proportions of time that taxa spend on relatively small branches were subjected to arcsine transformation and regressed against peroneal process length, peroneal process thickness, physiologic abduction angle, torsion, curvature A, and curvature B. Ordinary least squares (OLS) regressions were also performed between variables.

Finally, in order to examine whether or not the morphology of the Mt1 discriminates between 1) taxa that used substrates of different size and orientation (i.e., NG, T, S, LQ, SQ, and VCL), 2) between different grasp types (i.e., PNG, I-V, I-II, and DLG), and between 3) anthropoids, prosimians, and non-primates, canonical discriminant analyses (CDA) were conducted in SPSS 16.0 software. Because there are overall shape differences that tend to discriminate between anthropoid and prosimian Mt1s (Patel et al., 2012a), additional CDAs of grasp type among prosimians and of substrate preference in prosimians and in anthropoids were conducted. In all CDAs, linear measurements and the square root of proximal articular surface area were divided by the geometric mean, angular measurements were calculated in radians, and curvatures of the proximal articular surface remain scaled to the size of the articular surface. Classification results were compared between original CDA and CDAs using leave-one-out cross-validation. Extant specimens were assigned *a priori* to their respective groups (Table 1). Because we also wanted to see how fossil Mt1s would be classified, they were no assigned to any specific group before running the analyses.

RESULTS

Table 2 presents the species means and standard deviations for each of the six functional variables included in this study. Box-and-whiskers plots of the raw data for each variable within taxonomic groups, grasp types, and substrate preference groups are illustrated in Figure 6.

Overall, there appears to be a trend toward longer peroneal processes in vertical clingers and leapers, and relatedly, among I-V graspers. Peroneal process thickness, physiologic abduction angle, and curvature A do tend to be higher in vertical clingers and leapers, despite similarly lower means in all other grasp substrate preference groups. Among grasping primates, torsion tends to be similar across all groups; however, non-graspers (e.g., tree shrews and colugos as well as *Homo*), appear to have vastly lower torsion than all other groups. Vertical clingers and leapers do appear to have a more negative curvature B; however, this overlaps with some non-graspers.

ANOVAs

The phylogenetic ANOVA results indicate that peroneal process length, Mt1 torsion, curvature A, and curvature B are significantly different among substrate preference groups while peroneal process thickness and physiologic abduction angle are not significantly different. Table 3 shows the F-statistic and phylogenetic p-values from phylogenetic analysis. For comparison, the F-statistic and p-values from a standard ANOVA are included. Peroneal process length is significantly different in the phylogenetic ANOVA (phylogenetic $p<0.01$) in that vertical clingers and leapers have relatively longer peroneal processes when compared with those of all other substrate preference groups. Mt1 torsion is significantly different among substrate preference groups (phylogenetic $p<0.01$) and post-hoc comparisons indicate that non-grasping taxa are significantly different from all others in having lower torsion while comparisons between other substrate preference groups are non-significant.

Additionally, the first principal curvature, curvature A, is significantly different between substrate preference groups (phylogenetic $p<0.05$) and post-hoc comparisons indicate that only

vertical clingers and powerful arboreal graspers (phylogenetic $p < 0.05$) are significantly different from one another. Finally, curvature B is significantly different between vertical clingers and leapers and all other groups (phylogenetic $p < 0.05$ in all post hoc comparisons) except non-primates.

Among grasp types, only curvature A is significantly different. Curvature A is significantly higher in I-II graspers than in derived limited graspers. All other variables are not significantly related to differences in grasp type (Table 4).

The standard ANOVA results indicate that each of the six variables is significantly different among taxonomic groups (Table 5). Prosimians have longer peroneal processes than do anthropoids and non-primates ($p < 0.01$ in both comparisons) while peroneal process length is not different between anthropoids and non-primates. Peroneal process thickness and physiologic abduction angle are significantly different between prosimians and both anthropoids and non-primates ($p < 0.01$ and $p < 0.05$, respectively in peroneal process analysis, and $p < 0.01$ in both physiologic abduction angle analyses), with prosimians having thicker processes and higher physiologic abduction angles than anthropoids or non-primates. In these analyses, there are no significant differences between anthropoids and non-primates. Mt1 torsion is significantly lower ($p < 0.01$) in non-primates than in all primates, and anthropoids having lower torsion ($p < 0.01$) than prosimians. Curvature A is significantly different among all taxonomic groups ($p < 0.01$ in all post-hoc comparisons), with prosimians having the highest curvature, followed by non-primates, and then finally by anthropoids. Curvature B is significantly higher in prosimians than both anthropoids and non-primates, and significantly higher in anthropoids than in non-primates.

Regression

Results of the PGLS and OLS regressions are presented in Table 3. Because of the similar results in terms of both slope direction and p-value, only the PGLS results are discussed. There is a significant relationship between Mt1 torsion and proportion of time spent on small branches. Specifically, as the proportion of time spent on relatively small branches increases, there is trend toward higher torsion ($p<0.01$; Figure 7). Despite significant results, the proportion of variance explained in the torsion regression is small, at 0.27. All other variables show no significant relationship with percentage of time spent on small branches.

Canonical discriminant analysis

The results of this study indicate Mt1 morphology does not successfully discriminate between taxa with prior assignment to substrate preference groups. Only 67.3% of cases were originally classified correctly and 61.2% correctly classified using leave-one-out cross-validation (Table 7). Non-graspers and vertical clingers were, however, correctly classified with higher frequency than other substrate preference groups in this analysis (100% and 86.7%, respectively). Taxa assigned *a priori* as terrestrial were routinely classified as either semiterrestrial, large branch quadrupeds, or small branch quadrupeds. *A priori* semiterrestrial taxa were classified incorrectly in nearly two-thirds of all cases. Large branch quadrupeds and small branch quadrupeds were frequently misclassified as predicted to belonging to the other group, but less frequently misclassified as semiterrestrial, non-graspers, or even vertical clingers. *Carpolestes* was classified as a large branch quadruped (Table 9). Different adapids were classified as either semiterrestrial, terrestrial, and large branch quadrupeds. In this analysis,

Hemiacodon is predicted to be a non-grasper, but with relatively lower posterior probability (0.565). The fossil anthropoids are all predicted to be arboreal with the exception of *Proconsul.*

Substrate preference analyses of prosimians and anthropoids separately demonstrate a greater ability to discriminate between different substrate preference groups when overall differences between anthropoids and prosimians are negated. In the prosimian-only analysis, 87.7% of taxa were correctly classified and 76.5% correctly classified when cross-validated (Table 10). Taxa were separated along the first discriminant function by curvature B, relative maximum length and relative distal articular surface height (Table 11). Small branch quadrupeds fall along the more positive end of this spectrum, with higher curvature B, relatively higher distal articular height, and relatively lower maximum length of the bone whereas vertical clingers were clustered more negatively along the first discriminant function. Large branch quadrupeds and semiterrestrial taxa were distinguished from small branch quadrupeds along the second discriminant function in having a relatively shorter peroneal process and a higher curvature A. Semiterrestrial specimens were the group most frequently misclassified, which is not surprising in light of other studies that have found gross morphological similarities between semiterrestrial and arboreal taxa when compared with primarily terrestrial animals (e.g., Gebo and Sargis, 1994). In this analysis, posterior probabilities for fossil taxon assignment was substantially higher (Table 12). *Carpolestes, Adapis*, and *Adapoides* were predicted to belong to the semiterrestrial group with high posterior probability, and *Leptadapis* and *Hemiacodon* had relatively high probability of belonging to non-powerful arboreal graspers. As in the all-primate analysis, *Notharctus* was classified as a vertical clinger.

The anthropoid-only analysis yields correct classification 80.2% of the time and 69% with cross-validation. Anthropoid non-graspers (*Homo*) are classified correctly 100% of the time

whereas correct classification of other groups is less frequent, with large branch quadrupeds classified correctly most frequently at 83.7%. Interestingly, terrestrial taxa are routinely classified as large branch quadrupeds but do not appear to be misclassified as semierrestrial despite being more similar in substrate preference. Predicted group membership for fossil anthropoids places *Catopithecus* and *Epipliopithecus* as small branch quadrupeds, *Proconsul* as semiterrestrial, and *Aegyptopithecus* as terrestrial which contrasts with its predicted position as a small branch quadruped in the all-primate substrate preference analysis,

Among all taxa included in this study, Mt1 morphology successfully discriminated between different grasp types with 98.6% and 97.2% of all cases correctly classified and with leave-one-out cross-validation, respectively. The majority of taxa misclassified were taxa assigned to the I-V grasp type but were predicted to be I-II or derived limited graspers. In this analysis, primate grasp groups (I-V, I-II, and DLG) are separated along the first discriminant function (67.9% of the variance explained) which is primarily driven by relative peroneal process length, first principal curvature, and the physiologic abduction angle. I-V graspers are clustered together on the positive end of the first function in having higher peroneal process length, and higher curvature A, and a greater physiologic abduction angle. Derived limited graspers are clustered on the negative end of first function, and I-II graspers are situated in between. Primates and primitive non-graspers are separated along the second discriminant function (28.9% of variance explained) which is driven by a more negative curvature B and lower torsion than members of the primate grasp groups. With the exception of one *Adapis* specimen (NHMB QL 418), which was predicted to be a derived limited grasper, all of the adapids and *Hemiacodon* were predicted to be I-II graspers. As in the previous analysis, *Carpolestes* is grouped along with

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anthropoids as a derived limited grasper. Finally, all of the anthropoids included in this study had strong probability of assignment to the derived limited grasping group.

Results from the discriminant analysis of grasp type among prosimians showed a marginally higher success rate of distinguishing between I-V and I-II graspers, with 98.8% of correctly classified originally and 95.1% of cases correctly classified when cross-validated. While overall percentage of cross-validated correct classification is lower, 97.8% of I-V graspers and 91.3% of I-II graspers were correctly classified in cross-validation in the prosimian-only analysis whereas 97.1% (original) and 91.3% (cross-validated) were correctly classified in the analysis of all specimens. In contrast to the previous analysis, *Notharctus* and *Hemiacodon* were predicted in the prosimian-only analysis to belong to the I-V grasp group and *Carpolestes* fell out with I-II graspers when derived limited grasping was not one of the possible groups.

The results of this study indicate, like those previous studies (Patel et al, 2012a), that non-primate euarchontans, prosimians, and anthropoids can be distinguished on the basis of their Mt1 morphology with 98.6% of cases correctly classified, and 98.1% of cross-validated cases correctly classified. Prosimians are distinguished from anthropoids primarily along the first discriminant function (77.2% of the variance) in having a more positive curvature A, a more negative curvature B, and a longer peroneal process. Non-primates are distinguished from both anthropoids and prosimians along the second discriminant function (22.8% of the variance) in having a greaterphysiological length and lower torsion. In this analysis, the majority of adapids (*Adapis*, *Leptadapis*, *Adapoides*, and *Notharctus*) were classified as prosimians, with the exception of one *Adapis* specimen (NHMB QL 418) and one *Leptadapis* (NHMB QL 313), both of which were classified as anthropoids with probabilities of 0.892 and 0.501, respectively. *Hemiacodon* was predicted to belong to prosimians with a high probability (0.999), and all of the

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anthropoid fossils in the study were predicted as anthropoids with high probability. *Carpolestes simpsoni* was classified as an anthropoid and not as a non-primate.

DISCUSSION AND CONCLUSIONS

Several features of the primate first metatarsal, including a long and robust peroneal process, physiologic abduction angle, torsion, and curvatures of the proximal articular surface have been cited as a means with which to infer substrate preference and grasping power (Bloch and Boyer, 2002; Sargis et al, 2007; Patel et al, 2012a), make inferences about grasping type (sensu Gebo, 1985), and justify assignment of isolated Mt1s as belonging to anthropoids or prosimians (Patel et al, 2012a).

Results of this study suggest that the variables studied here are good indicators of taxonomic affinity and supports the suggestion that isolated fossil Mt1s may be attributed to their taxonomic group based on isolated morphology. Furthermore, high percentages of correct classification in the CDA further indicate that attribution to taxonomic group is possible.

While Mt1 morphology successfully distinguished different grasp types based on overall Mt1 shape, isolated morphology (e.g., high curvature B, or low torsion) is not a useful means by which to infer grasp type. High percentage of correct classification of taxa to their respective grasp type may largely be due to the fact that grasp type is largely, though not entirely, distributed along phylogenetic lines.

With regard to substrate preference, relatively longer peroneal processes were predicted to be associated substrate use that requires more 'powerful' grasping. Vertical clingers and leapers, which may use foot postures that require more powerful pedal grasping (Gebo, 1993; but see Boyer et al, 2007) (though it should be reiterated that no experimental work has

demonstrated this), did have significantly longer peroneal processes. However, the overall relationship between use of relatively smaller substrates and peroneal process length was weak as evidenced by the fact that no other substrate preference groups could be distinguished from one another and that the PGLS regression was not significant between proportion of time in small branches and peroneal process length.

Results for the association between both peroneal process thickness and physiologic abduction angle and substrate preference, did not fit the predictions that both measures would be higher in taxa that grasp more frequently. Neither variable had a significant association with substrate preference or a significant relationship in the PGLS regression.

The prediction that higher torsion is associated with use of substrates that require grasping was partially supported. Non-grasping taxa, including both non-primate euarchontans, *Tupaia* and *Cynocephalus*, and a primate that represents an evolutionary reversal away from grasping, *Homo*, have significantly lower torsion than all of the grasping primates in this analysis. Torsion, however, did not differentiate between any of the other substrate preference groups. The PGLS regression yielded a significant relationship between increased small branch use and higher torsion. Despite significance, the predictive value of torsion as a way to estimate proportion of time on small branches is minimal.

Both curvature A and curvature B are significantly related to grasping power, and like peroneal process length, are only significantly different between vertical clingers and leapers and all other grasping groups. Curvature A is significantly higher while curvature B is significantly more negative in vertical clingers and leapers when compared with other substrate preference groups.

Overall, the results of this study indicate that Mt1 morphology may not be a good means by which to infer substrate preference based on the limited significant differences between substrate preference groups, non-significance of the linear relationship between proportion of time spent on relatively small branches and most of the variables, and relatively low percentage of correctly classified cases in the discriminant function analyses. While this study attempted to create a metric by which to justify classification of some taxa on a continuum of grasping 'power', it is possible that some of the inconsistency between the results and predictions arise from inherent problems with using existing behavioral data. Some authors have argued that different methodology for collecting behavioral data may greatly influence results in positional behavior studies and may render positional behavior studies incomparable (Dagosto and Gebo, 1998) while others have shown that there may be a great deal of inaccuracy in estimating substrate properties by researchers (Bezanson et al, 2012). Additionally, there is a great deal of inconsistency in the way that some authors assign substrate size bins which makes the comparison of time spent on small branches difficult. Perhaps with increasing methodological consistency, more accurate methods for assessing substrate properties, and assignment of substrate bins with an eye toward dividing substrate sizes into those that reflect relatively small and relatively large sizes it will be possible to better examine the relationship of Mt1 morphology to substrate preference.

Despite the difficulty of inferring substrate preference from Mt1 morphology, vertical clingers and leapers have relatively longer peroneal processes, and a strongly saddle-shaped (higher dorsovolar curvature and more a more negative tiboperoneal curvature) and these features may be useful indicators of substrate preference in fossil primate Mt1s. Significant differences in peroneal process length that differentiate vertical clingers and leapers from taxa

with different substrate preferences are interesting in light of Jacobs et al's (2009) findings that grasp-leaping behavior was not associated with differences in peroneal process length. It is possible that these conflicting results may be due to differences in group membership. In this study, the only taxa included in the VCL substrate group were those that are primarily orthograde during leaping whereas Jacobs et al (2009) included *Pithecia,* which tends to use pronograde leaping (Fleagle and Mittermeier, 1980), in their 'leaper' group. Furthermore, this analysis included *Galagoides demidoff* in the vertical clinging and leaping group while Jacobs et al (2009) included it in the 'intermediate leaper' category. It is possible that peroneal process length does not correlate with overall leaping frequency, but may be different among taxa that go about leaping in orthogrady.

Mt1 torsion, too, may be useful for reconstructing substrate preference and perhaps help shed light on grasping evolution. Torsion did not differentiate primates that possess a grasping hallux regardless of differences in substrate use; however, both non-primates non-graspers and *Homo* which lacks a grasping hallux have similarly low torsion. It is possible that having high torsion is associated with primate-like pedal grasping and that non-primates lack this feature and that as humans lost their ability to abduct and adduct their hallux they convergently reverted to lower torsion. As such, it is possible that torsion is a reflection of grasping ability and may be useful as a means by which to infer this behavior in stem primates and in hominins. In this analysis, all of the crown primate fossils included fall well within the range of torsion exhibited by extant grasping primates. Adapids (*Adapis, Leptadapis, Notharcus,* and *Adapoides*) have torsion values that fall in line with primate graspers and differ from the values in non-graspers which may suggest that early euprimates had a primate hallucal grasping mechanism. Torsion in the Mt1 of *Carpolestes simpsoni* is on the low end of the range of all grasping primates, but is

much higher than in non-graspers. This may indicate a transition toward primate-like grasping in this stem primate.

Overall, the results of this study indicate that caution should be taken in making inferences about substrate preference in fossil taxa as it relates to the evolution of grasping among primates (e.g., Patel et al, 2012a). Alternatively, the results of this study indicate that it may be possible to identify vertical clingers and leapers from other groups and that torsion may be of interest to those who wish to reconstruct the evolution of grasping among stem primates lineage or the transition away from pedal grasping along the hominin lineage.

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APPENDIX

Taxon	Grasp Type	Substrate	Proportion Small Branch Use	Reference
Allenopithecus nigroviridis	DLG	S	—	Gautier-Hion 1988
Alouatta seniculus	DLG	SQ	0.3836	Fleagle and Mittermeier, 1980; Schon-Ybarra and Ybarra, 1987; Youlatos, 1998
Aotus azarae	DLG	SQ	—	Sussman, 2000
Arctocebus calabarensis	I-V	SQ	0.4	Charles-Dominique, 1974
Ateles belzebuth	DLG	LQ	0.0521	Cant et al, 2001
Ateles fusciceps	DLG	LQ	—	Cant, 1986**
Ateles geoffroyi	DLG	LQ	0.23	Cant, 1986
Avahi laniger	I-II	LQ	—	Warren, 1997
Bunopithecus hooloch	DLG	LQ	—	Islam and Feeroz, 1992
Callimico goeldii	DLG	LQ	—	Garber and Leigh, 2001
Callithrix jacchus	DLG	LQ	—	Young, 2008; Beattie, 1927
Cebus apella	DLG	SQ	0.472	Fleagle et al. 1980; Youlatos, 1998
Cercocebus agilis	DLG	S	—	Walker, 2004
Cercopithecus mona	DLG	S	—	Gartlan and Struhsaker, 1972
Cercopithecus neglectus	DLG	LQ	0.143	Gautier-Hion 1988
Cercopithecus nictitans	DLG	S	—	Bitty and McGraw, 2007
Cheirogaleus major	I-V	LQ	—	Charles-Dominique,
Chiropotes satanas	DLG	LQ	0.1198	Rose, 1979
Chlorocebus aethiops	DLG	SQ	0.3009	Rose, 1978; Rose, 1979; Gebo and Chapman, 1995
Colobus guereza	DLG	LQ	0.2037	McGraw, 1998
Colobus polykomos	DLG	SQ	0.25	—
Daubentonia madagascariensis	I-V	SQ	—	Petter and Peyrieras, 1970
Erythrocebus patas	DLG	T	—	Isbell et al, 1998
Eulemur albifrons	I-II	LQ	0.2	Dagosto, 1994
Eulemur collaris	I-II	LQ	0.2	Dagosto, 1994
Eulemur coronatus	I-II	LQ	—	Dagosto, 1994**
Eulemur macacao	I-II	LQ	—	Dagosto, 1994**
Eulemur mongoz	I-II	LQ	—	Tattersall and Sussman, 1975
Galago moholi	I-V	VC	0.19	Harcourt and Bearder, 1989
Galago senegalensis	I-V	VC	0.19	Crompton, 1984
Galagoides demidoff	I-V	VC	0.25	Charles-Dominique, 1974
Gorilla gorilla gorilla	DLG	S	—	Remis, 1995
Hapalemur griseus	I-II	VC	—	Gebo, 1987*
Homo sapiens	DNG	NG	0	—
Indri indri	I-II	VC	—	Napier and Walker, 1967
Lagothrix lagotricha	DLG	NA	0.0784	Cant et al, 2001
Lemur catta	I-II	S	—	Sussman, 1974; Ward and Sussman, 1979
Lepilemur mustelinus	I-V	VC	—	Hladik and Charles-Dominique 1974
Lophocebus galleritus	DLG	S	—	Nakatsukasa, 1996
Loris tardigradus	I-V	SQ	0.761	Nekaris and Rasmussen, 2003
Macaca arctoides	DLG	SQ	—	Cant, 1988

Taxon	Grasp Type	Substrate	Proportion Small Branch Use	Reference
Macaca fasicularis	DLG	SQ	0.399	Cant, 1988
Macaca fuscata	DLG	S	—	Chatani, 2003
Macaca mulatta	DLG	S	0.1772	Wells and Turnquist, 2001; Goldstein and Richard, 1989
Macaca nemestrina	DLG	S	—	Rodman, 1979
Macaca nigra	DLG	S	—	*Rodman, 1979
Mandrillus leucophaeus	DLG	T	—	Gartlan and Struhsaker, 1972
Mandrillus sphinx	DLG	T	—	Norris, 1988
Microcebus murinus	I-V	SQ	—	Martin, 1973
Nasalis larvatus	DLG	LQ	—	Su and Jablonski, 2009
Nycticebus coucang	I-V	SQ	0.555	Glassman and Wells, 1984*
Otolemur crassicadatus	I-V	LQ	0.2	Crompton, 1984
Pan paniscus	DLG	S	—	Susman, 1980; Doran, 1993
Pan troglodytes	DLG	S	0.0218	Hunt, 1992
Papio anubis	DLG	T	—	Rose, 1977.; Dunbar and Dunbar, 1974
Papio ursinus	DLG	T	—	Hall, 1962; Patel et al., 2009
Perodicticus potto	I-V	LQ	—	Oates, 1984; Charles-Dominique, 1977
Pithecia pithecia	DLG	SQ	0.2691	Fleagle and Mittermeier, 1980; Walker, 1996
Pongo pygmaeus	DLG	SQ	0.2577	Cant, 1987
Presbytis rubicunda	DLG	LQ	0.1136	Fleagle, 1977
Piliocolobus badius	DLG	LQ	0.2012	Gebo and Chapman, 1995; 1996
Propithecus coquereli	I-II	VC	—	Richard, 1978**
Propithecus edwardsi	I-II	VC	—	Richard, 1978**
Propithecus vereauxi	I-II	VC	0.11	Richard, 1978
Propithecus diadema	I-II	VC	0.067	Dagosto, 1995; Dagosto and Yamashita, 1998
Pygathrix nemaeus	DLG	LQ	—	Workman and Covert, 2005
Rhinopithecus roxellana	DLG	LQ	—	Isler and Gruter, 2005
Saguinus midas	DLG	LQ	—	Fleagle and Mittermeier, 1980
Saguinus mystax	DLG	LQ	—	Garber, 1991; Garber and Pruetz, 1995
Saguinus oedipus	DLG	SQ	0.502	Garber and Sussman, 1984
Saimiri boliviensis	DLG	SQ	0.2956	Fontaine, 1990
Saimiri sciureus	DLG	SQ	0.6371	Fleagle and Mittermeier, 1980; Youlatos, 1999
Semnopithecus entellus	DLG	S	—	Newton, 1992
Theropithecus gelada	DLG	T	—	Dunbar and Dunbar, 1974
Trachypithecus cristata	DLG	LQ	—	Fleagle, 1978
Varecia variegata	I-II	LQ	0.214	Dagosto, 1995
Tarsius bancanus	I-V	VC	0.18	Crompton and Andau, 1986
Tarsius syrichta	I-V	VC	0.11	Dagosto et al, 2001
Cynocephalus volans	PNG	NG	—	Byrnes, 2011**
Tupaia tana	PNG	NG	—	Emmons, 2000; Sargis, 2001

Table 1: Substrate preference and grasp type groups of taxa in this study. Grasp type from Gebo (1985) and Patel et al (2012a). Grasp power defined in the text and based on the literature referenced. * Captive study. ** Grouping of taxon was based on literature reference of a closely related species.

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	n		PPL	PPT	PAA	Torsion	Curve A	Curve B
Allenopithecus nigroviridis	1	Mean	4.62	1.99	96.38	55.16	0.866	-0.063
		SD	--	--	--	--	--	--
Alouatta seniculus	4	Mean	1.39	4.46	98.97	59.44	1.17	-0.07
		SD	0.28	0.42	4.24	12.61	0.05	0.15
Aotus azarai boliviensis	5	Mean	0.63	1.86	109.08	51.92	0.71	-0.013
		SD	0.12	0.16	4.54	5	0.09	0.05
Arctocebus calabarensis	3	Mean	1.29	1.87	116.03	76.98	1.5	-0.27
		SD	0.17	0.19	4.505	3.2	0.1	0.05
Ateles belzebuth	2	Mean	0.85	4.13	104.58	53.65	0.75	-0.15
		SD	0.22	0.37	6	21.17	0.0003	0.07
Ateles fusciceps	1	Mean	1.02	4.75	99.42	50.76	0.93	0.097
		SD	--	--	--	--	--	--
Ateles geoffroyi	2	Mean	1.14	3.99	99.98	50.65	0.84	-0.08
		SD	0.05	0.007	0.77	8.83	0.07	0.01
Avahi laniger	1	Mean	3.71	1.58	126.41	48.75	1.23	-0.52
		SD	--	--	--	--	--	--
Bunopithecus hoolock	2	Mean	1.11	3.56	96.02	44.54	1.02	0.05
		SD	0.77	0.16	2.37	4.41	0.19	0.08
Callimico goeldii	2	Mean	0.345	1.54	102.76	53.86	0.68	-0.22
		SD	0.12	0.33	0.62	7.33	0.14	0.25
Callithrix jacchus	1	Mean	1.26	0.32	103.4	36.97	0.67	-0.56
		SD	--	--	--	--	--	--
Cebus apella	6	Mean	1.37	3.36	98.57	56.64	1.08	-0.05
		SD	0.36	0.18	2.31	3.74	0.08	0.06
Cercocebus agilis	1	Mean	5.25	1.26	96.97	52.20	0.83	0.038
		SD	--	--	--	--	--	--
Cercocebus galeritus	1	Mean	3.37	1.07	99.84	43.27	0	0.063
		SD	--	--	--	--	--	--
Cercopithecus mona	1	Mean	2.48	0.36	105.04	53.29	0.75	0.012
		SD	--	--	--	--	--	--
Cercopithecus neglectus	1	Mean	4.69	0.46	97.36	52.92	1.09	0.12
		SD	--	--	--	--	--	--
Cercopithecus nictitans	1	Mean	3.45	0.76	98.31	43.49	1.07	-0.04
		SD	--	--	--	--	--	--
Cheirogaleus major	2	Mean	1.57	3.24	120.85	50.56	1.57	-0.45
		SD	0.29	0.12	0.21	0.63	0.07	0.01
Chiropotes satanas	2	Mean	0.68	3.08	102.52	55.86	0.87	-0.02
		SD	0.18	0.41	1.23	3.65	0.16	0.05
Chlorocebus aethiops	5	Mean	0.69	2.54	98.56	56.46	0.93	0.07
		SD	0.1	0.43	3.7	2.76	0.08	0.07
Colobus guereza	4	Mean	0.56	2.93	97.36	46.15	0.84	0.12
		SD	0.12	0.09	2.42	4.76	0.05	0.08
Colobus polykomos	1	Mean	0.99	3.34	89.67	33.86	0.88	-0.0095
		SD	--	--	--	--	--	--
Cynocephalus	1	Mean	0.1	0.66	108.4	-4.44	0.77	-0.34
		SD	--	--	--	--	--	--
Daubentonia madagascariensis	1	Mean	5.23	1.83	123.28	45.42	1.63	-0.38
		SD	--	--	--	--	--	--
Erythrocebus patas	1	Mean	4.41	0.84	93.01	34.51	0.73	0.041
		SD	--	--	--	--	--	--
Eulemur coronatus	1	Mean	2.71	5.11	108.79	47.37	1.48	-0.47
		SD	--	--	--	--	--	--
Eulemur fulvus albifrons	4	Mean	2.44	5.27	111.49	49.46	1.77	-0.52
		SD	0.35	0.35	4.54	4.21	0.19	0.05
Eulemur fulvus collaris	5	Mean	2.56	5.19	110.11	50.49	1.83	-0.47
		SD	0.17	0.38	7.97	4.52	0.11	0.03

	n		PPL	PPT	PAA	Torsion	Curve A	Curve B
Eulemur macaco macaco	1	Mean	5.32	2.66	108.55	40.56	1.68	-0.43
		SD	--	--	--	--	--	--
Eulemur mongoz	1	Mean	4.73	1.95	109.05	54.27	1.41	-0.46
		SD	--	--	--	--	--	--
Galago moholi	4	Mean	1.42	2.32	140.99	58.57	2.2	-0.71
		SD	0.06	0.08	9.11	4.95	0.13	0.1
Galago senegalensis	1	Mean	2.31	1.76	133.80	69.63	2.42	-0.59
		SD	--	--	--	--	--	--
Galagoides demidoff	3	Mean	1.16	1.55	130.69	67.05	2.08	-0.54
		SD	0.38	0.17	7.86	5.94	0.45	0.09
Gorilla gorilla gorilla	7	Mean	4.75	10.01	95.50	40.47	1.16	-0.05
		SD	1.25	1.34	3.09	6.15	0.16	0.1
Hapalemur griseus	3	Mean	2.05	4.12	112.24	48.81	2.02	-0.51
		SD	0.38	0.38	2.06	3.33	0.3	0.03
Homo sapiens	9	Mean	2.49	9.69	94.00	15.78	0.52	0.04
		SD	0.89	0.78	2.72	9.87	0.07	0.04
Indri indri	3	Mean	2.95	7.72	105.41	61.54	1.66	-0.56
		SD	0.3	0.14	5.65	8.6	0.18	0.05
Lagothrix lagotricha	1	Mean	4.09	0.96	96.81	62.34	0.79	-0.06
		SD	--	--	--	--	--	--
Lemur catta	4	Mean	1.88	5.18	114.51	53.46	1.82	-0.46
		SD	0.14	0.14	7.36	3.88	0.13	0.09
Lepilemur leucopus	4	Mean	2.20	3.24	101.26	50.80	1.59	-0.977
		SD	0.55	0.97	7.58	1.20	0.38	0.053
Loris tardigradus	3	Mean	0.99	2.04	121.8	74.39	1.29	-0.16
		SD	0.15	0.39	2.12	6.58	0.35	0.03
Macaca arctoides	1	Mean	3.69	0.7	98.89	45.69	0.87	0.071
		SD	--	--	--	--	--	--
Macaca fascicularis	2	Mean	0.51	3.185	98.25	46.61	0.97	0.05
		SD	0.08	0.26	2.23	1.37	0.01	0.02
Macaca fuscata	1	Mean	4.56	0.64	98.99	53.37	1.13	0.037
		SD	--	--	--	--	--	--
Macaca mulatta	1	Mean	4.18	0.41	104.34	41.11	1	0.099
		SD	--	--	--	--	--	--
Macaca nemestrina	5	Mean	0.73	4.68	101.74	55.38	1	0.02
		SD	0.36	1.09	3.33	4.39	0.08	0.05
Macaca nigra	1	Mean	3.53	0.65	94.25	45.68	1.12	0.024
		SD	--	--	--	--	--	--
Mandrillus leucophaeus	1	Mean	5.43	0.5	99.91	41.30	0.73	0.11
		SD	--	--	--	--	--	--
Mandrillus sphinx	2	Mean	1.10	6.26	100.19	57.29	0.83	0.014
		SD	0.18	0.18	3.17	12.04	0.019	0.022
Microcebus murinus	5	Mean	0.77	1.61	125.92	60.23	1.79	-0.56
		SD	0.13	0.12	5.19	3.24	0.1	0.062
Nasalis larvatus	10	Mean	0.86	4.28	93.30	59.39	0.99	0.099
		SD	0.12	0.45	3.56	9.82	0.091	0.11
Nycticebus coucang	4	Mean	0.98	2.23	116.73	65.88	1.31	-0.19
		SD	0.14	0.12	6.04	8.04	0.27	0.086
Otolemur crassicaudatus	7	Mean	2.81	4.17	124.45	73.60	2.16	-0.73
		SD	0.27	0.34	10.03	2.89	0.10	0.076
Pan paniscus	1	Mean	7.50	1.2	97.16	38.95	1.22	0.13
		SD	--	--	--	--	--	--
Pan troglodytes schweinfurthii	3	Mean	2.15	8.07	95.76	37.32	1.29	0.059
		SD	0.84	1.35	5.05	9.62	0.12	0.087
Papio anubis	1	Mean	4.64	0.61	97.25	53.62	0.90	0.10
		SD	--	--	--	--	--	--
Papio ursinus	4	Mean	0.49	3.88	97.54	42.10	0.83	0.16
		SD	0.11	0.8	4.72	6.75	0.084	0.068

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	n		PPL	PPT	PAA	Torsion	Curve A	Curve B
Perodicticus potto	6	Mean	2.45	3.04	118.83	77.33	1.92	-0.25
		SD	0.32	0.25	8.49	8.49	0.24	0.13
Piliocolobus badius	3	Mean	0.88	4.45	93.68	46.43	1.07	0.15
		SD	0.072	0.067	1.49	8.07	0.21	0.11
Pithecia pithecia	1	Mean	3.56	0.85	100.19	63.70	0.92	-0.19
		SD	--	--	--	--	--	--
Pongo pygmaeus	6	Mean	2.32	7.24	89.23	52.29	0.92	-0.25
		SD	0.51	0.85	3	11.89	0.17	0.15
Presbytis melalophos	1	Mean	2.97	0.5	100.05	58.13	0.81	-0.12
		SD	--	--	--	--	--	--
Propithecus coquereli	1	Mean	6.75	3.17	118.21	58.97	2.01	-0.92
		SD	--	--	--	--	--	--
Propithecus diadema	1	Mean	6.58	3.03	99.16	50.87	1.81	-0.63
		SD	--	--	--	--	--	--
Propithecus edwardsi	1	Mean	8.89	3.83	112.82	54.83	1.87	-0.53
		SD	--	--	--	--	--	--
Propithecus verreauxi	6	Mean	2.73	5.87	114.54	56.48	1.78	-0.63
		SD	0.51	0.54	9.48	4.39	0.11	0.06
Pygathrix nemaeus	1	Mean	5.05	1.69	97.37	70.69	0.85	-0.0063
		SD	--	--	--	--	--	--
Rhinopithecus roxellana	1	Mean	2.16	5.13	90.64	34.84	1	0.043
		SD	0.11	0.83	4.46	7.98	0.014	0.012
Saguinus mystax	1	Mean	0.29	1.07	100.09	39.53	0.57	-0.48
		SD	--	--	--	--	--	--
Saguinus niger	4	Mean	0.40	1.24	95.47	36.54	0.68	-0.0058
		SD	0.39	0.67	4.38	10.14	0.16	0.13
Saguinus oedipus	1	Mean	1.05	0.13	91.05	58.44	0.48	-0.27
		SD	--	--	--	--	--	--
Saimiri boliviensis	7	Mean	0.48	1.84	100.01	60.00	0.67	-0.1
		SD	0.12	0.18	3.17	6.97	0.11	0.099
Saimiri sciureus	2	Mean	0.20	0.81	101.45	72.55	0.53	-0.41
		SD	0.021	0.099	1.45	2.97	0.12	0.014
Semnopithecus entellus	1	Mean	3.61	1.22	96.16	39.56	0.8	0.058
		SD	--	--	--	--	--	--
Tarsius_bancanus	2	Mean	1.28	1.76	114.68	55.86	1.77	-0.59
		SD	0.25	0.34	1.24	4.05	0.14	0.11
Tarsius syrichta	1	Mean	1.4	1.83	117.53	57.26	1.96	-0.6
		SD	--	--	--	--	--	--
Theropithecus gelada	1	Mean	4.39	0.77	94.55	44.88	0.99	0.2
		SD	--	--	--	--	--	--
Trachypithecus cristatus	1	Mean	3.60	0.72	95.57	66.44	0.83	0.19
		SD	--	--	--	--	--	--
Tupaia tana	6	Mean	0.35	1.01	87.94	14.26	1.4	-0.88
		SD	0.13	0.17	4.64	1.45	0.15	0.2
Varecia variegata variegata	3	Mean	5.37	6.04	110.69	44.64	1.46	-0.36
		SD	0.51	0.33	7.66	7.29	0.33	0.046
†*Carpolestes* UM 101963			0.24	0.90	96.00	39.82	1.33	-0.12
†*Adapis* AMNH 140719			1.12	2.30	110.00	54.78	1.18	-0.45
†*Adapis* NHMB QE 646			0.42	2.44	106.95	56.53	1.43	-0.49
†*Adapis* NHMB QL 418			0.39	2.57	115.56	51.05	1.16	-0.41
†*Adapoides* IVPP v13015			1.12	2.30	119.26	53.15	1.75	-0.43
†*Leptadapis* NHMB QD 650			2.49	5.06	104.34	63.14	1.30	-0.33
†*Leptadapis* NHMB QL 383			2.08	5.77	113.81	64.35	1.74	-0.27
†*Leptadapis* NHMB QL 616			2.39	6.20	104.50	60.53	1.43	-0.38
†*Leptadapis* NHMB QL 660			2.09	5.82	109.56	52.29	1.77	-0.37
†*Notharctus* AMNH 11474			2.61	5.28	110.00	42.39	1.47	-0.59
†*Hemiacodon* AMNH 12613			2.23	3.83	127.27	71.84	1.57	-0.83
†*Aegyptopithecus* DPC 13318			0.91	4.62	96.75	53.00	0.78	-0.27
†*Catopithecus* DPC 20939			0.25	1.66	100.50	57.95	0.65	-0.39
†*Proconsul* KNM RU 5872			2.54	8.23	100.93	52.74	1.21	-0.03

Table 2: Descriptive statistics for each variable discussed in this study. † Indicates fossil taxon.

Substrate Analysis				
Variable	F	p-value	F	phylogenetic p-value
PPL	21.375	<0.001	12.55	0.006
PPT	16.76	<0.001	5.22	0.066
PAA	11.93	<0.001	5.48	0.064
Torsion	41.28	<0.001	15.28	0.005
Curve A	18.78	<0.001	13.15	0.048
Curve B	19.16	<0.001	16.3	0.039

Table 3: ANOVA results from substrate preference analysis.

Grasp Type Analysis				
Variable	F	p-value	F	phylogenetic p-value
PPL	103.49	<0.001	103.09	0.13
PPT	64.98	<0.001	25.35	0.22
PAA	116.98	<0.001	67.94	0.15
Torsion	39.48	<0.001	21.29	0.57
Curve A	132.76	<0.001	85.27	0.039
Curve B	119.27	<0.001	52.16	0.15

Table 4: ANOVA results from grasp type analysis.

Taxon Analysis		
Variable	F	p-value
PPL	<0.001	242.67
PPT	<0.001	136.08
PAA	<0.001	167.04
Torsion	<0.001	52.54
Curve A	<0.001	286.78
Curve B	<0.001	231.65

Table 5: ANOVA results from taxon analysis.

Variable	Method	R²	F	p-value	df	Slope	SEE Slope	Intercept	SEE Intercept	Lambda
PPL	OLS	0.007	0.209	0.651	1, 31	0.106	0.232	0.476	0.068	
	PGLS	3.53E-05	0.001	0.999	2, 31	0.137	0.415	0.499	0.169	0.730**
PPT	OLS	0.072	2.416	0.13	1, 31	0.499	0.321	0.192	0.202	
	PGLS	0.041	1.326	0.28	2, 31	0.47	0.408	0.193	0.287	0.716**
PAA	OLS	0.022	0.691	0.412	1, 31	0.003	0.003	0.216	0.346	
	PGLS	0.011	0.345	0.711	2, 31	-6.003	0.005	0.855	0.608	0.758**
Torsion	OLS	0.361	17.517	< 0.01	1, 31	0.01	0.002	-0.073	0.141	
	PGLS	0.2737	11.68	< 0.01	2, 31	0.0108	0.0032	-0.114	0.198	0.660*
QuadA	OLS	0.01	0.301	0.587	1, 31	-0.043	0.078	0.553	0.101	
	PGLS	0.345	1.107	0.343	2, 31	-0.126	0.12	0.685	0.197	0.668*
QuadB	OLS	0	0.0001	1	1, 31	6.98E-05	0.15	0.501	0.05	
	PGLS	0.0018	0.055	0.947	2, 31	-0.0527	0.225	0.485	0.131	0.751**

Table 6: Results of ordinary least squares (OLS) regression and phylogenetic generalized least squares regression (PGLS). * Lambda is significantly different from 1. ** Lambda is significantly different from both 0 and 1.

Substrate Analysis		Original Group Classification							
			Predicted Group Membership						CV
			NG	T	S	LQ	SQ	VCL	
Original Correct	67.3%	NG	100	0	0	0	0	0	100
		T	0	50	10	30	10	0	50
CV Correct	61.2%	S	0	14.8	37	33.3	11.1	3.7	37
		LQ	1.4	0	4.1	64.9	20.3	9.5	56.8
		SQ	0	0	7	22.8	68.4	1.8	68.4
		VCL	0	0	0	10	3.3	86.7	86.7

Table 7: Canonical discriminant analysis results: classification results for grasp power analysis (all primates).

Variable	Function				
	1	2	3	4	5
Torsion	-0.699	-0.073	-0.222	0.099	0.169
Curve B	-0.03	0.799	0.269	-0.185	0.037
Rel. DAH	0.139	0.695	0.167	0.148	0.177
Curve A	-0.176	-0.688	0.218	0.226	-0.393
Rel. PPL	-0.168	-0.648	-0.134	0.227	-0.277
Rel. AL	0.323	0.631	0.23	-0.204	0.535
Rel. PPT	-0.206	-0.459	0.117	0.153	-0.185
PAA	-0.232	-0.445	-0.076	0.131	0.081
Rel. DAW	0.182	0.313	0.217	0.289	0.116
Rel. APD	0.34	0.488	0.213	-0.524	0.161
Rel. ML	0.007	0.127	-0.063	0.184	0.372
Rel. PL	0.069	0.205	-0.083	0.149	0.321
Rel. PAS	-0.001	-0.216	0.223	-0.085	0.293

Table 8: Canonical discriminant analysis results: loadings for grasp power analysis (all primates).

Fossil Specimen	Substrate (All Primates)	
	Predicted Group	Probability
UM 101963 *(Carpolestes)*	LQ	0.84
NHMB QE 646 (*Adapis*)	S	0.5
NHMB QL 418 (*Adapis*)	T	0.54
IVPP v13015 (*Adapoides*)	LQ	0.624
NHMB QD 650 (*Leptadapis*)	S	0.928
NHMB QL 383 (*Leptadapis*)	LQ	0.455
NHMB QL 616 (*Leptadapis*)	S	0.693
NHMB QL 660 (*Leptadapis*)	S	0.621
AMNH 11474 *(Notharctus)*	VCL	0.815
AMNH 12613 (*Hemiacodon*)	NG	0.565
DPC 11318 (*Aegyptopithecus*)	LQ	0.833
DPC 20939 (*Catopithecus*)	SQ	0.794
25C (*Epipliopithecus*)	LQ	0.622
E4 (*Epipliopithecus*)	SQ	0.695
KNM RU 5872 (*Proconsul*)	S	0.781

Table 9: Canonical discriminant analysis results: group membership and posterior probability for fossil Mt1s in grasp power analysis (all primates).

			Predicted Group Membership				CV
			S	LQ	SQ	VCL	
Original Correct	87.7%	S	75	25	0	0	25
		LQ	0	90.3	3.2	6.5	80.6
CV Correct	76.5%	SQ	0	18.8	81.3	0	68.8
		VCL	0	10	0	90	83.3

Table 10: Canonical discriminant analysis results: classification results for grasp power analysis (prosimians).

Variable	Function
	1
Torsion	0.351
Rel. PL	-0.347
Rel. PPL	0.312
Rel. ML	-0.249
PAA	0.241
Rel. DAW	0.146
Rel. PAS	0.109
Rel. PPT	-0.089
Rel. DAH	-0.075
Rel. APD	-0.074
Curve A	0.048
Rel. AL	-0.29
Curve B	0.013

Table 11: Canonical discriminant analysis results: loadings for grasp power analysis (prosimians).

Fossil Specimen	Substrate (Prosimian)	
	Predicted Group	Probability
UM 101963 (*Carpolestes*)	S	0.998
NHMB QE 646 (*Adapis*)	S	0.973
NHMB QL 418 (*Adapis*)	S	0.918
IVPP v13015 (*Adapoides*)	S	0.999
NHMB QD 650 (*Leptadapis*)	LQ	0.975
NHMB QL 383 (*Leptadapis*)	LQ	0.989
NHMB QL 616 (*Leptadapis*)	LQ	0.993
NHMB QL 660 (*Leptadapis*)	LQ	0.744
AMNH 11474 (*Notharctus*)	VCL	0.997
AMNH 12613 (*Hemiacodon*)	LQ	0.879

Table 12: Canonical discriminant analysis results: group membership and posterior probability for fossil Mt1s in grasp power analysis (prosimians).

Anthropoid Substrate Analysis	Original Group Classification		Predicted Group Membership					CV
			NG	T	S	LQ	SQ	
Original Correct	80.2%	NG	100	0	0	0	0	100
		T	0	70	0	20	10	60
CV Correct	69.0%	S	0	4.3	73.9	13	8.7	56.5
		LQ	0	0	0	83.7	16.3	74.4
		SQ	0	0	4.9	17.1	78	78

Table 13: Canonical discriminant analysis results: classification results for grasp power analysis (anthropoids).

Variable	Function			
	1	2	3	4
Rel. APD	-0.339	0.291	-0.128	-0.042
Rel. PL	0.223	-0.397	0.36	0.368
Rel. PPT	0.092	0.19	-0.008	-0.023
Curve B	-0.073	0.096	0.499	0.001
Rel. PPL	0.036	0.136	-0.497	-0.367
Rel. DAH	-0.08	-0.207	0.469	0.214
Rel. PAS	-0.021	0.364	0.425	0.098
Rel. AL	-0.377	0.037	0.414	0.338
Rel. DAW	-0.15	0.003	0.354	0.08
Curve A	0.184	0.552	0.162	-0.566
Rel. ML	0.238	-0.32	0.332	0.396
Torsion	0.355	0.064	-0.13	0.361
PAA	0.071	0.097	-0.097	0.126

Table 14: Canonical discriminant analysis results: loadings for grasp power analysis (anthropoids).

Fossil Specimen	Substrate (Anthropoid)	
	Predicted Group	Probability
DPC 11318 (*Aegyptopithecus*)	T	0.974
DPC 20939 (*Catopithecus*)	SQ	0.981
25C (*Epiliopithecus*)	SQ	0.902
E4 (*Epipliopithecus*)	SQ	0.975
KNM RU 5872 (*Proconsul*)	S	0.85

Table 15: Canonical discriminant analysis results: group membership and posterior probability for fossil Mt1s in grasp power analysis (anthropoids).

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Grasp Analysis		Original Group Classification	Predicted Group Membership				CV
			PNG	I-V	I-II	DLG	
Original Correct	98.6%	PNG	100	0	0	0	85.7
		I-V	0	93.5	2.2	4.3	91.3
CV Correct	97.2%	I-II	0	0	100	0	97.1
		DLG	0	0	0	100	100

Table 16: Canonical discriminant analysis results: classification results for grasp type analysis (all primates)

Variable	Function		
	1	2	3
Rel. PPL	0.642	-0.066	0.026
Curve A	0.577	-0.266	-0.366
PAA	0.523	0.067	-0.11
Rel. AL	-0.376	0.196	0.254
Rel. DAH	-0.369	0.184	0.151
Rel. APD	-0.275	0.145	0.088
Curve B	-0.434	0.504	-0.047
Torsion	0.222	0.306	-0.163
Rel. PPT	0.387	-0.121	-0.691
Rel. PL	-0.32	-0.213	0.334
Rel. PAS	0.009	0.076	0.315
Rel. HW	-0.066	0.078	0.29
Rel. ML	-0.277	-0.18	0.29

Table 17: Canonical discriminant analysis results: loadings for grasp type analysis (all primates).

Fossil Specimen	Grasp Type (All Primates)	
	Predicted Group	Probability
UM 101963 (*Carpolestes*)	DLG	0.8
NHMB QE 646 (*Adapis*)	I-II	0.94
NHMB QL 418 (*Adapis*)	DLG	0.737
IVPP v13015 (*Adapoides*)	I-II	0.999
NHMB QD 650 (*Leptadapis*)	I-II	0.985
NHMB QL 383 (*Leptadapis*)	I-II	0.58
NHMB QL 616 (*Leptadapis*)	I-II	0.749
NHMB QL 660 (*Leptadapis*)	I-II	0.999
AMNH 11474 (*Notharctus*)	I-II	0.981
AMNH 12613 (*Hemiacodon*)	I-II	0.937
DPC 11318 (*Aegyptopithecus*)	DLG	0.999
DPC 20939 (*Catopithecus*)	DLG	0.999
25C (*Epipliopithecus*)	DLG	0.999
E4 (*Epipliopithecus*)	DLG	0.999
KNM RU 5872 (*Proconsul*)	DLG	0.999

Table 18: Canonical discriminant analysis results: group membership and posterior probability for fossil Mt1s in grasp type analysis (all primates)

Prosimian Grasp Analysis		Original Group Classification				
				Predicted Group Membership		CV
				I-V	I-II	
Original Correct	98.8%		I-V	97.8	2.2	97.8
			I-II	0	100	91.4
CV Correct	95.1%					

Table 19: Canonical discriminant analysis results: classification results for grasp type analysis (prosimians).

Variable	Function
	1
Torsion	0.351
Rel. PL	-0.347
Rel. PPL	0.312
Rel. ML	-0.249
PAA	0.241
Rel. DAW	0.146
Rel. PAS	0.109
Rel. PPT	-0.089
Rel. DAH	-0.075
Rel. APD	-0.074
Curve A	0.048
Rel. AL	-0.29
Curve B	0.013

Table 20: Canonical discriminant analysis results: loadings for grasp type analysis (prosimians).

Fossil Specimen	Grasp Type (Prosimian)	
	Predicted Group	Probability
UM 101963 (*Carpolestes*)	I-II	0.999
NHMB QE 646 (*Adapis*)	I-II	0.999
NHMB QL 418 (*Adapis*)	I-II	0.829
IVPP v13015 (*Adapoides*)	I-II	0.999
NHMB QD 650 (*Leptadapis*)	I-II	0.999
NHMB QL 383 (*Leptadapis*)	I-II	0.998
NHMB QL 616 (*Leptadapis*)	I-II	0.999
NHMB QL 660 (*Leptadapis*)	I-II	0.999
AMNH 11474 (*Notharctus*)	I-V	0.999
AMNH 12613 (*Hemiacodon*)	I-V	0.503

Table 21: Canonical discriminant analysis: group membership and posterior probability for fossil Mt1s in grasp type analysis (prosimians)

Taxon Analysis		Original Group Classification				
			Predicted Group Membership			CV
			Non-primate	Prosimian	Anthropoid	
Original Correct	98.6%	Non-primate	100	0	0	100
		Prosimian	0	96.3	3.7	95.1
CV Correct	98.1%	Anthropoid	0	0	100	100

Table 22: Canonical discriminant analysis results: classification results for taxon analysis.

Variable	Function	
	1	2
Curve A	0.679	0.126
Rel. PPL	0.611	0.261
Curve B	-0.589	0.312
PAA	0.481	0.367
Rel. AL	-0.451	-0.061
Rel. PPT	0.45	0.25
Rel. DAH	-0.435	-0.046
Rel. APD	0.326	-0.02
Rel. DAW	-0.098	-0.02
Rel. PAS	0.021	0.014
Rel. PL	-0.269	-0.479
Torsion	0.138	0.473
Rel. ML	-0.188	-0.389

Table 23: Canonical discriminant analysis results: loadings for taxon analysis.

Fossil Specimen	Taxon Analysis	
	Predicted Group	Probability
UM 101963 (*Carpolestes*)	Anthropoid	0.964
NHMB QE 646 (*Adapis*)	Prosimian	0.708
NHMB QL 418 (*Adapis*)	Anthropoid	0.892
IVPP v13015 (*Adapoides*)	Prosimian	0.997
NHMB QD 650 (*Leptadapis*)	Prosimian	0.957
NHMB QL 383 (*Leptadapis*)	Anthropoid	0.501
NHMB QL 616 (*Leptadapis*)	Prosimian	0.522
NHMB QL 660 (*Leptadapis*)	Prosimian	0.997
AMNH 11474 (*Notharctus*)	Prosimian	0.975
AMNH 12613 (*Hemiacodon*)	Prosimian	0.999
DPC 11318 (*Aegyptopithecus*)	Anthropoid	0.999
DPC 20939 (*Catopithecus*)	Anthropoid	0.999
25C (*Epipliopithecus*)	Anthropoid	0.999
E4 (*Epipliopithecus*)	Anthropoid	0.999
KNM RU 5872 (*Proconsul*)	Anthropoid	0.999

Table 24: Canonical discriminant analysis results: group membership and posterior probability for fossil Mt1s (taxon analysis).
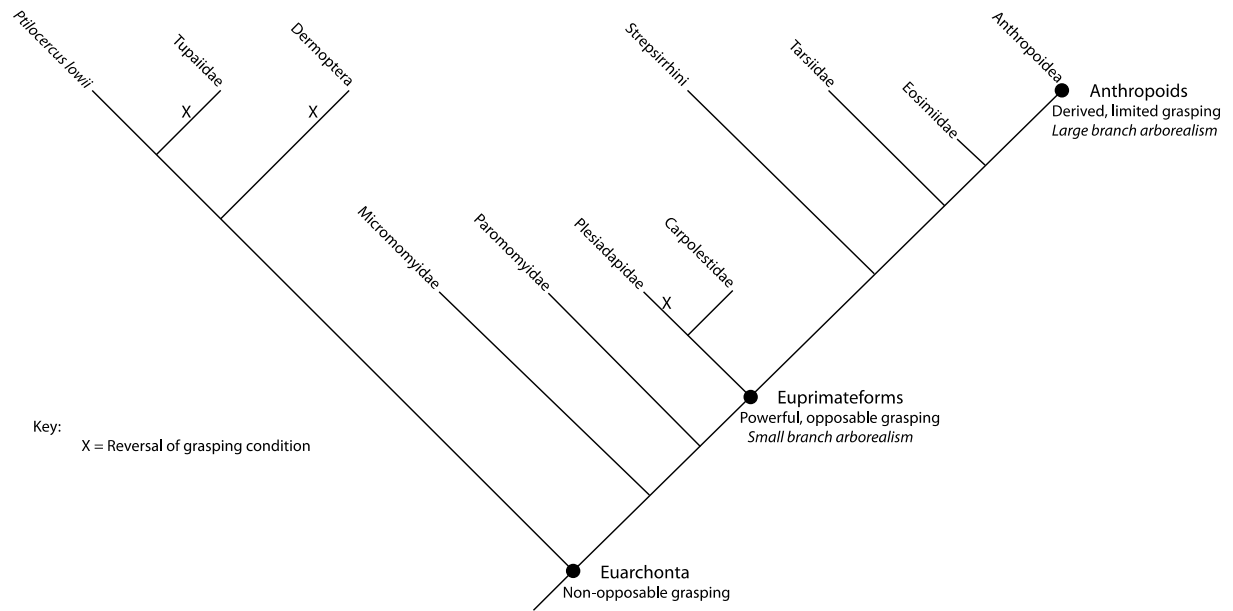
Figure 1: Scenario of evolution of primate pedal grasping presented in the text. Composite from Rollinson and Martin (1981), Gebo (1986), Sargis et al (2007), and Patel et al (2012a)
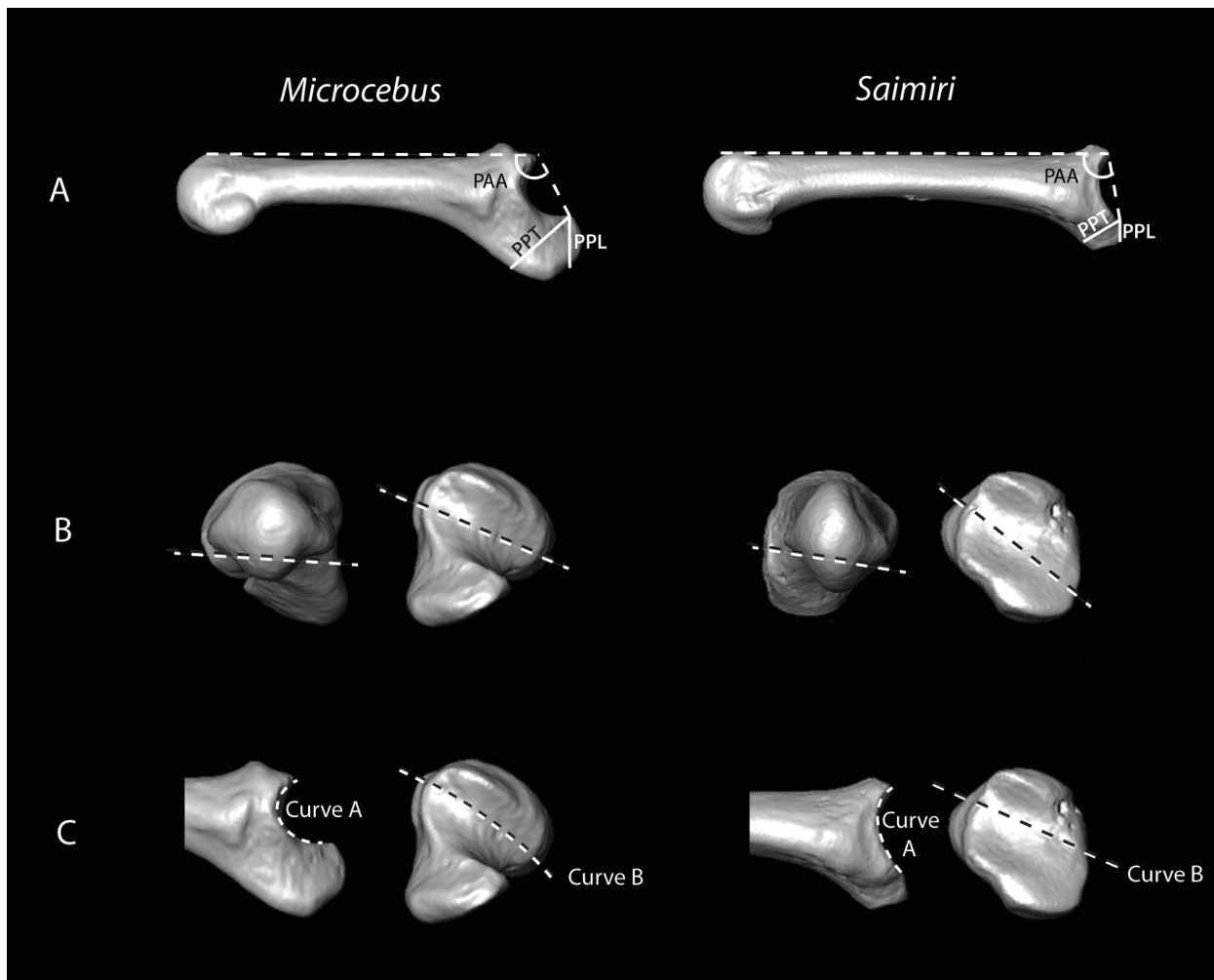
Figure 2: Illustration of variables often associated with powerful hallucal grasping. A.) PPL: peroneal process length, PPT: peroneal process thickness, PAA: physiologic abduction angle; B.) Illustration of torsion: angle between axes of rotation on proximal and distal articular surfaces; C.) curve A: the first principal curvature (in the dorsovolar aspect), curve B: the second principal curvature (in the tibio-peroneal aspect).
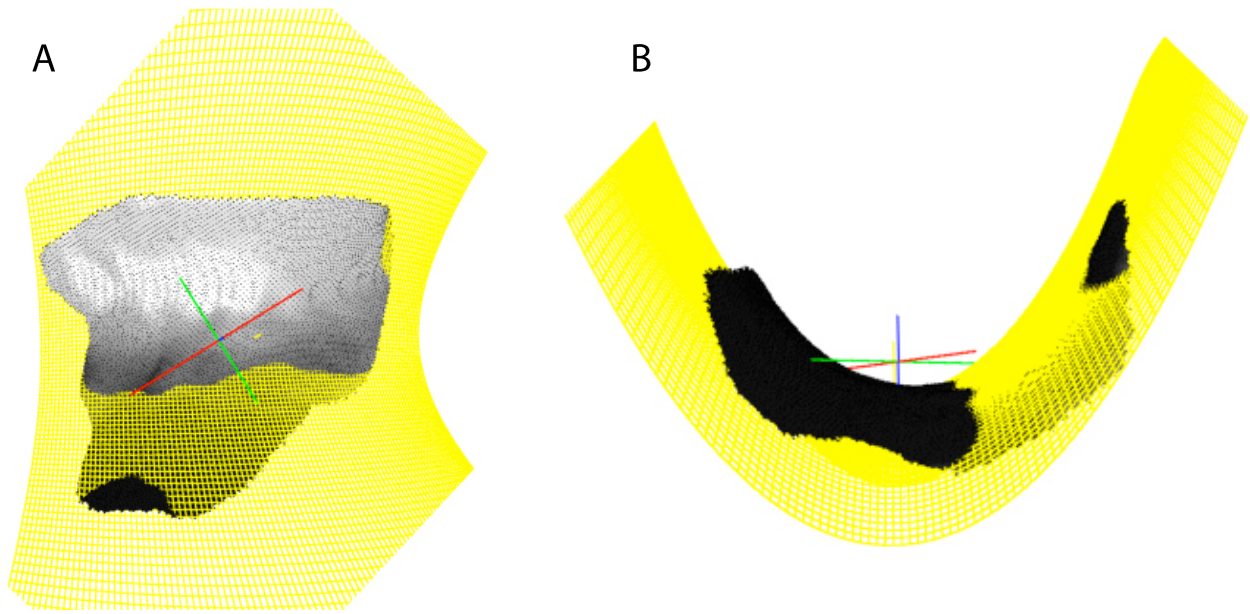
Figure 3: Segmented proximal articular surfaces of *Microcebus* with quadric functions fit to surface curvature. A. Proximal view. B. Lateral view.
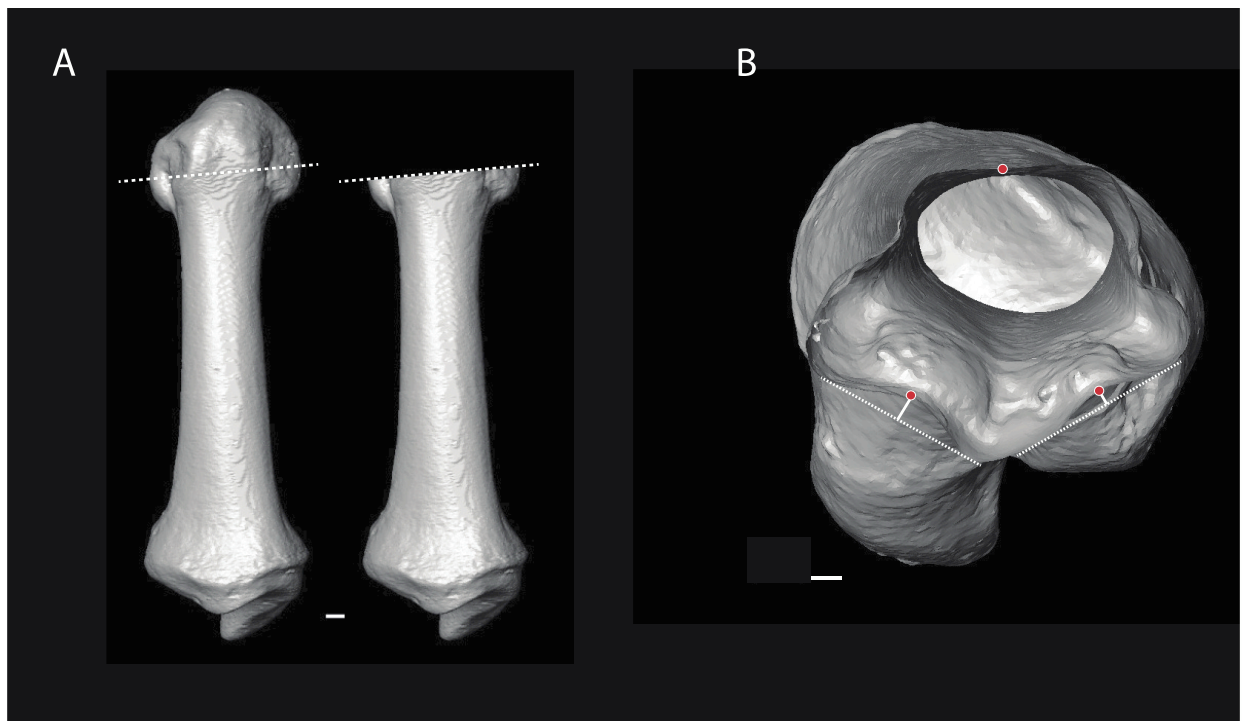
Figure 4: A.) Dorsal orientation of the Mt1 with dotted line representing location of widest epicondylar breadth. The distal aspect beyond the widest epicondylar breadth has been removed on the right. B.) The cut proximal end with three landmarks placed on it: two landmarks in the sesamoid grooves at the deepest perpendicular distance from the dotted lines connecting the midline keel and the epicondyle, and one on the dorsal aspect of the surface at the midpoint between the epicondyles.
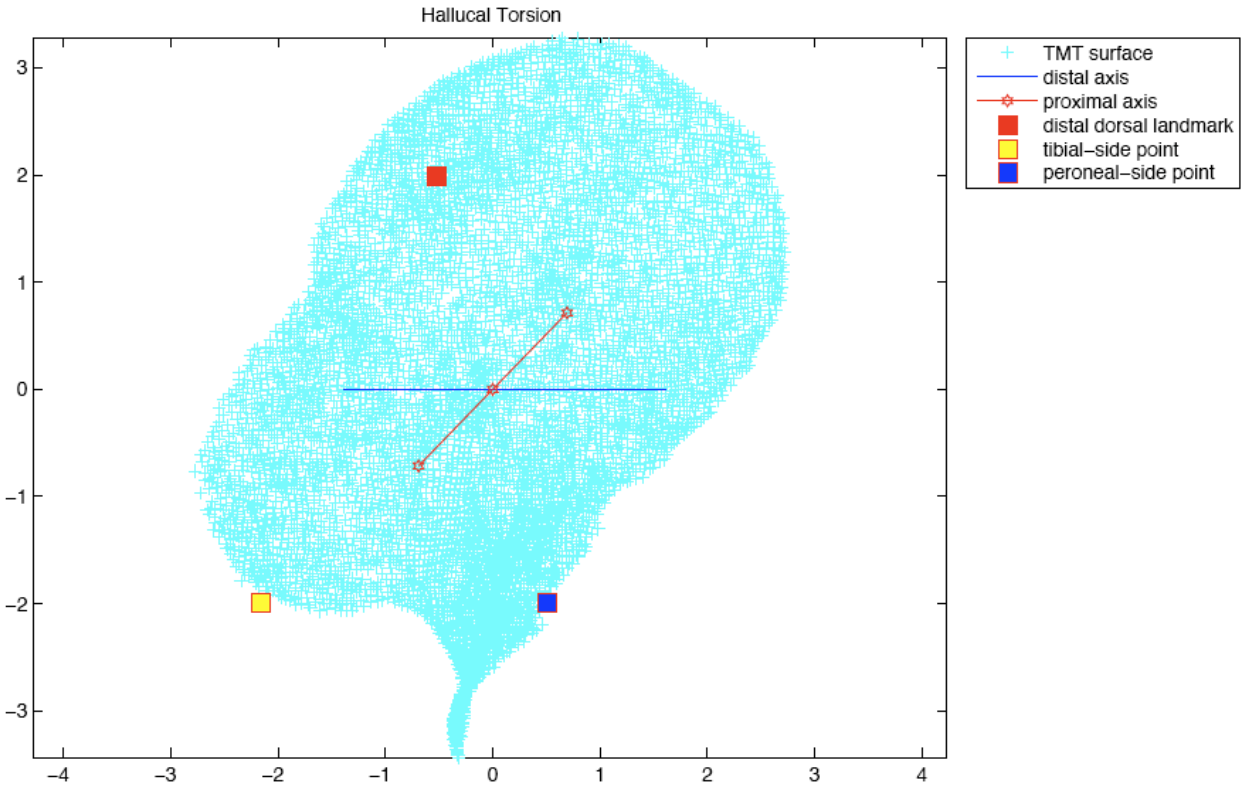
Figure 5: Matlab output showing the points of the proximal articular surface (teal), each of the three landmarks (red, blue, yellow), the eigenvector of the first principal curvature (red line) and the orientation of the distal axis (blue line) projected into two dimensional space. Torsion is measured as the angle between the blue and red lines.
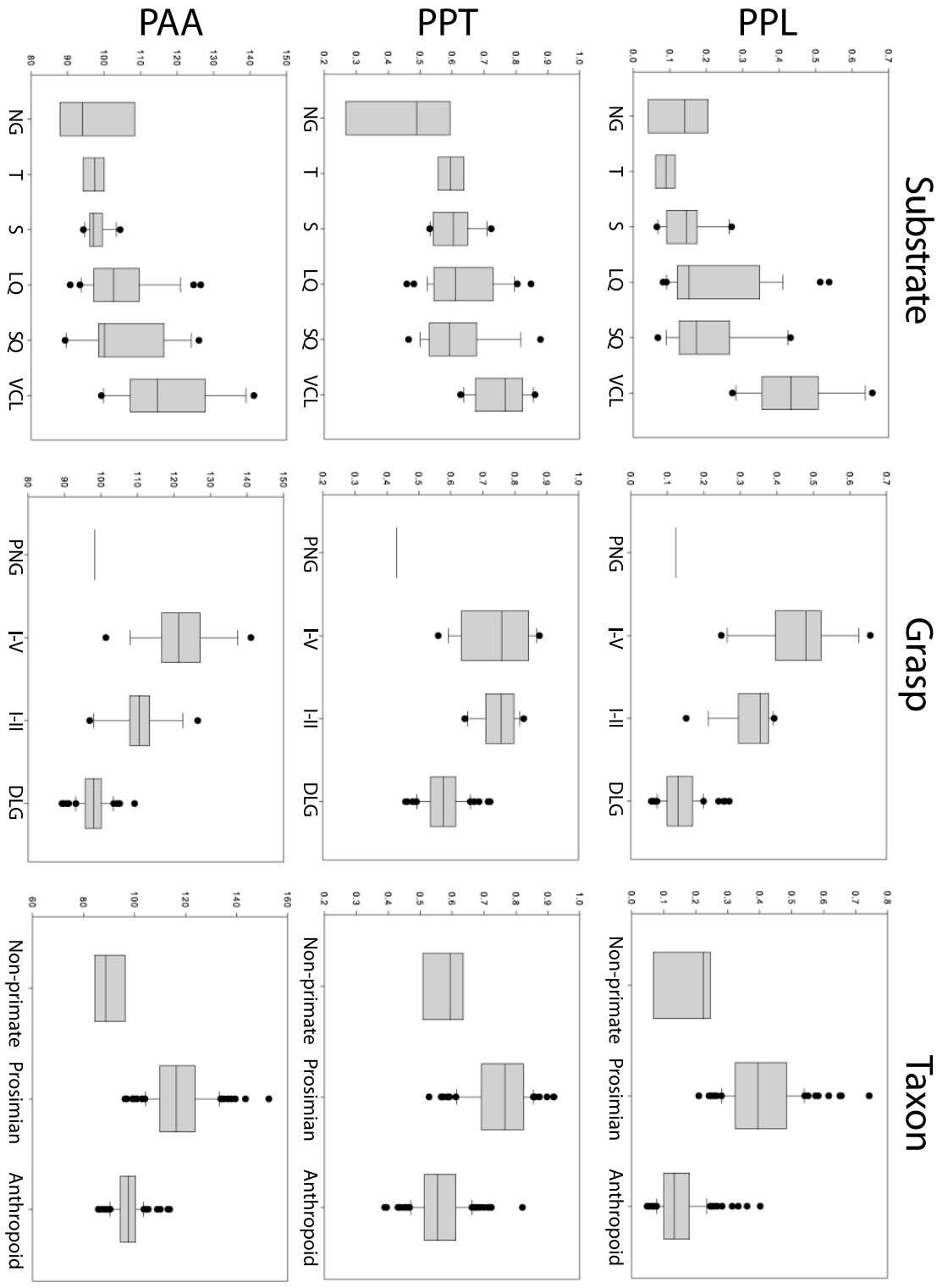
Figure 6: Results: means and interquartile ranges each variable in substrate, grasp type, and taxon analyses.
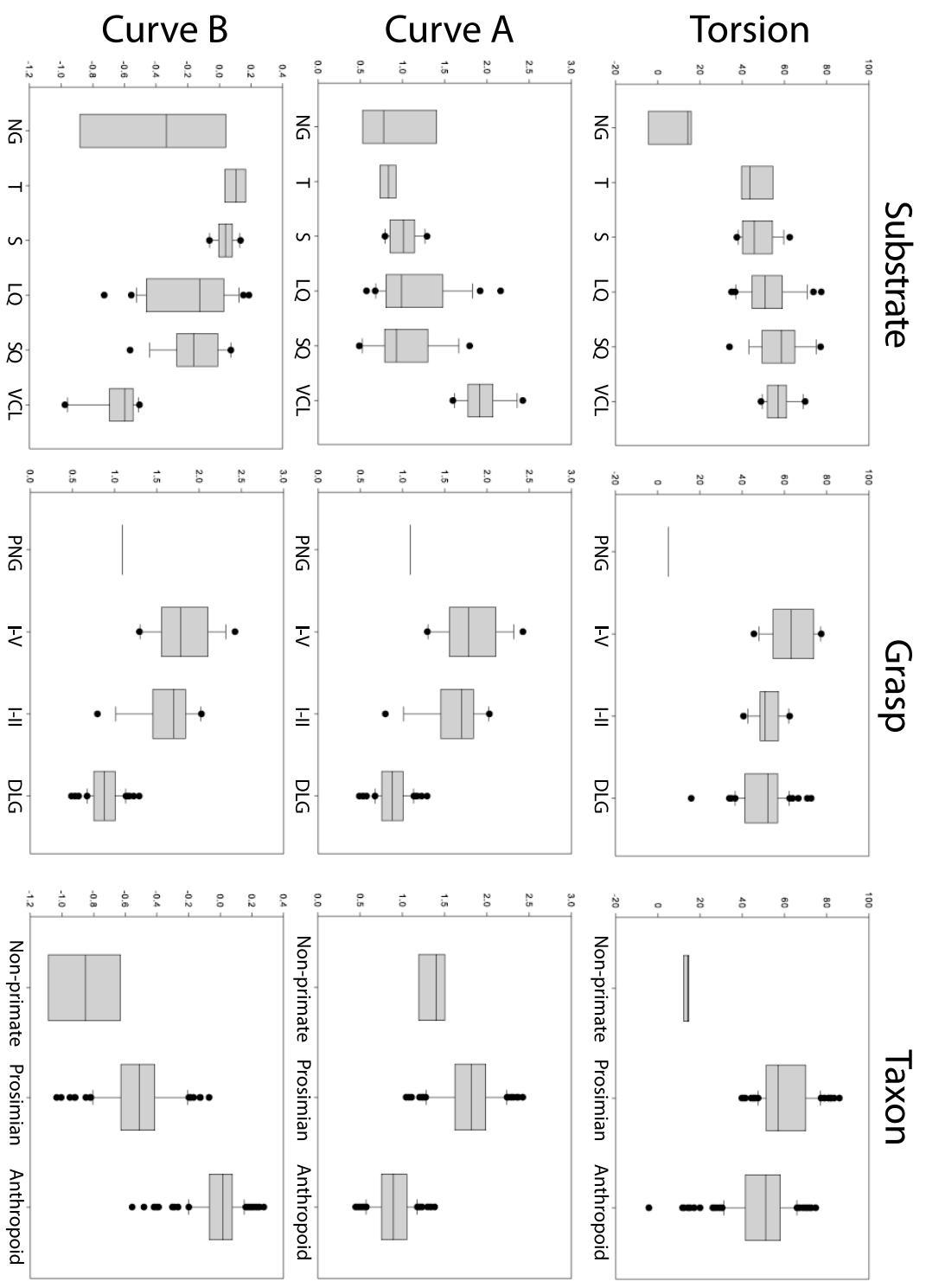
Figure 6: Results: means and interquartile ranges each variable in substrate, grasp type, and taxon analyses.
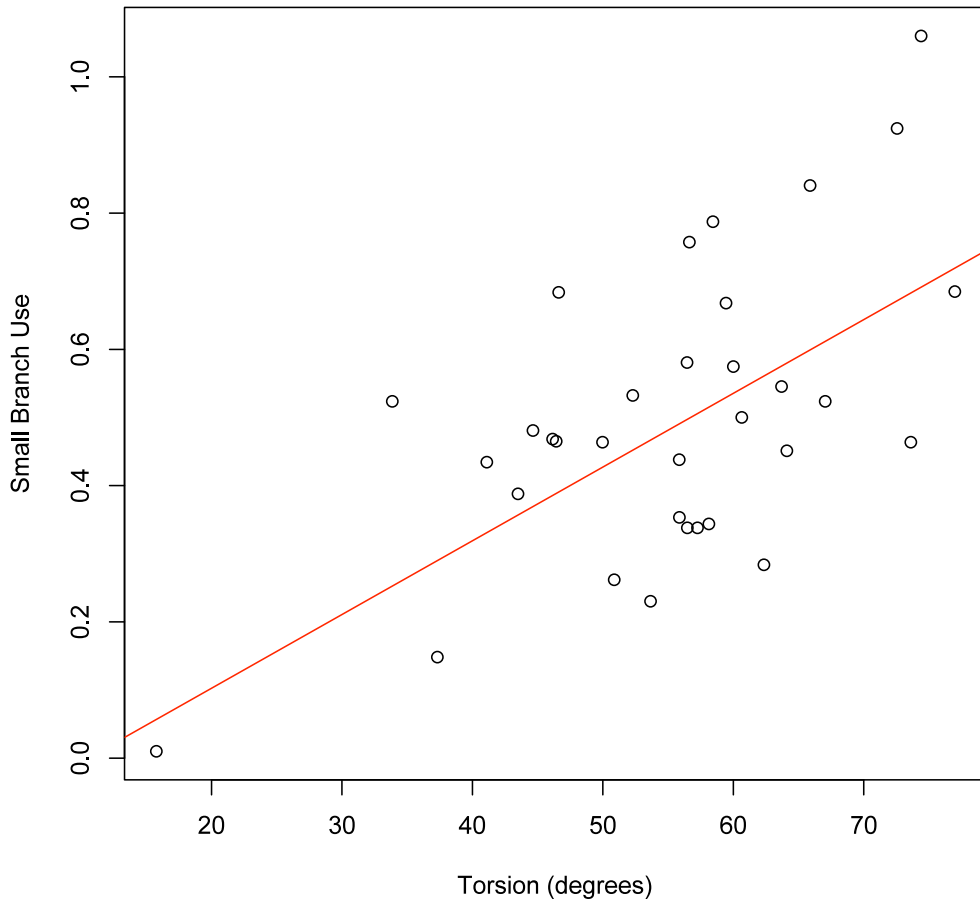
Figure 7: Results of PGLS regression of torsion (degrees) and Arcsine transformation of proportion of small branch use.