Distinguishing Subcategories within Arboreal Quadrupedalism: Morphological Markers of Slow Climbing

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Abstract of the Thesis

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Among primates, an arboreal quadruped is one whose primary locomotor method is running and/or walking in an arboreal setting. Within this category, primates take on a variety of secondary locomotor methods, such as slow climbing (SC), in which a primate uses vertical climbing, bridging, and suspension to cross gaps. Leaping (L) is another secondary locomotor method, also used for gap crossing. Finally, an arboreal quadrupedal generalist (G) would be a primate which does not frequently utilize a specialized gap-crossing method. This study aims to discover the skeletal differences between these three subcategories. In particular, it concentrates on slow climbing, as it is proposed to be utilized by several Miocene apes. Two phylogenetic groups were examined: a platyrrhine group - *Alouatta seniculus* (SC), *Cebus apella* (G), and *Saimiri boliviensis* (L); and a Lorisiformes group - *Nycticebus coucang* (SC), *Otolemur crassicaudatus* (G), and *Galago demidovii* (L). One-way ANOVAs were run on skeletal measurements within each phylogenetic group, and then PCAs were run on the same measurements with the groups combined. This study found that, compared to closely-related arboreal quadrupeds, slow climbers had alterations in their skeleton that allowed for a greater range of abduction at the shoulder, greater mobility and stability at the elbow and knee, and greater abduction and rotation at the hip. In several cases, these structural modifications parallel those seen elsewhere in brachiators. These findings may help to explain apparent morphological contradictions in the hominoid fossil record.

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Introduction

Arboreal quadrupedalism is a locomotor category applied to a wide range of extinct and extant primates. It is defined as the principal locomotor activity being running and/or walking in a small branch setting (Rose 1973). Its broad definition applies to such a large group of highly variable primates that it is somewhat surprising that subcategories within arboreal quadrupedalism have not been frequently employed as descriptors for locomotor behavior. The simplest way to devise such subcategories is to look at secondary modes of locomotion, and determine what morphological characteristics can set these subcategories apart from one another. In this way, fossil taxa that have fallen under the broad category of arboreal quadrupedalism can begin to be better understood in terms of locomotion.

By referring to taxa as arboreal quadrupeds, secondary modes of locomotion often get overlooked. Ignoring secondary modes of locomotion may result in misleading conclusions in primate morphological studies, as secondary modes often have great adaptive value (Rose 1973, Senturia 1995). One specific group which has suffered from this vague locomotor title is the early Miocene hominoids. Rose (1993) describes Miocene hominoids as a unique form of arboreal quadrupeds, without a clear modern analogue. Early Miocene hominoids are hypothesized to be more mobile at their joints than most arboreal quadrupeds, and some may be more cautious and slow in their climbing, due to their size (Rose 1993). Some have compared this form of locomotion to that of *Alouatta*, or even to that of *Nycticebus*, if you disregard the notion that size is solely responsible for slow climbing behaviors (Cartmill and Milton 1977). These two primate genera have been objects of some confusion in locomotor classification. They have been considered semi-brachiators (a category that no longer has meaning), slow climbing quadrupeds, incipient brachiators, or just simply arboreal quadrupeds (Erikson 1963, Napier and Napier 1967, Rose 1973, Mittermeier and Fleagle 1976, Cartmill and Milton 1977, Rose 1993, Senturia 1995). They are a prime example of why the category of arboreal quadrupedalism is not a precise descriptor of locomotion. Referring to *Alouatta*, *Nycticebus*, or early Miocene hominoids as arboreal quadrupeds misses a great deal of their unique nuances of locomotion that, in early studies, once set *Alouatta* apart from arboreal quadrupeds in the group known as semi-brachiators (Rose 1973, Mittermeier and Fleagle 1976). Semi-brachiation was shown to be an inaccurate locomotor category description, as it is not actually a method of locomotion and was applied to a very wide group of primates who, upon closer inspection, had little overlap with one another concerning locomotion and movement (Mittermeier and Fleagle 1976). Semi-brachiation was correct in one regard, and that was in noticing that certain arboreal quadrupeds were actually more like intermediates between quadrupedal and suspensory animals. Here, slow climbing is proposed to be a preferred title for the form of locomotion shared by *Alouatta, Nycticebus*, and potentially early Miocene hominoids - uniting them in cautious quadrupedalism and in their great range of joint mobility, which is surpassed only by true suspensory primates like modern hominoids.

By creating subcategories within arboreal quadrupedalism, such as slow climbing, it will be easier to both discuss and determine the locomotor patterns of extinct primates.

This study looks to understand the skeletal morphology of various extant arboreal quadrupedal subcategories, to help determine a more precise locomotion pattern of extinct arboreal quadrupeds.

For the purposes of this study, arboreal quadrupedalism is broken down into three subcategories. These three different locomotor subcategories are assigned to two different primate phylogenetic groups – a platyrrhine group and a Lorisiformes group. The three locomotor subcategories are slow climbers (platyrrhine: *Alouatta seniculus*; Lorisiformes: *Nycticebus coucang*), generalists (platyrrhine: *Cebus apella*; Lorisiformes: *Otolemur crassicaudatus*), and leapers (platyrrhine: *Saimiri boliviensis*; Lorisiformes: *Galago demidovii*) (Erikson 1963, Charles-Dominique and Martin 1970, Mendel 1976, Cartmill and Milton 1977, Fleagle and Mittermeier 1981, Gebo 1992, Fleagle 1999). These three categories were chosen to cover the basic variation in the broader locomotor category of arboreal quadrupedalism.

Slow climbers are here defined as arboreal quadrupeds that use vertical climbing, bridging, and suspension in their repertoire, without frequent brachiation. They use these behaviors to cross gaps in arboreal settings. These primates generally move in a slower fashion than others, and have been described as “cautious quadrupeds” (Cartmill and Milton 1977). Early hominoids are hypothesized to have moved in a similar fashion (Rose 1988, Rose 1993, Ward 1993, Gebo 1996, Madar et al. 2002).

Generalists are here defined as arboreal quadrupeds which do not frequently utilize any specialized locomotor mode (Gebo 1992). These may be thought of as strict arboreal quadrupeds, participating in running and walking arboreal behaviors far more frequently than either leaping or suspensory behaviors.

Leapers are here defined as arboreal quadrupeds which frequently leap as a means of locomotion and a method for crossing gaps. Their primary method of locomotion is not necessarily leaping, as they still retain a large percentage of quadrupedal behaviors in their repertoire (Charles-Dominique and Martin 1970, Fleagle 1999). The term “leaper” in this paper will thus refer to primates who leap as a secondary locomotor method, rather than as a primary locomotor method.

Suspensory primates, such as hominoids and *Ateles*, have several features that seem to differentiate them from primates practicing arboreal quadrupedalism. Such traits include a dorsally positioned scapula, a long clavicle, a globular humeral head, an enlarged capitulum, a round radial head, a spool-shaped trochlea, a deep olecranon fossa, a mobile hip, and a shallow patellar groove (Cartmill and Milton 1977, Fleagle 1977, Rose 1988, Anemone 1993, Larson 1993, MacLatchy et al. 1996, Richmond et al. 1998). However, in the fossil record, Miocene hominoids have been shown to have some of these traits, while maintaining other traits which are more characteristic of quadrupedal species. Miocene hominoids such as *Proconsul*, *Sivapithecus*, and *Dryopithecus* all have morphologies which indicate a strange mixture between arboreal quadrupedal traits, and traits common to modern hominoids, which practice suspension (Fleagle 1984, Harrison 1987, Rose 1993, Andrews and Pilbeam 1996, Ward 1997, Moya Sola et al. 2004). Thus, the current Miocene fossil record seems to suggest that these traits may have evolved in a mosaic fashion. For example, modern ape-like features of the distal humerus accompany more primitive quadrupedal traits in *Sivapithecus* (Pilbeam et al. 1990). This implies either that not all of the traits shared by suspensory crown hominoids are necessary for that behavior (i.e., *Sivapithecus* was suspensory despite its apparent shoulder morphology), or that some of the presumed suspensory traits actually evolved for some other purpose (i.e., *Sivapithecus* has an ape-like distal humerus for some purpose other than suspensory behavior). Indeed, it has been suggested previously that behaviors other than suspension or brachiation might select for ape-like musculoskeletal features (Cartmill & Milton, 1977). It may be that slow climbing and bridging preceded modern ape-like suspensory and brachiating behaviors, and that a portion of the modern ape package was acquired during this stage. To understand the range of Miocene ape locomotor abilities and the pattern of locomotor development through that time period, a closer look at the morphologies of modern arboreal quadrupedal subcategories must be taken. Specifically, it must be understood how slow climbers differ from other arboreal quadrupeds, and if any of the traits in which they differ are traits previously thought to indicate suspensory locomotion. If so, some of the early traits of Miocene hominoids which seem to imply a contradiction in locomotor styles may instead be a simple adaptation to a form of arboreal quadrupedalism which places more emphasis on climbing. If not, then an alternative explanation for the mosaic of skeletal features in early hominoids must be found.

Hypotheses:

1. The slow climbers *Alouatta* and *Nycticebus* will share alterations of their skeletal anatomy when they are compared to other arboreal quadrupeds of their respective phylogenetic groups. These shared traits may indicate parallel evolution for a slow climbing lifestyle, allowing them to use a variety of climbing postures, including bridging behaviors and some suspension.

2. Features distinguishing slow climbing will be similar to some of those which have been said to distinguish suspensory locomotion, due to the similar nature of requiring a wider range of limb mobility and extension.

To test these hypotheses, slow climbers will be compared to other arboreal quadrupeds using traits which have also been known to distinguish suspensory primates from other groups. In this fashion, Hypothesis 1 will test when slow climbers can be differentiated from other arboreal quadrupeds in a given set of traits, and Hypothesis 2 will test if markers of slow climbing are similar to those of suspension. The predictions will be based on previous claims in the literature of traits which apply to suspensory and/or climbing primates.

Predictions:

Prediction 1: Limb Proportions

1a: Slow climbers will have a higher intermembral index. Reaching behaviors, coupled with any degree of forelimb suspension, should select for an increase in the length of the forelimb in relation to the hind limb (Jungers 1985). Generalists will have intermediate intermembral indices, while leapers will have the lowest with their longer hind limbs.

1b: Slow climbers will have a longer forelimb than the other arboreal quadrupeds when compared to their global geometric mean (see reasons above). Generalists will have short forelimbs to keep them close to the branches they move on (Rose 1973). Leapers will have forelimb lengths like generalists, since they do not specialize in any forelimb motion.

1c: Leapers will have a longer hind limb than the other arboreal quadrupeds compared to their global geometric mean, because of the need for a great deal of hind limb extension in leaping (Jungers 1979). Generalists will have shorter hind limbs to help them stay near the branches during quadrupedal locomotion, and slow climbers will either be similar to generalists because they have no need to specialize the hind limb.

Prediction 2: Shoulder

2a: Slow climbers will have a larger, more globular humeral head to allow for greater range of motion at the shoulder in comparison to other arboreal quadrupeds. The head will be higher than the greater tubercle to allow for further abduction (Larson 1993).

2b: Slow climbers will have larger muscle insertions and originations for muscles that move the shoulder - in particular those of the rotator cuff and the deltoid, which may retract, abduct, or flex the shoulder, to allow for positions such as extreme protraction in bridging, and extreme abduction and retracting in suspension and climbing postures (Erikson 1963, Larson 1993).

2c: Slow climbers will have more dorsally positioned scapulae compared to other arboreal quadrupeds. Proxies for this will include more humeral torsion in comparison to other arboreal quadrupeds, which may be seen by a wider distance between the greater and lesser tubercles as they rotate back around the humeral head (Harrison 1989). Other proxies will be longer clavicles in slow climbers, and more projecting acromian processes (Erikson 1963, Larson 1993).

Prediction 3: Elbow

3a: Slow climbers will have expanded articular surfaces at the trochlea for greater range of flexion and extension. Additionally, the trochlea and trochlear notch will be expanded mediolaterally with more of a keel than seen in other arboreal quadrupeds to allow for stability in a wide range of positions (Rose 1988, Gebo 1996). Furthermore, they will have deep olecranon fossae for great extension, as seen in suspensory primates (Feldesman 1982).

3b: Slow climbers will have an expanded articular surface at the capitulum, and a rounder radial head for greater pronation and supination (Rose 1988).

3c: Slow climbers will have large epicondyles for attachments of pronators and supinators, as well as for wrist extensors and flexors, so that these joints may have a greater range of motion (Rose 1988).

Prediction 4: Hip

4a: Slow climbers will have a rounder and larger femoral head for greater hip mobility, with a large acetabulum to match (Ruff and Runestad 1992, MacLatchy et al. 1996).

4b: Slow climbers will have a high femoral neck angle to allow for greater mobility during abduction (Anemone 1993).

4c: Slow climbers will have a larger fossa for the ligamentum teres attachment in the acetabulum to allow for more freedom of movement (Ward 1991).

4d: Slow climbers will have a shallower acetabulum, permitting a wider range of abduction (MacLatchy 1998).

Prediction 5: Knee

5a: Slow climbers will have an expanded bicondylar width and shallow condyles to allow for stabilized side to side movements and/or rotation movements, rather than specialized flexion and extension, which require antero-posteriorly deep condyles (Gebo 1989, Anemone 1993).

5b: Slow climbers will have larger medial condyles than lateral condyles for support during extreme climbing postures, while leapers and generalists will be more symmetrical. In addition, leapers will have a larger lip to their lateral condyles than seen on their medial condyles for support during flexion/extension (Fleagle 1977, Madar et al. 2002).

5c: Slow climbers will have a shorter, broader patellar groove to allow for more movement of the patella, aiding in movements which require a combination of extension/flexion and medial and lateral rotation (Madar et al. 2002). Leapers will have a tall, raised patellar groove to improve the leverage of quadriceps femoris across the knee during extension (Gebo 1989, Anenome 1993).

Methods

To determine if a slow loris differs from its arboreal quadrupedal relatives in the same ways the howler monkey differs, the two phylogenetic groups were first analyzed separately in one-way ANOVAs. If *Nycticebus* was statistically different from its group in a feature the same way *Alouatta* was, the feature was considered a distinguishing marker of slow climbers. This separation allowed for reducing the effects of phylogeny. For example, if trait X had sizes 1, 2, 3, 4, 5, and 6, and these relative sizes were matched with *Alouatta, Cebus, Saimiri, Nycticebus, Otolemur,* and *Galago,* respectively, one might argue that the size of trait X cannot be an indicator slow climbing, as the slow climbers are not near each other in size. However, by dividing it up by phylogeny, it becomes clear that the groups have sizes 1, 2, 3 and 4, 5, 6, indicating that amongst a related group of primates, slow climbers always have the smallest size for trait X.

To emphasize if those distinguishing markers were important in variation, the groups were then combined in five Principle Components Analyses (PCAs). These will determine how well slow climbers can be differentiated in a morphospace from other arboreal quadrupeds. It is noted that phylogeny could be a factor, as *Cebus* and *Saimiri* are more closely related to one another than either is to *Alouatta*, just as *Otolemur* and *Galago* are to one another at the expense of *Nycticebus*. This issue will be kept in mind as the evaluations proceed.

Digital calipers and protractors were used to measure the distances and angles in this study. Circumference and curved measurements were taken by aligning thin string along the curvature, and then measuring the distance of the straightened string. All measurements were tested for accuracy by five repeated tests. Measurements with high error rates were not included in the final analysis.

One-hundred and twenty-six measurements were used, and from these, thirty-six indices were derived. Figures 1-22 demonstrate the majority of the measurements as taken on the bones. Tables A and B give the abbreviations for these measurements and indices. The indices are for the most part straightforward, though some require additional explanation. ML and AP NCMAs are the measurement of the curve of a long bone as described in Swartz (1990). They are the distance between the long cord of the bone to the center of the shaft divided by the diameter of the midshaft, and can be represented in Figure 23 (chord labeled “C”, diameter labeled “D”. Normalized curvature moment arms were taken for both the anteroposterior direction to check for retroflexion, and the mediolateral direction to check for medial inclination. Moment arm in curvature was deduced based on a normalized curvature moment arm (NCMA) used by Swartz (1990). Curvature moment arm was defined by Biewener (1983) as the distance from the cord length (a line from the distal to proximal ends of a bone) to a midpoint on the shaft. Swartz (1990) modified Biewener’s measurement by dividing it by the cross sectional diameter of the midshaft. Insertion Indices are demonstrations of how far down a muscle or ligament attaches on a long shaft, to understand its leverage. Robusticity is measured by dividing the midshaft width by the length of the long bone, to determine how robust a shaft of a long bone is.

Osteological specimens were from the Stony Brook University Museum, the University of Michigan: Museum of Zoology, and the American Museum of Natural History: Mammalogy Department. Eight specimens from each species were examined, with the exception of *Galago demidovii*, for which only six specimens could be obtained. Only adult specimens were measured, determined by the fusion of the long bone epiphyses to their diaphyses.

The measurements were then normalized by first dividing each by the geometric mean, and then logging each result using the normal log. Indices were first calculated by using the measurements that had been divided by their geometric mean. After calculation, these were then logged for normalcy. A student's t-test was then used to determine which measurements were significantly different within phylogenetic groups. This was done to narrow down which measurements were useful to test further for the purposes of differentiating locomotor groups. Those measurements which were significant were then run through a one-way ANOVA, comparing the locomotor categories to one another. This was done twice – once for the platyrrhine group, and again separately for the Lorisiformes group. A Bonferroni correction was run on the ANOVA results, so that a significance level would be below $p = 0.01667$, rather than below $p = 0.05$. This was determined by dividing the original p-value of 0.05 by 3, due to there being 3 contrasts run for each ANOVA (slow climbers compared to generalists, generalists compared to leapers, and slow climbers compared to leapers). Comparisons were then made to see which traits were significantly different among groups in identical fashions between the platyrrhine results and the Lorisiformes results. Table C lists the ANOVA results. Traits which separate slow climbers from other arboreal quadrupeds to a significant degree are highlighted in red. Traits which separate slow climbers from other arboreal quadrupeds at a level of $p \leq 0.05$ are highlighted in orange. Table D lists these results in a summarized fashion.

Principle Components Analyses were run using selected measurements and indices which represented key features of the limb proportions, shoulder, elbow, hip, and knee. A separate analysis was run for each joint, as well as for the limb proportions. The results are depicted in Figures 24-38 and Tables E-I.

Results

ANOVA

For *p*-values for each test, refer to the ANOVA results summarized in Table C. All measurements are in relation to the global geometric mean of the subject. Unless otherwise stated as non-significant or approaching significance, traits which are listed as separating slow climbers from other arboreal quadrupeds are significant at a $p = .01667$ level.

Prediction 1a: upheld.

Slow climbers have a higher Intermembral Index than the other arboreal quadrupeds in their phylogenetic groups.

Prediction 1b: partially upheld.

Slow climbers have longer forelimbs than generalists, but in Lorisiformes, the leaper *Galago* has a longer forelimb than the slow climber *Nycticebus*. Generalists have the shortest forelimbs.

Prediction 1c: partially upheld.

Leapers have the longest hind limbs. However, generalists and slow climbers do not have similar hind limb length as was originally predicted. Generalists have longer hind limbs than slow climbers.

Prediction 2a: partially upheld.

Slow climbers have humeral heads rising highest above their greater tubercles in relation to other arboreal quadrupeds. However, the heads of the humeri were not any larger in slow climbers than any other arboreal quadruped, nor any more rounded. The only dimension in which they were separated from other arboreal quadrupeds was in height, where they approached significance. Depth, width, and circumference of the humeral head were not different among arboreal quadrupeds.

Prediction 2b: partially upheld.

Slow climbers have taller supraspinous fossae, indicating a large supraspinatus muscle. However, their greater and lesser tubercles are no larger than any other arboreal quadruped. Their deltoid insertion is intermediate among the arboreal quadrupeds, with the longest insertion in generalists, and the shortest in leapers. Their infraspinous fossae are not significantly different from other arboreal quadrupeds.

Prediction 2c: not upheld.

While the pattern of slow climbers having the greatest distance between tubercles was present, it was not a significant value. Slow climbers did have longer clavicles than other arboreal quadrupeds, and these values approached significance, but they did not have longer acromian processes.

Prediction 3a: partially upheld.

The length of the articular surface in the trochlear notch was longest in slow climbers, but their olecranon fossae were not the deepest. The measure of olecranon fossa depth was not found to be significant. The width at the waist of the trochlear notch was greatest in slow climbers, but there was no keeling that could be seen as greater than other arboreal quadrupeds.

Prediction 3b: partially upheld.

Slow climbers do have the largest capitula. However, they do not consistently have the roundest radial heads, which was determined by dividing the mediolateral diameter of the head by the anteroposterior diameter. In Lorisiformes, the slow climber has the roundest radial head, but in platyrrhines, the slow climber *Alouatta* is near equal in symmetry with the generalist *Cebus*.

Prediction 3c: not upheld.

Leapers had the smallest humeral epicondyles, but generalists and slow climbers had interchangeable values. In platyrrhines, the slow climber had a larger medial epicondyle and a smaller lateral epicondyle than the generalist, while this was the opposite in Lorisiformes.

Prediction 4a: partially upheld.

Slow climbers consistently had larger femoral heads, as well as larger acetabulae. Their femoral heads were significantly taller and wider than other arboreal quadrupeds, and approached significance in their depth. Slow climbers do not always have rounder acetabulae or femoral heads, but these are always rounder in slow climbers than in leapers.

Prediction 4b: upheld.

Slow climbers have the largest angle of their femoral angle to their shaft.

Prediction 4c: almost upheld.

Slow climbers have the widest notches for the ligamentum teres, though this only approached significance.

Prediction 4d: not upheld.

There was no relation between acetabular depth and locomotor method.

Prediction 5a: partially upheld.

Slow climbers had the widest bicondylar widths. However, this was not found to be statistically significant. Slow climbers did not have the shallowest condyles overall, though they were shallower than seen in leapers.

Prediction 5b: upheld.

Slow climbers had smaller lateral condyles than medial condyles. Additionally, this ratio was shown to become larger in generalists, and largest in leapers, with their raised lateral lip.

Prediction 5c: not upheld.

Slow climbers had the widest patellar grooves, which were significantly different in width from other arboreal quadrupeds. Slow climbers also had a shorter patellar groove than leapers, and in Lorisiformes, they had a shorter patellar groove than generalists as well. However, in platyrrhines, the slow climber *Alouatta* had a patellar groove about the same height as the generalist *Cebus*.

PCA

The PCA results were similar to the ANOVA results. As mentioned the PCAs were divided up based on five categories: limb proportions, shoulder morphology, elbow morphology, hip morphology, and knee morphology. See Figures 24-38 and Tables E-I for reference. On the figures, red indicates slow climbers, blue indicates generalists, and green indicates leapers.

In its first three components, the Limb Proportion PCA accounts for 97% of the variance. Likewise, the Shoulder PCA accounts for 61% of the variation, the Elbow PCA accounts for 58% of the variation, the Hip PCA accounts for 71% of the variation, and the Knee PCA accounts for 73% of the variation.

Limb Proportion PCA:

PC I is driven by lower limb length. Leapers have the longest hind limbs, while slow climbers have shorter hind limbs. This accounts for 54% of the variation. *Cebus* actually places closer to the slow climbers than to the other generalist (*Otolemur)* or the leapers. This may indicate that either *Alouatta* has not decreased its lower limb length considerably, or that *Cebus* has shortened its hind limb relatively more than *Otolemur*. (See Figures 24 and 25; Table E.)

PC II is driven by upper limb length. Generalists have shortened their upper limb, while leapers and slow climbers have kept them longer. This accounts for 40% of the variation. Each phylogeny demonstrates a clear distinction between its generalist member and the other two members. In platyrrhines, the slow climber *Alouatta* demonstrates a longer upper limb than the leaper *Saimiri.* However in Lorisiformes, the slow climber *Nycticebus* and the leaper *Galago* have similar upper limb lengths, with *Galago* even longer than *Nycticebus* due to its long radius and ulna. (See Figures 24 and 26; Table E.)

PC III is a measure of forearm to arm length, mimicking the brachial index. A long femur is correlated with a longer humerus on this axis. As established, *Galago* has a long forearm and a short humerus, and so has a high brachial index. The slow climbers have both a long upper and forearm, and so place near the center. Generalists have a short upper and forearms, but since neither is dramatic in length, they end near the middle as well. *Saimiri* clearly does not have as long of a radius or ulna as *Galago,* and would place near the middle if it weren't for its long femur pulling it down. This accounts for 3% of the variation, and therefore is of much less importance than the first two components. (See Figures 25 and 26; Table E.)

Shoulder PCA:

PC I is driven by the shape of the scapula, along with the shape of the humeral head. A scapula with a long medial border and a large supraspinous fossa, and a tall humeral head that sits higher above the greater tubercle pull slow climbers to the left on the PC I axis. Meanwhile other arboreal quadrupeds are farther right. This accounts for 31% of the variation. (See Figures 27 and 28; Table F.)

PC II is driven by glenoid cavity height, the length of the acromian process, and the protrusion of the spine of the scapula. A tall glenoid fossa is contrasted to a long acromian process and a spine which protrudes out far. These traits appear to be dividing the primates by phylogenetic relations, though a trend in locomotor groups can potentially be seen within the divided phylogenetic groups. The Lorisiformes of this study have taller glenoid cavities, shorter acromian processes, and spines which protrude less off the scapula. The platyrrhines are the opposite. Therefore, PC II is not a good indicator of locomotor group, as much as it is an indicator of the phylogenetic group. This accounts for 20% of the variation. (See Figures 27 and 29; Table F.)

PC III is derived from how far down the humerus the deltoid tuberosity runs. This component is also influenced by humeral head width and the greater tubercle height, neither of which distinguish the locomotor categories apart from one another, nor the phylogenetic groups apart from one another well. The result is a component which does not separate any groups. This accounts for 10% of the variation. (See Figures 28 and 29; Table F.)

Elbow PCA:

PC I is derived from the size of articular surfaces. The larger capitulum, radial head, and trochlear notch surfaces of slow climbers pull them left, since they have the greatest expansion of articular surfaces. This accounts for 30% of the variation. (See Figures 30 and 31; Table G.)

PC II is driven by the trochlea medial and lateral lip heights, the size of the capitulum, and the protrusion of the humeral epicondyles. Tall medial and/or lateral lips to the trochlea and/or a large capitulum are contrasted to large epicondyles. Leapers have high medial and lateral lips to their trochlea and small epicondyles. Generalists have reasonable sized epicondyles, and a small capitulum. Slow climbers are in the middle, because while they have a large capitulum and reasonable height of their trochlea lips, they also have large epicondyles. This accounts for 18% of the variation. (See Figures 30 and 32; Table G.)

PC III is made up of the shape of the radial head and the depth of the olecranon fossa. A rounder radial head and a deeper olecranon fossa are contrasted to a larger radial tuberosity. *Nycticebus* has a round radial head and a deep olecranon fossa. *Alouatta* has a deep olecranon fossa but a larger radial tuberosity, which places it slightly above *Nycticebus*. The generalists and leapers have a combination which causes them to fall in the center of the axis. This accounts for 10% of the variation. (See Figures 31 and 32; Table G.)

Hip PCA:

PC I is derived from the general size of the femoral head, and greater trochanter, as well as the width of the notch for the ligamentum teres in the acetabulum. Those are contrasted to a larger third trochanter and a larger neck circumference. Slow climbers place farthest left with their large femoral heads and small third trochanters; meanwhile their closest arboreal quadrupedal relatives place farther right. Notably, the platyrrhines group closer to one another than the Lorisiformes do. *Cebus* and *Saimiri* are farther to the right than *Alouatta*, but are much closer to *Alouatta* than *Otolemur* or *Galago* are to *Nycticebus*. Another way to look at this is that *Nycticebus* places among the platyrrhines for PC I. This accounts for 35% of the variation. (See Figures 33 and 34; Table H.)

PC II is derived from the size and shape of the femoral head and acetabulum. Slow climbers have roughly the largest and roundest femoral heads and acetabulae of their group, followed by generalists, and then by leapers. Leapers are not going to have very symmetrical surfaces because they just need front to back motion, not side to side. Generalists still need to participate in a fair amount of abduction and adduction, to move quadrupedally on tree branches. However, *Cebus* is very close to the range of *Saimiri,* whereas *Otolemur* is distinctly lower than *Galago*. All platyrrhines are farther up on the axis than Lorisiformes. So there may be some phylogeny influencing this axis, as well. This accounts for 28% of the variation. (See Figures 33 and 35; Table H.)

PC III is driven by the size of the greater trochanter and the width of the entrance to the acetabular notch. A large greater trochanter accompanies a large acetabular entrance width on this axis. Because of the combination of these two, it is not easy to distinguish locomotor groups. *Saimiri* and *Nycticebus* have small notch entrances, while *Alouatta* has the largest greater trochanter in relation to its femoral length. The traits of PCIII may be best looked at on their own, rather than in a group, as they do not separate groups by locomotor method or phylogeny. This accounts for 8% of the variation. (See Figures 34 and 35; Table H.)

Knee PCA:

PC I is derived from the general shape of the femoral condyles. The size of the lateral condyle is contrasted to the size of the medial condyle. Same with patellar groove height – a tall patellar groove is contrasted to a wide patellar groove, and to a large bicondylar width. There is a clear distinction here between the leapers and the slow climbers. However, the generalists are not as easy to place as a group. *Otolemur* places with the leapers, and *Cebus* with the slow climbers. This is likely due to the larger bicondylar width in *Cebus* than seen in *Otolemur*. Also, the height of the patellar groove is similar between *Cebus* and *Alouatta*, and between *Otolemur* and *Galago*, so they group accordingly. This component is very influential, accounting for 48% of the variation seen. (See Figures 36 and 37; Table I.)

PC II is derived from the size of the epicondyles and the size of the articular surface at the distal end of the femur. Large epicondyles are contrasted to large articular surface area. Leapers have a small articular surface, due to the lack of medial/lateral expansion, so they are slightly lower. Slow climbers have a large articular surface, but also have large epicondyles, so they are towards the middle. Generalists have large articular surfaces, and mid-size epicondyles, so they also in the middle. Overall, this component clearly does not separate locomotor groups well. It does separate groups based on phylogeny, however, with Lorisiformes placing higher, and platyrrhines placing lower. This is likely due to platyrrhines having larger epicondyles than the Lorisiformes. This component accounts for 14% of the variation. (See Figures 36 and 38; Table I.)

PC III is driven by the tibial tuberosity insertion and the size of the articular surface. Generalists have large articular surfaces and tibial tuberosity insertions farther down the shaft, while slow climbers and leapers have shorter tibial tuberosity insertions. This accounts for 11% of the variation. (See Figures 37 and 38; Table I.)

Discussion

For each of the five major morphological discussion categories, the ANOVA results will first be discussed, followed by a discussion of the PCA, and lastly, a summary of any distinguishing characters the category revealed. Afterwards, there will be a discussion of how these morphologies may apply to the fossil record.

Limb Proportions:

Slow climbers have a higher intermembral index than the other arboreal quadrupeds in their phylogenetic groups. This is a result of the slow climbers having a longer forelimb than generalists, and shorter hind limbs than both the generalists and the leapers.

In Lorisiformes, the leaper *Galago* has a longer forelimb than the slow climber *Nycticebus*. Specifically, it is the radius and ulna which appear longer in *Galago* than in *Nycticebus.* Forelimb length scales negatively in lorises (Jungers 1979). As such, forelimb length is inversely proportional to body size in lorises, and *Nycticebus* is on the upper end of body size for lorises. This scaling is due more to the antebrachial than brachial arm segments changing (Jungers 1979). Since *Nycticebus* is larger, it has limbs that appear shorter relatively than in smaller lorises. Forelimb length is also negatively allometric in Lemuridae, but it is not clear if it is in Galagidae. *Galago* has an elongated radius and ulna, and being the smallest primate of the study, its limb length might scale differently (Jungers 1979, Demes and Jungers 1989). The platyrrhine leaper has a shorter forelimb than the slow climber, and does not go against the prediction like the Lorisiformes group does.

Leapers have the longest hind limbs. However, generalists and slow climbers do not have similar hind limb length. Generalists have longer hind limbs than slow climbers. This may be due to the need of slow climbers to generate more pedal friction to avoid slipping during clinging and climbing, as hypothesized by Jungers (1985). Negative allometry of the hind limb may allow a larger individual to “lean away” from the support, which can optimize friction against the tree. Or it could be a result of generalists needing maintain a slightly longer hind limb for the times that they do participate in leaping behaviors. Likely, it is a combination of these. A long hind limb is useful for leaping. Leaping is not frequently seen (or not seen at all) in slow climbers, while is seen more often in generalists (though not as often as in leapers) (Fleagle 1999).

These findings are corroborated in the limb proportion PCA, in which both phylogenetic groups were included together. Leapers had the longest hind limbs and slow climbers had the shortest, as PC I demonstrates. Generalists place between leapers and slow climbers, though *Otolemur* places closer to the leapers while *Cebus* places closer to the slow climbers. As *Otolemur* is closely related to many extreme leapers, it may be an artifact of phylogeny that allows it to have a longer lower limb, depending on the primitive condition of its clade. On the other hand, the shortened hind limb of *Cebus* may be a result of their role in the suspensory tripod between the hind limbs and the tail. Hind limbs longer than the prehensile tail would be cumbersome for suspensory feeding postures.

In PC II, it is shown that generalists had the shortest forelimbs, while slow climbers and leapers maintained longer forelimbs. The PC I/PC II graph is essentially illustrating an intermembral index.

Intermembral indices seem a reliable method of separating slow climbers from other forms of arboreal quadrupedalism. Hind limb length alone cannot be used assuredly, as *Cebus* falls near the range of the slow climbers on the PC I axis. Likewise, forelimb length cannot be used with confidence, as the leaper *Saimiri* places near the slow climbers, and the leaper *Galago* actually shows a longer forelimb than its slow climbing relative, *Nycticebus*. Therefore, it is best to use the intermembral index to determine if a primate is likely a slow climber in comparison to its relatives.

Shoulder:

The heads of the humeri were not any larger in slow climbers than any other arboreal quadruped, nor any more rounded. The only thing distinguishing the humeral head of slow climbers from other arboreal quadrupeds is that the humeral heads of slow climbers are taller. A tall humeral head gives surface area for adduction and abduction (Jolly 1967, Harrison 1989, Larson 1993). In relation to the other arboreal quadrupeds of this study, slow climbers have humeral heads rising higher above their greater tubercles, though this is a non-significant difference. Lowering the greater tubercle, plus increasing the height of the humeral head, creates a larger surface area for articulation of the humerus, to allow it to move at the shoulder even when fully flexed (Rose 1989, Larson 1993). This allows for locomotor, postural, and manipulative events to occur when the arm is raised farther up over the head (Rose 1989).

Lowering the greater tubercle can create a complication, though, as the greater tubercle is the attachment site for the abductor, supraspinatus. Larson and Stern (1989 and 1992) concluded that the only way for an animal with a low greater tubercle to deal with heavy demands on supraspinatus for abduction and joint stabilization is to increase the size of supraspinatus. Acrobatic species have larger supraspinatus fossae than terrestrial species, and hominoids and atelines have largest of them all (Larson 1993). Supraspinatus is critical in arm elevation. The early phase of arm elevation is brought about solely by deltoid/supraspinatus interaction, as opposed to the earlier idea that arm elevation is a result of the muscle couple of deltoid/supraspinatus with the remaining members of the rotator cuff assisting to resist superior displacement of the humerus by the power of the deltoid (Innman 1944, Larson and Stern 1986, Larson 1993). Supraspinatus itself actually prevents humeral displacement in the early phase of arm elevation. This responsibility can shift to infraspinatus or upper subscapularis as the direction of movement and orientation of humerus changes. Mostly, however, supraspinatus is a pure abductor (Larson and Stern 1986). Quadrupedally, supraspinatus does not act as a protractor of the humerus during swing phase as historically hypothesized, but does act during the support phase, as demonstrated by macaques, vervet monkeys, and chimpanzees (Larson and Stern 1987, Larson and Stern 1989, Larson and Stern 1992). In this study, slow climbers have taller supraspinous fossae, indicating a large supraspinatus muscle (Erikson 1963). It is unlikely that they require this size increase for greater support during typical support phases, since they do not move more often in quadrupedal locomotion than the other members of the study. It is more likely that they are employing the supraspinatus muscle in abduction and arm elevation for climbing, and atypical support phases during bridging behaviors.

Other muscle size enlargements are not clearly evident. The greater and lesser tubercles of the slow climbers are no larger than any other arboreal quadruped. The deltoid insertion of the slow climbers is intermediate among the arboreal quadrupeds, with the longest insertion in generalists, and the shortest in leapers. The infraspinous fossae of slow climbers are not significantly different from those of other arboreal quadrupeds. The only muscle proxied in this study that distinguishes slow climbers from other arboreal quadrupeds at the shoulder is supraspinatus. Abduction at the shoulder is therefore likely an important movement in slow climbers, but due to the lack of change in other muscles, it appears movements such as lateral rotation and circumduction are no more frequently employed than in other arboreal quadrupeds.

The medial border of the scapula is longer in slow climbers, but this is probably due to the increased height of the supraspinous fossa. This elongation could provide more space for attachments of rhomboids and levator scapulae, which are suggested to be stabilizers of the shoulder girdle (Ashton and Oxnard 1963). However, without soft tissue comparisons, it is difficult to say which muscles are truly being increased.

Torsion of the humeral head has long been debated as to its value and as to the proper way to measure it. In this study, humeral torsion was measured using the method of Harrison (1989), which measured potential torsion by how far the greater and lesser tubercle were apart from one another. Humeral torsion is suggested to really be a result of the migration of the tubercles around the humeral head (Harrison 1989, Larson 1993). Slow climbers had the greatest distance between tubercles, though not at a significant value.

High torsion has long been thought to be a trait of suspensory behavior (Inman 1944). However, gibbons, a highly suspensory primate, have low torsion (Larson 1988). African apes, which this theory often was based on, have high torsion, which could potentially be explained as an accommodation to quadrupedal postures by animals with dorsally placed scapulae (Larson 1988). Humeral torsion might not actually be a hallmark of suspensory behavior (Larson 1988, Larson 1993). If humeral torsion accommodates quadrupedal postures for animals with more dorsally placed scapulae, it provides an interesting explanation to why slow climbers would have an increase in distance between their tubercles, even if it was to a non-significant degree.

Another key feature that was able to separate slow climbers from other arboreal quadrupeds was the length of the clavicle. Slow climbers have longer clavicles than other arboreal quadrupeds, just as more suspensory species have longer clavicles than slow climbers (Larson 1993). A long clavicle is hypothesized to increase the breadth of the shoulders, and therefore the arm span, in primates. It is important in hominoids and

Ateles, who have moved their scapula dorsally, to have a longer clavicle to reach between the scapula and the sternum (Ashton and Oxnard 1962).

The final proxy for dorsal scapula positioning is the acromian process length. The acromian process of hominoid and atelines projects noticeably beyond the glenoid (Larson 1993). This may be to improve leverage of deltoid (Inman 1944). A long acromian process was not seen in slow climbers.

As already known from living species, slow climbers do not have a scapula as dorsally positioned as suspensory primates. However, it is interesting to note that some features indicating at least a small migration of the scapula dorsally may be present in slow climbers, such as the higher humeral torsion and a longer clavicle.

The PCA for the shoulder is very poor. It only accounts for 61% of the variation, and does not do a good job of distinguishing locomotor groups. PC I is the only component which separates locomotor groups along its axis, and the only group it consistently separates from the others is the slow climber group. PC II separates the groups based on phylogenetic relations, and PC III does not succeed in separating any groups. The driving forces behind PC I are the scapular shape and the shape of the head of the humerus. This confirms the importance of the variation in length of the medial border of the scapula, the height of the supraspinous fossa, and the height of the humeral head. Slow climbers increase the height of all of those, though again, the length of the medial border of the scapula is probably related to the height of the supraspinous fossa.

There does not appear to be significant caudal elongation of this border as is found in suspensory species for increasing serratus anterior (Ashton and Oxnard 1962).

The best characters of the shoulder for distinguishing slow climbing are the height of the supraspinous fossa, the height of the humeral head, and the length of the clavicle. The degree to which the humeral head rises above the greater tubercle could also be informative, if a good sample size exists for comparison. Other traits, such as how round and globular the humeral head is and how large the tubercles are, are not informative in this study.

Elbow:

The length of the articular surface in the trochlear notch was longest in slow climbers, but their olecranon fossae were not the deepest. The measure of olecranon fossa depth was not found to be significant. This implies that extension and flexion were important, but not to the same degree as in suspensory species, in which there is considerable extension of articular surface into the olecranon fossa (Rose 1988). Of importance to note, is that olecranon fossa depth is often not a reliable measurement, and there is subjectivity to how much articular surface extends within the fossa (Senturia 1995). Height, width, and depth of the olecranon process were not found to be significant.

There is also expansion of the trochlear notch mediolaterally in slow climbers, which represents some stabilization at the elbow, though not to the extent it would if it also included a trochlear keel (Rose 1988, Rose 1993). In hominoids there is thought to be universal stability at the elbow, no matter what position the animal is in at the time, due in part to its keel (Rose 1988). This stability is also provided by other aspects of the humeroulnar and humeroradial articulations. However, in non-hominoids there is usually only one particular stable position, because they have close-packing in full pronation (Rose 1988).

Ateles is an exception among non-hominoids. While it does not have a keel, it does have a large capitulum and a relatively symmetrical radial head so it is not so restricted to one stable position. This humeroradial morphology is partially reflected in the slow climbing group.

Slow climbers have the largest capitula of the arboreal quadrupeds in this study, determined by directly comparing the height and width of the capitula among the primates, and by multiplying the height by the width of the capitula to create a rough estimate of surface area. In all regards, slow climbers tended to be largest. However, slow climbers did not consistently have the most symmetrical radial heads. The roundness of the radial head was determined by dividing the mediolateral diameter of the head by the anteroposterior diameter. In Lorisiformes, the slow climber *Nycticebus* has the roundest radial head, but in platyrrhines, the slow climber *Alouatta* is near equal in symmetry with the generalist *Cebus*. This does not mean that generalists and slow climbers have the same stability at the elbow. *Cebus* may have a range of pronation and supination similar to the range of that seen in *Alouatta*, but it still has a smaller capitulum, indicating that it may have less stability than *Alouatta*.

Suspensory primates have larger medial epicondyles than other primates (Senturia 1995). It had been previously hypothesized that arboreal quadrupeds would have larger medial epicondyles than other primates, but it was not upheld when put under further inspection (Senturia 1995). Instead, arboreal quadrupeds were shown to have larger medial epicondyles in relation to most primates, but not in relation to suspensory primates. However, this leads to the hypothesis that slow climbers may have increased their humeral epicondyles if they are practicing any form of suspensory behavior, particularly their medial epicondyle. This study demonstrated that this was not always the case. Leapers had the smallest humeral epicondyles, but generalists and slow climbers had interchangeable values. In platyrrhines, the slow climber had a larger medial epicondyle and a smaller lateral epicondyle than the generalist, while this was the opposite in Lorisiformes. These findings suggest that to be a slow climber, it may not be required to increase the size of the muscle attachment sites for wrist flexors and pronators, or extensors and supinators. This somewhat contradicts the finding of a large capitulum, which indicates a potentially more stable system for pronation and supination, implying they are of greater importance in slow climbers. However, this study only measured the amount that these epicondyles protruded from the humerus and not the length of them proximo-distally. Measuring the height of the epicondyles may give further clues to this contradiction.

In the PCA, PC I and II seem to distinguish slow climbers apart from other arboreal quadrupeds. However, the traits in total only account for 58% of the variation seen in the elbow features. This analysis is therefore weak. The strongest traits are the articular surface area traits, particularly that of the capitulum, as that is influential on PC I and PC II.

PC I is derived from the size of articular surfaces, and separates the locomotor groups with a large degree of certainty. Slow climbers are to one side of the axis, and within each phylogenetic group, the order then proceeds to generalists being centered, and leapers being farthest to the other side. Without looking at phylogeny, it would appear that the generalists and the leapers are in one jumble, but with respect to their relationships, an order can be discovered. This pull for locomotor method, however, is not strong enough to overcome the pull of phylogeny.

PC II is driven by the trochlear shape, the size of the capitulum, and the protrusion of the humeral epicondyles. Large epicondyles indicate one half of the axis, while a taller trochlea plus a larger capitulum make up the other side. Slow climbers place in the middle, because they have large articular surfaces and large muscle attachments. Generalists have small articular surfaces and larger muscle attachments, placing less value on stability. Leapers have smaller muscle attachment sites at the elbow, but have a tall trochlea which could potentially be useful in extension/flexion at the elbow during a jump from quadrupedal postures.

PC III is not successful at separating locomotor groups and will not be discussed.

The best characters to look at for separating locomotor groups by the elbow are the sizes of the articular surfaces. An expanded trochlear notch and capitulum could indicate a slow climber, if compared to other members of its phylogenetic group. Muscle attachment sites are not consistent amongst locomotor groups and should not be used with confidence until further study is done.

Hip:

Slow climbers consistently had larger femoral heads, as well as larger acetabula than other arboreal quadrupeds in this study. Large femoral heads serve the same purpose as large humeral heads – to give a large and broader surface area for motion at the joint. This is a key feature demonstrating the degree of mobility at the hip joint. Another feature lending to this is the large angle (approximately 135 degrees; range of 129-145 degrees) of the femoral neck to the shaft seen in slow climbers (MacLatchy et al. 1996). The generalists and leapers follow as expected, with their angles becoming smaller (approximately 128 degrees; range of 121-133 degrees) and even smaller (approximately 126 degrees; range 119-132 degrees), respectively. A large angle allows for greater abduction and rotation at the hip, both necessary to suspension and bridging actions.

Slow climbers have the widest notches for the ligamentum teres, implying great mobility at the hip (Ward 1991, MacLatchy et al. 1996). A large notch means that the ligamentum teres can be repositioned with ease, as the femoral head moves within the acetabulum.

Acetabular depth was not found to be an indicator of locomotor method. This is similar to MacLatchy (1998), in which strepsirrhine acetabula were found to be remarkably similar in morphology despite differences in locomotor method.

There were no major distinctions in any of the muscular attachments at the proximal femur. This may suggest that muscles were likely not being recruited to any extreme different degree at the hip in any of the locomotor groups.

The PCA for the hip is more useful than the shoulder or elbow, as it accounts for 71% of the variation seen. Overall, PC I and II are the best components to look at for locomotor groupings. Femoral head size in particular is important, as it plays a role in both PC I and PC II, distinguishing slow climbers from other locomotor groups each time.

PC I is a measure of femoral head size, greater trochanter size, and the width of the notch for the ligamentum teres in the center of the acetabulum. In general, platyrrhines have a larger femoral head and a taller greater trochanter, so they end up on one end of the axis. However, among them it is clear that there is a gradient of the size of these features, with them largest in the slow climber, then the generalist, and finally the leaper. This same gradient is seen in the Lorisiformes, however they are spread farther across the axis than the platyrrhines. This component is useful in separating phylogenetic groups and locomotor groups from one another.

PC II is also useful. It is a measure of femoral head and acetabular size and symmetry. The larger and more symmetrical femoral heads and acetabula belong to the slow climbers, while the leapers display the smallest heads and least round acetabula. This axis is less dramatic in separating the locomotor groups, but the same trend from PC I can be seen.

PC III is not as useful. It is a measure of greater trochanter height and width of the entrance to the acetabular notch. Overall, this axis separates leapers from generalists. Leapers have small notch entrances and shorter greater trochanters than generalists.

However, the slow climbers are split. The short greater trochanter of *Nycticebus* places it higher, while the longer greater trochanter of *Alouatta* places it lower. The width of the acetabular notch entrance is variable, and does not seem to distinguish groups. Greater trochanter height is clearly demonstrated to not be a good indicator of whether an arboreal quadruped is a slow climber or not.

Overall, the best traits of the hip to look at are femoral head size, shape of the acetabulum, width of the notch for the ligamentum teres, and the angle of the neck to the shaft, as long as these can be compared within phylogenetic groups.

Knee:

Slow climbers had the widest bicondylar widths, though this was not found to be statistically significant. The patellar groove is wider in slow climbers than other arboreal quadrupeds. Additionally, the condyles are shallowest in slow climbers. This allows for stabilized side to side movements and/or rotation movements, rather than specialized flexion and extension, which require antero-posteriorly deep condyles and a high patellar groove (Gebo 1989).

Slow climbers have smaller lateral condyles than medial condyles on the femur. The ratio of lateral to medial condyle size was shown to become larger in generalists, and largest in leapers. A taller, raised patellar groove improves the leverage of quadriceps femoris across the knee during extension, which facilitates leaping (Gebo 1989, Anemone 1993). A prominent lateral border, as well as an increased height and depth of the lateral condyle, reflect the disproportionally large size of vastus lateralis among leapers, and also suggest an adducted hind limb (Fleagle 1977). In contrast, an enlarged medial condyle compared to the lateral condyle has been suggested to aid in stabilization during abduction and eccentric loading in hominoids (Gebo 1989, Madar et al. 2002). As slow climbers are closer to the hominoid condition than the leaping condition, this may demonstrate that slow climbers have a more stable knee structure for when their leg is abducted, rotated, or experiencing abnormal loads (Madar et al. 2002).

Slow climbers have a shorter patellar groove than leapers overall, and in Lorisiformes, they have a shorter patellar groove than generalists as well. However, in platyrrhines, the slow climber *Alouatta* has a patellar groove about the same height as the generalist *Cebus*. A tall patellar groove is good for extension at the knee, as would be needed in a leaping primate (Fleagle 1977). A shorter, broader patellar groove may allow for more movement of the patella, aiding in movements which require a combination of extension/flexion and medial and lateral rotation (Madar et al. 2002). *Cebus* may be exhibiting the condition seen in slow climbers, because it requires similar types of stabilization. As *Cebus* practices a degree of hind limb suspension via a prehensile tail, it would need to mimic the stabilization for extreme postures which is seen in slow climbers.

The PCA for the knee is fairly powerful, as it accounts for 73% of the variation. PC I is derived from the general shape of the femoral condyles and patellar groove height. Tall patellar grooves with larger lateral condyles than medial condyles are indicative of leapers, who need these features for their methods of leg extension during locomotion (Fleagle 1977). Bicondylar width also factors in to this component. A large bicondylar width and larger medial condyles than lateral condyles is indicative of slow climbers, which need such arrangements for more stability at the knee during abducted postures (Madar et al. 2002). However, the generalists are not as easy to place as a group. *Cebus* has a larger bicondylar width and shorter patellar groove height than its fellow generalist, *Otolemur*. *Otolemur* is more similar to *Galago* in these regards. This may be a result of phylogeny on the part of the Lorisiformes, and a result of the suspensory tail in platyrrhines. As mentioned earlier, *Cebus* participates in a degree of tail and hind limb suspension, which may drive it to need stability at the knee similar to *Alouatta* or *Nycticebus* (Fleagle 1999, Madar et al. 2002).

PC II is derived from the size of the epicondyles and the size of the articular surface at the distal end of the femur. Leapers have a small articular surface, because they do not have much expansion medial-laterally at the knee. Meanwhile, generalists and slow climbers do have larger articular surfaces. Pulling in the other direction, epicondyle size is small in leapers and larger in generalists and slow climbers. However, this axis does not separate the groups based on locomotor method. Rather, it is heavily influenced by phylogeny. Platyrrhines have much larger epicondyles than Lorisiformes, and so the groups cluster based on relationships.

PC III is driven by the tibial tuberosity insertion and the size of the articular surface. Generalists have large articular surfaces and tibial tuberosity insertions farther down the shaft, while slow climbers and leapers have shorter tibial tuberosity insertions.

A lower or longer tibial tuberosity insertion may increase the ability for extension at the knee, which is conceivably useful both in leaping and in hind limb suspensory postures (Fleagle 1977).

Overall, the knee is a useful area for determining if a primate could be a slow climber. The most critical characteristics are clearly the ratio of medial to lateral femoral condyle size for slow climbers, as well as the shortened height of the patellar groove. A longer tibial tuberosity is also an indicator, if it can be determined before that the primate is not a leaper. However, knee morphology must be viewed cautiously. *Cebus* demonstrates that a generalist can fall close to the range of slow climbers in regards to knee morphology, most likely because it does participate in a degree of hind limb and tail suspension. Therefore, the knee on its own should not be the only area looked at to determine if a primate could be a slow climber rather than a generalist.

The Hominoid Fossil Record:

The following traits from the regions examined in this study have been used to describe hominoids and their suspensory pattern of locomotion: long clavicle, long vertebral border of the scapula, long humerus, large capitulum, long trochlear notch, short femur and tibia, large femoral head, high femoral neck-to-shaft angle, wide and shallow patellar groove, a larger medial femoral condyle than lateral, and a high intermembral index (Erikson 1963, Rose 1988, Anenome 1993, Larson 1993, Rose 1993, Gebo 1996, Madar et al. 2002). Many times, traits found within Hominoidea are assumed to then be adaptations for brachiation. However, the traits listed above are also found, though potentially to a lesser degree, in slow climbing primates. It is likely that these traits relate to joint mobility, but not necessarily for the purposes of true brachiation. Therefore, it is prudent to keep in mind this alternative use for these traits when examining the fossil record.

There are also several traits from the regions of this study which have been previously used to describe the anatomy of brachiators and are not seen in slow climbers. These include a globular humeral head, a true spooled-shaped trochlea, a short olecranon process, and a deep olecranon fossa.

In previous studies, the olecranon fossa depth was found not to be a distinctive hominoid synapomorphy, as its degree of depth overlapped with many other catarrhines (Larson 1998). Additionally, it is not seen in *Ateles*, who can be included as a suspensory primate (Larson 1998). In this study, a deep olecranon was not shown to be a necessary adaptation for slow climbing.

A spool-shaped trochlea is only found in hominoids, not in *Ateles*, and therefore may or may not be an adaptation for suspension (Larson 1998). However, a large humeral head size and short olecranon processes are traits that hominoids share with *Ateles*, so therefore likely are suspensory adaptations (Larson 1998).

In the fossil record, Miocene hominoids have a variety of these potential suspensory traits in combination – including traits that can be found in slow climbers and those traits that are not. Some also have several traits that appear to be unlike suspensory primates or slow climbers.

Proconsul is an early Miocene hominoid from Africa, classified as an arboreal quadruped (Walker 1997). It does not seem to have any features suggesting orthogrady. Instead, its axial skeleton is very pronograde in nature. It likely had six lumbar vertebrae, and the torso of *Proconsul* would have been mediolaterally narrow and dorsoventrally deep, unlike modern hominoids, but like modern cercopithecoids and ceboids (Ward 1993, Walker 1997). The scapula of *Proconsul africanus* resembles platyrrhine morphology with a potentially elongated vertebral border, though this is difficult to be certain of as the medial portion of the scapula is distorted (Walker and Pickford 1983, Harrison 1987). The humeral head of *P. africanus* lacks the medial torsion seen in modern apes, though the distal humerus is almost similar to that of hylobatids, except that the lateral keel of the trochlea is less prominent (Harrison 1987, Walker 1997). Any spooling of its trochlea is slight and may not definitively indicate stabilization for suspensory behavior, anyway, as that trait is not present in *Ateles.* The ulna articulates with carpal bones, which is not seen in modern hominoids, though its hallux is designed for strong grasping (Rose 1993). Additionally, the narrow iliac blades suggest pronograde behavior (Walker 1997). The femur does show some similarities to modern hominoids, in its high neck-to-shaft angle and larger head (Ward et al. 1993). Also, the distal femur of *Proconsul* has a broad, shallow patellar groove with fairly symmetrical condyles (Fleagle 1983, Kelley and Pilbeam 1986). Finally, the hallux of *Proconsul* is strong and likely was capable of a large degree of motion at the midtarsal joint (Walker 1997).

Of the features found to correlate with slow climbing behavior in this study, only the high femoral neck-to-shaft angle, the broad patellar groove, and the large capitulum are preserved in *Proconsul*. This may potentially imply the beginnings of slow climbing behaviors, but perhaps is not as specialized toward them as the slow climbing primates in this study.

The potentially elongated vertebral border of *Proconsul* may be indicative of a larger supraspinous fossa, which also is a trait found in slow climbers. However, given the position of the scapular spine, the supraspinous fossa is likely not exceedingly tall, as seen in slow climbers. Rather, it may be deep, which was not a trait which could separate arboreal quadrupeds apart into more specific locomotor groups (Walker and Pickford 1983). The larger capitulum may allow for increased elbow stability in pronation and supination, as seen in slow climbers and suspensory primates (Rose 1988). The neck-to-shaft angle of *Proconsul nyanzae* is in the range of the slow climbers in this study, as well as hominoids. The broad, shallow patellar groove is similar to what is described in this study for slow climbers, as well as *Cebus*, but the slow climbers in this study demonstrated some asymmetry to the femoral condyles in favor of a larger medial condyle than lateral.

The intermembral index of *Proconsul heseloni* is estimated to be 86.9 (Walker and Pickford 1983). This is lower than what is seen in the slow climbers of this study (average 96.4 for *Alouatta*; 87.1 for *Nycticebus*; 82.9 for *Cebus;* 68.0 for *Otolemur*; 78.7 for *Saimiri*; 68.4 for *Galago*). As *Proconsul* is closer in size and relationship to the platyrrhine group, it may be more fitting to compare it to the intermembral indices that group demonstrates. In comparison to the platyrrhines, *Proconsul* falls between the generalists and the slow climbers.

Other than the spooling trochlea, *Proconsul* has very few traits that indicate it is overly mobile in the trees. Its higher neck-to-shaft angle and large femoral head do indicate a greater range of hind limb mobility, though the symmetry of the femoral condyles indicates its knee was not as well adapted to extreme postures as the slow climbers in this study likely are. It seems there is potential that *Proconsul* was capable of behaviors found in modern slow climbers, but perhaps not as specialized towards them. *Proconsul,* therefore, is best described as an arboreal quadruped with some abilities for careful climbing and grasping, but nothing to suggest more suspensory capabilities.

Dendropithecus is a small bodied catarrhine from the early Miocene of Africa, previously suggested to be on the lineage to modern gibbons (Andrews and Simons 1977, Fleagle 1984). There is nothing in particular that ties it to the hominoid lineage, but nevertheless has often been considered to be a Miocene ape (Harrison 1987, Fleagle 1999). It has an elongation of its forelimbs and a shortening of its hind limbs, similar to *Ateles* (Rose 1993, Rose 1996). The humeral shaft is relatively gracile, and slightly retroflected, more like *Cebus* than *Ateles* (Rose 1993). It does not have a large degree of humeral torsion and its bicipital groove is narrow (Fleagle 1983). The distal end of the humerus has a rounded capitulum, a medially expanded trochlea without any obvious spooling, a well defined lateral keel, and an expanded medial epicondyle (Fleagle 1983, Rose 1993). The radius is very robust, and the proximal end of the ulna has a tall cross-section, both of which appear to be more monkey-like than ape-like (Andrews and Simons 1977). Its phalanges are not strongly curved as would be seen in hominoids (Rose 1993). What exist of its lower limb bones may resemble primitive catarrhine morphology

(Fleagle 1984; Rose 1993). In a principal components analysis done by McHenry and Corruccini (1976) on the proximal femora of several extant and extinct catarrhines, *Limnopithecus* (here, *Dendropithecus*) placed in between *Hylobates* and *Presbytis* in terms of proximal femoral shape. The results were nearly identical in a previous principal components analysis that analyzed the shape of the distal humerus among extant and extinct catarrhines (McHenry and Corrunccini 1975). There were no platyrrhines or strepsirrhines included in these studies, however, so it is impossible to say how these studies tie into potential slow climbing morphology, and therefore very difficult to determine if *Dendropithecus'* similar morphology to *Hylobates* is due to suspensory practices, or to climbing and bridging. From the descriptions of the postcrania, however, it appears that *Dendropithecus* was less specialized in limb morphology than *Hylobates* for suspensory-type locomotion.

Dendropithecus possibly shares the following traits with slow climbers: a large capitulum, a trochlea without any obvious spooling, an expanded medial epicondyle, elongated forelimbs, and shortened hind limbs. Of those, only the rounded, enlarged capitulum and the elongated forelimb with a shortened hind limb can really possibly connect *Dendropithecus* to a slow climbing lifestyle, as the other traits can be found in other arboreal quadrupeds as well.

With an intermembral index in the range of atelines, a distal humerus similar to slow climbers, and a proximal femur approaching a hylobatid-like morphology, it is likely safe to say that *Dendropithecus* was an arboreal quadruped, with potential for some more mobile locomotor patterns, such as those which may be exhibited in slow climbing.

If suspension was included in its repertoire, it likely was confined to postural hind limb suspension with assistance from a hand, or forelimb suspension with assistance from a foot (Rose 1996).

Sivapithecus is a well-studied late Miocene ape from several regions of Asia. Its postcrania have been under the spotlight for decades, due to their primitive appearance which contrast to the suite of shared derived craniofacial features it has in common with the highly orthograde *Pongo* (Ward 1997). The humerus of *Sivapithecus* is retroflected to a larger degree than seen in any modern hominoid (Pilbeam et al. 1990). The degree of mediolateral curvature is similar to that of cercopithecoids, while its anteroposterior curvature falls within the range of platyrrhines (Slivensky, unpublished data). Despite the primitive nature of the humeral shaft, its capitulum is globular without a proximolateral tail, its trochlea is clearly spooled, and its medial epicondyle, while not completely present, is clearly beginning to flare medially (Rose 1988; Senturia 1995). These are traits of the modern hominoid complex. A juvenile radius is similar to that of *Proconsul*, and the carpals are closest in resemblance to generalized platyrrhines (Rose 1993). The manual phalanges are robust and curved, as in modern hominoids, but their joints more closely resemble those of platyrrhines (Rose 1993). Overall, the forelimb of *Sivapithecus* indicates an arboreal quadrupedal form of locomotion, with some abilities to climb vertically and grasp more than *Proconsul* demonstrated.

The hind limb presents a similar story, though it indicates more mobility than seen in the forelimb. The femur has asymmetrical condyles, which represent the ability to medially rotate on the tibia (Madar et al. 2002). The patella is similarly unrestrictive.

Madar et al. (2002) concludes that the knee morphology would allow for foot placement and load bearing on supports not directly under the center of mass, which can be construed as the beginnings of bridging behavior. The transverse tarsal joints of *Sivapithecus* have a supination degree as great as that seen in African apes (Madar et al. 2002). Finally, the pedal phalanges are robust, and likely used for grasping purposes (Madar et al. 2002).

Perhaps the seemingly more mobile hind limb may be a result of it being from a separate and smaller species, *S. sivalensis,* than the often-studied large humerus, which is from *S. parvada*. The smaller species, *S. sivalensis,* has a humerus to study as well, but it is smashed and therefore difficult to create accurate measurements from. Previously, it has been suggested that the two species may have had different locomotor methods based upon the two humeri of the respective species (Koehler et al. 2001). This has been contested based on the curvatures of the two humeri being almost perfect matches, despite their size differences (Richmond and Whalen 2001). Whether the two species of *Sivapithecus* would have participated in significantly different forms of locomotion is a question which will not be able to be answered until more overlapping postcrania is found.

Slow climbing and/or suspensory traits which are evident in *Sivapithecus* include a large capitulum, a large medial epicondyle on the humerus, asymmetrical femoral condyles, and a broad patellar groove. Additionally, the pattern of a potentially less mobile forelimb and more mobile hind limb is similar to what is seen in the slow climbers of this study. In conclusion, a shoulder joint which likely does not include a globular humeral head, an elbow with a large capitulum, and a distal femur that also shows the ability for an increased range of extreme postures make *Sivapithecus* readily comparable to the slow climbers of this study. The overarching theme with *Sivapithecus* is that it is an arboreal quadruped, which likely had several antipronograde activities in its repertoire allowing it to participate in slow climbing behaviors. Other than its spool-shaped trochlea, *Sivapithecus* is very similar to the slow climbers in this study, particularly *Alouatta* (Madar et al. 2002).

Dryopithecus is a late Miocene taxon from Europe. It has a large clavicle (Koehler et al. 2001). Its humeral shaft is relatively straight, though it inclines medially (Rose 1997). The torsion of the humeral head is debated, as it is missing (Begun and Kordos 1997). Some suggest it does not have torsion, due to its bicipital groove seeming wide and shallow, and its lesser tubercle not being reflected anteriorly (Rose 1997). However, the relevance of humeral torsion to suspensory behavior is debatable (Larson 1993). The distal humerus resembles the *Sivapithecus* humerus in most regards, having a large capitulum and spool-shaped trochlea, though its olecranon fossa is relatively shallow in comparison (Rose 1997). The carpals are similar to those of extant hominoids, while the phalanges are more primitive (Rose 1997). The foot is in a way, opposite of the hand, in that its tarsals are primitive while its metatarsals and phalanges more closely resemble modern hominoids (Ward 1997). In the hind limb, *Dryopithecus* has a neck-to-shaft femoral angle of 133 degrees (Moya Sola and Koehler 1996). The femur is also shallow distally, suggesting abducted postures as seen in primates which practice hind limb suspension. Its intermembral index is 114, which is higher than what is seen in the slow climbers of this study as well as the African apes (Moya Sola and Koehler 1996).

Dryopithecus is similar to slow climbers in the following ways: it has a large clavicle, a humerus with a large capitulum and shallow olecranon fossa, a neck-to-shaft femoral angle which falls in the range of both slow climbers and hominoids, and a femur which is shallow distally. However, its intermembral index is higher than what is seen in slow climbers.

Because of having an intermembral index above that of the slow climbers in this study, it is likely that *Dryopithecus* was more suspensory in behavior than modern slow climbers. Its possibly primitive shoulder joint, shallow olecranon fossa, and primitive manual phalanges mean that it likely maintained a quadrupedal posture, while having antipronograde behaviors to a larger extent than seen in *Sivapithecus* or *Proconsul* (Rose 1997; Ward 1997). The shallow olecranon fossa and primitive shoulder joint are also found in slow climbers, so it is possible to have these features and still use a variety of climbing postures. Traits such as a large capitulum, high femoral neck-to-shaft angle, and shallow distal femur are common to both slow climbers and suspensory primates, and could potentially allow for *Dryopithecus* to participate in either form of locomotion. It seems likely that *Dryopithecus* is a perfect example of a transitionary hominoid, moving from practicing climbing postures alone, to practicing suspension more frequently.

It is a strong possibility that certain traits of hominoids may exist due to their ability to use extreme climbing postures, much like the slow climbers in this study and several fossil specimens. To practice frequent suspension, features such as a dorsally placed scapula and a globular head are needed. A deep olecranon fossa and a spooled-shaped trochlea may or may not be necessary for brachiation, as they are not found in the suspensory atelines. However, if these traits are of aid in stabilization, they may not be needed in atelines, who can use their tail as a “fifth limb” to help stabilize them in the trees. Larger bodied animals tend to have more spooled trochlea, likely for stabilization, and apes are quite large in their body size and require a lot of stabilization for the locomotor activities they participate in (Feldesman 1982). Many of the other features that unite modern hominoids, however, may be evolved for extreme climbing rather than brachiation. This may help to explain some of the apparent modern traits in earlier Miocene hominoids, though it does not explain the spooled trochlea. If a spool-shaped trochlea is indeed useful for suspension in larger bodied animals, *Sivapithecus* remains a mystery. It lacks the straighter humeral shaft likely required for suspension, and has a primitive shoulder joint. One possible explanation is that *Sivapithecus parvada* is large enough that the stabilization of the elbow is needed for its body size for even climbing and bridging postures. However, this idea would be difficult to test, and still would not answer some of the more pressing questions of hominoid evolution, such as the potential for parallelism.

Conclusions

The slow climbers *Alouatta* and *Nycticebus* share a number of alterations of their skeletal anatomy in comparison to other arboreal quadrupeds of their respective phylogenetic groups. These shared traits are likely due to convergent evolution for a slow climbing lifestyle, allowing them to use a variety of climbing postures, including bridging behaviors and some suspension.

The traits shared amongst slow climbers all pertain to allowing a greater range of motion to permit extreme postures, and stability in such extreme postures. The shoulder and hip are altered for increased abduction, and the hip also altered for increased rotation. The elbow is given more stability during greater extension, flexion, pronation, and supination. The knee is also more stable in slow climbers. These trends all resemble the trends seen in the switch from quadrupedalism to suspension, and give credence to the hypothesis that slow climbing may have given rise to suspensory behaviors. This also has implications for ideas behind what skeletal traits indicate a suspensory lifestyle. Previously, traits such as an elongated clavicle, enlarged capitulum, widened trochlear notch, enlarged and rounded femoral head and widened knee were considered to be traits distinguishing suspensory primates from other locomotor groups (Rose 1988, Larson 1993, Anenome 1993, MacLatchy et al. 1996, Richmond 1998). Several of these traits have been applied to the fossil record as such (Pilbeam et al. 1990, Rose 1993,Rose 1997, Ward 1997). However, these traits may merely be indicating that a primate was an adept climber, rather than suspensory. Caution needs to be used in arguing any suspensory implications of these traits for extinct primates.

A few traits of suspensory primates which are not seen in slow climbers mostly come from the forelimb. These traits include a long acromian process, which may indicate a less dorsally positioned scapula; a globular humeral head, which indicates that circumduction at the shoulder in slow climbers is not near what it is in suspensory primates; a spool-shaped trochlea, which has been suggested to be a trait of stability, implying that slow climbers do not have elbows as stable as suspensory primates; and finally, a deep olecranon fossa, which means that slow climbers are likely not as able to extend the elbow as far as suspensory primates (Rose 1988, Larson 1993, Rose 1993). Together, these traits imply increased mobility at the shoulder and elbow beyond what is seen in slow climbers, which is likely due to participating in true brachiation. A comparison of the groups in this study to true suspensory primate skeletons would be of great importance in order to truly confirm any shared features between slow climbers and suspensory primates.

Miocene hominoids appear to be utilizing slow climbing behaviors to different extents, and, as is the case for *Dryopithecus*, may be moving towards more frequent suspension in such behaviors. It is difficult to make quantified comparisons, however, because that can only be accomplished with having the same elements to measure in a phylogenetic group. Due to the fragmented nature of the fossil record, this would be difficult to achieve. Until more postcranial elements are found that overlap across species, the Miocene hominoid fossil record can continue to be superficially reexamined to determine if any of the distinguishing traits of slow climbing are present in fossil hominoids, and if any purely suspensory traits can be confirmed.

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Appendix A: Figures and Tables

Figures

Figure 1

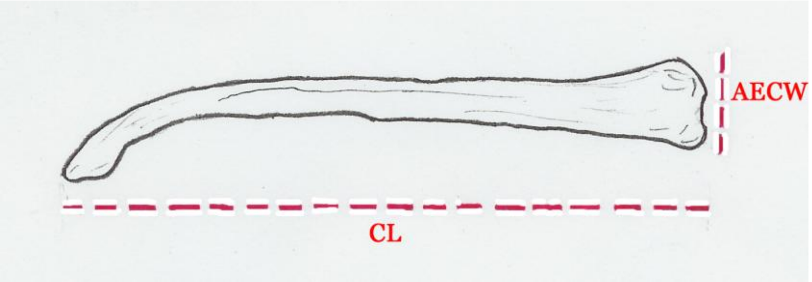


Figure 2

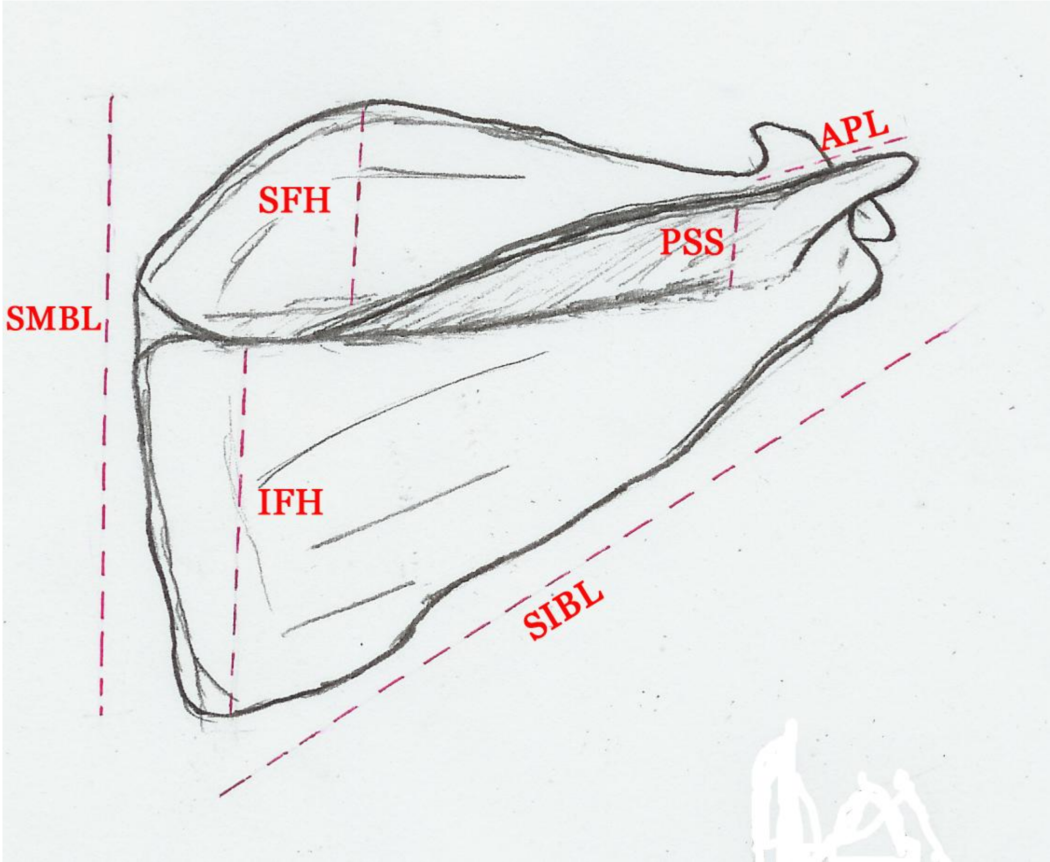


Figure 3

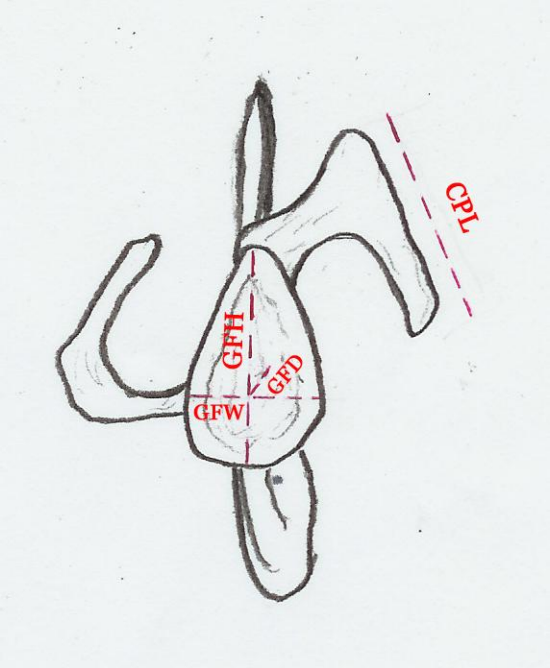
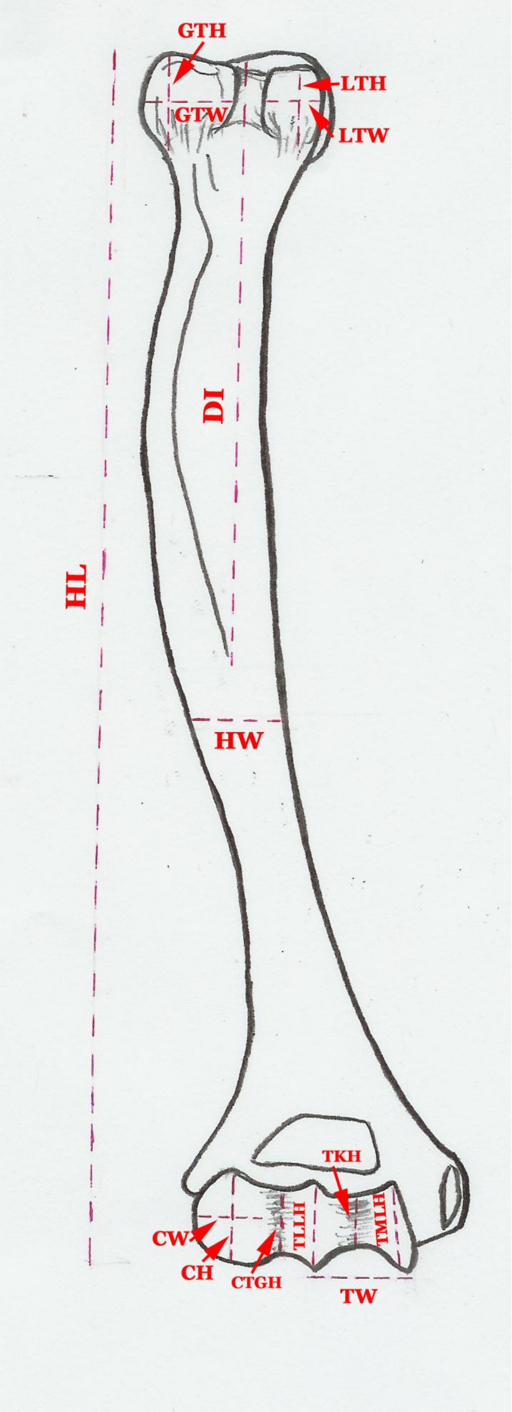


Figure 4



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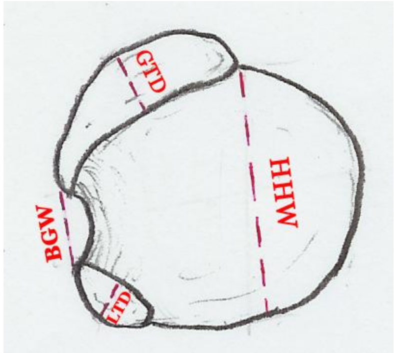

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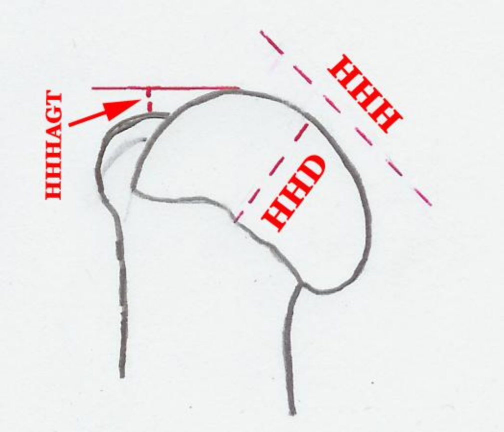

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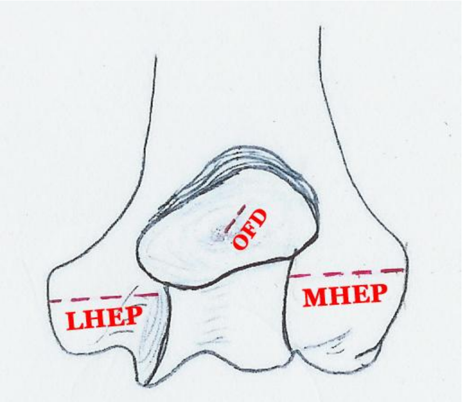

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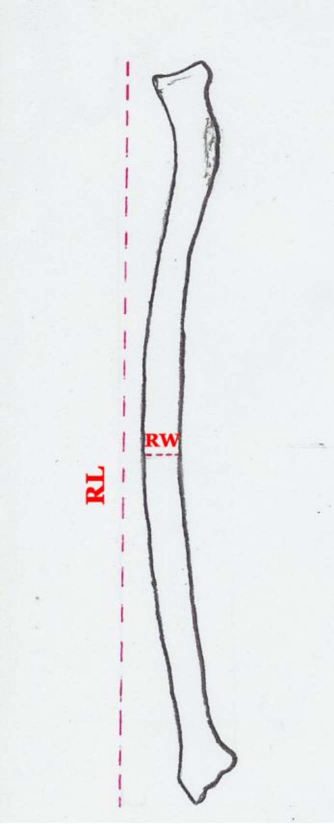

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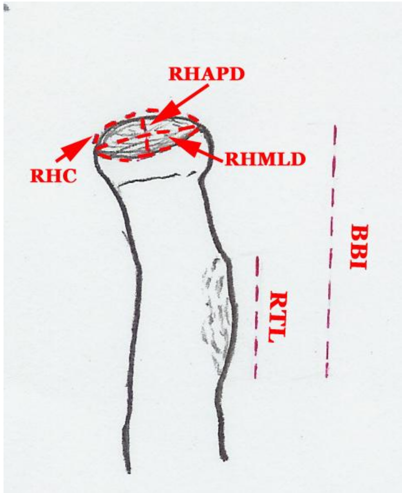

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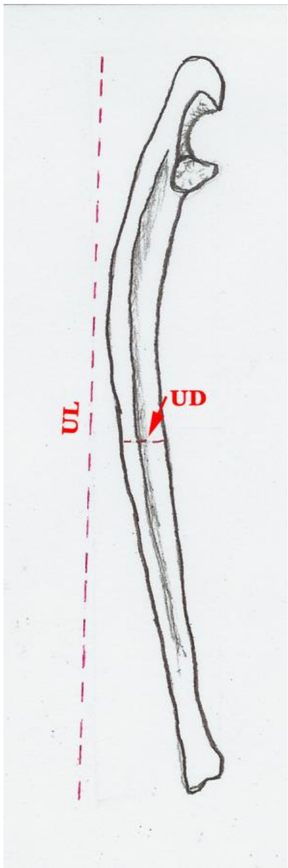

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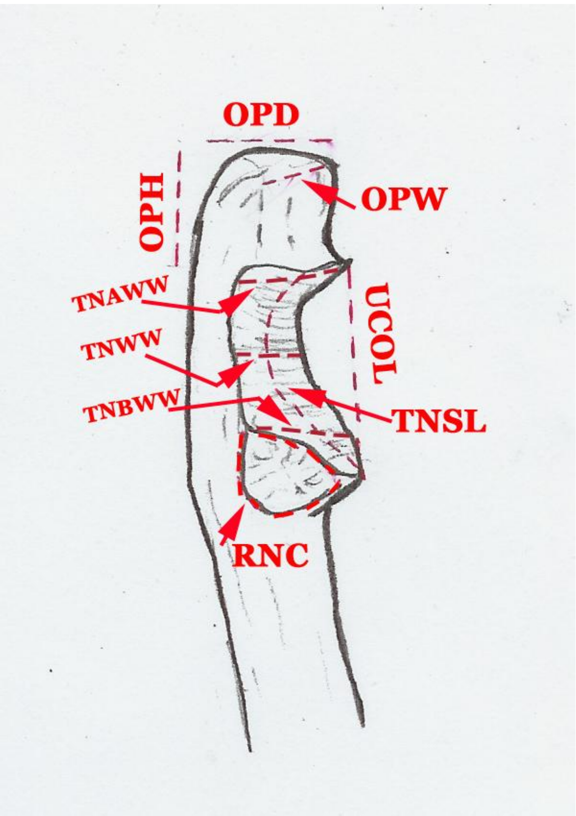

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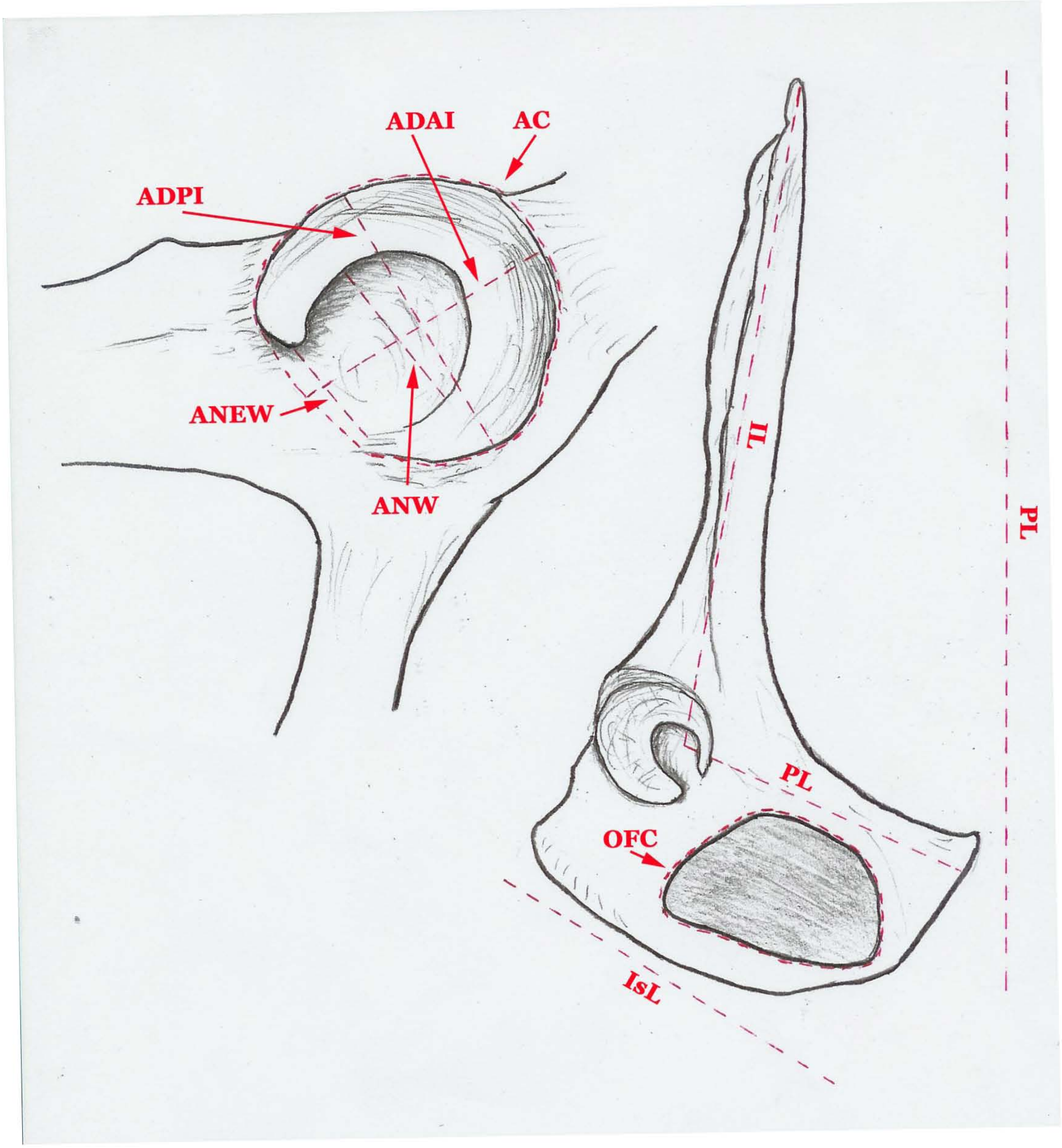

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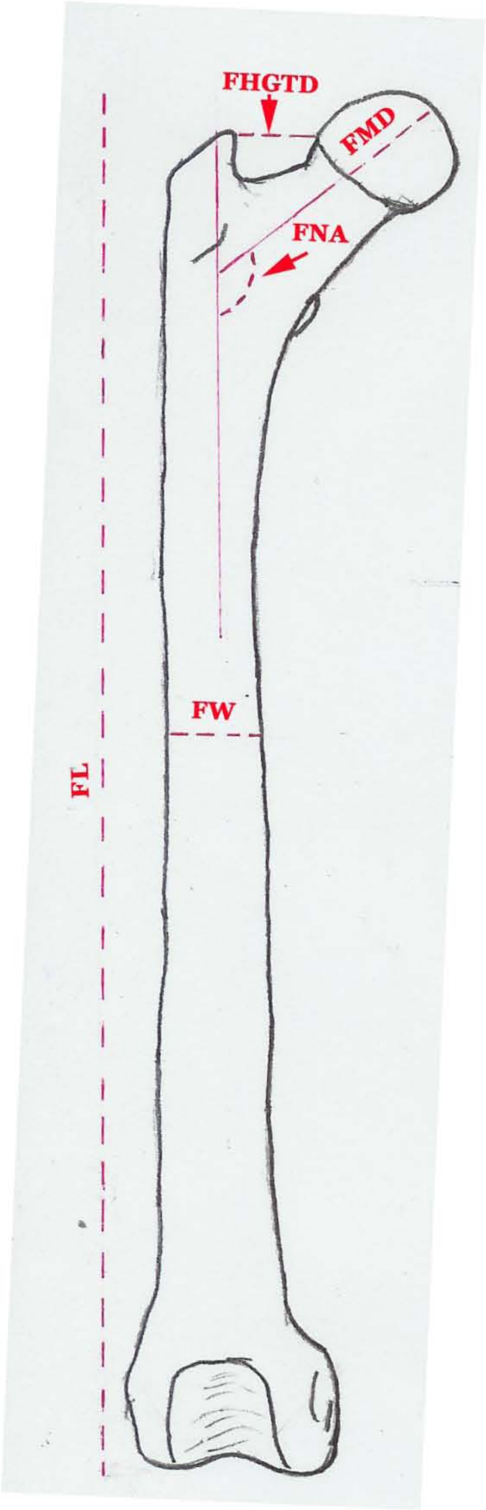

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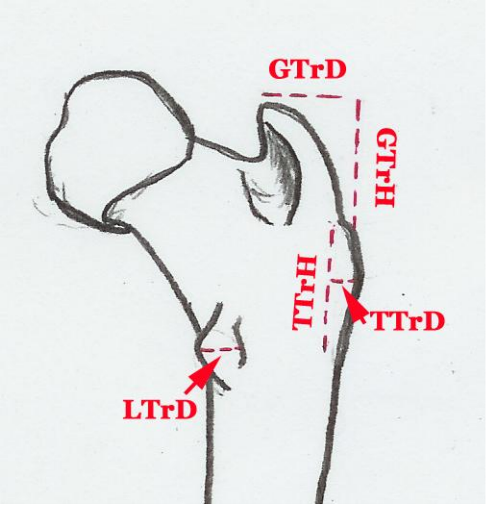

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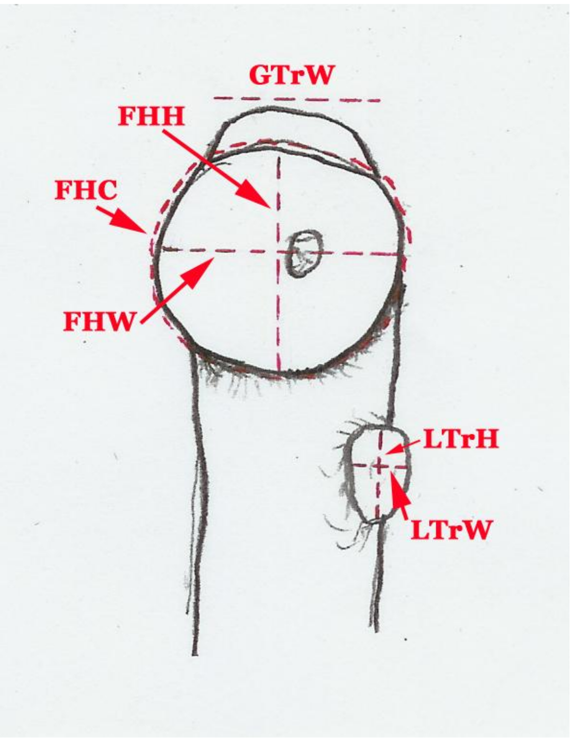

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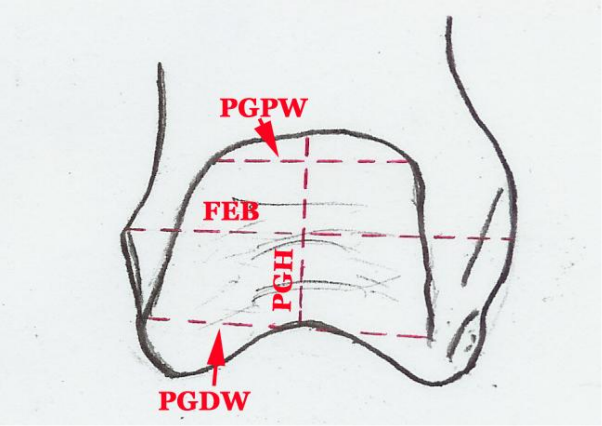

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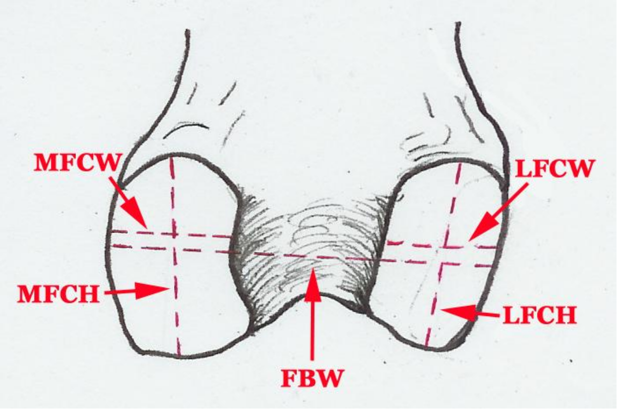

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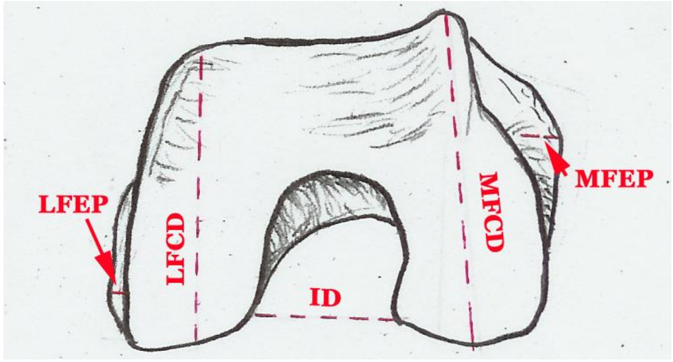

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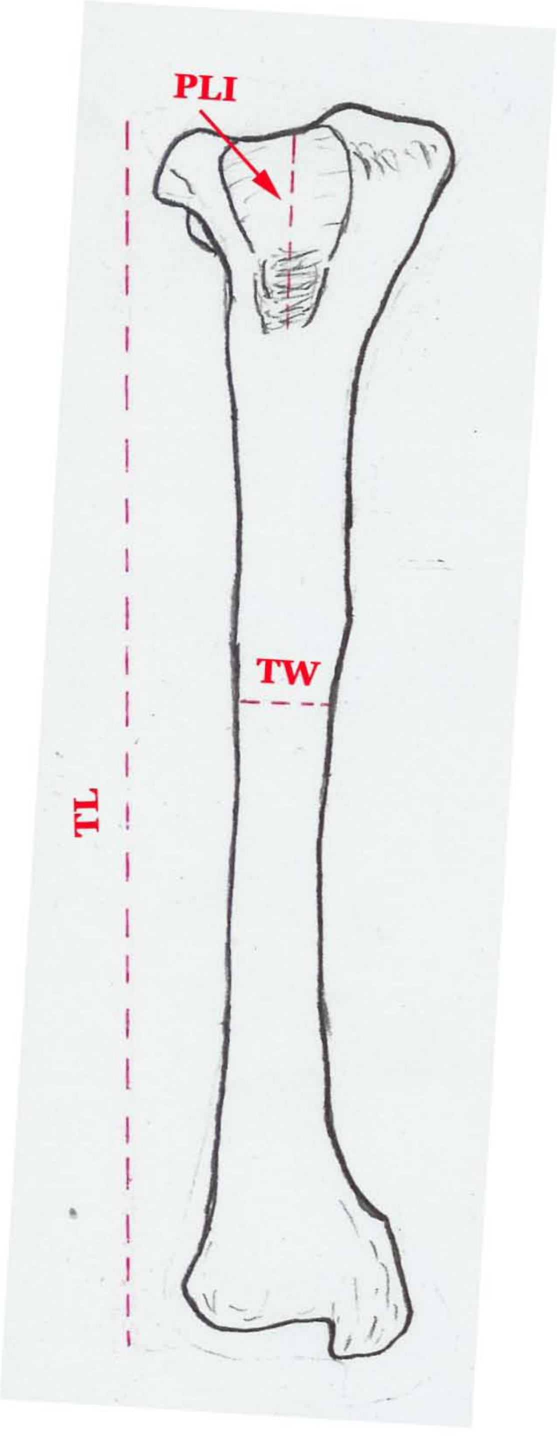

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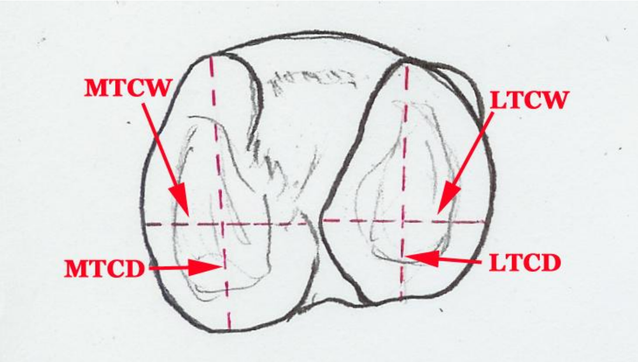

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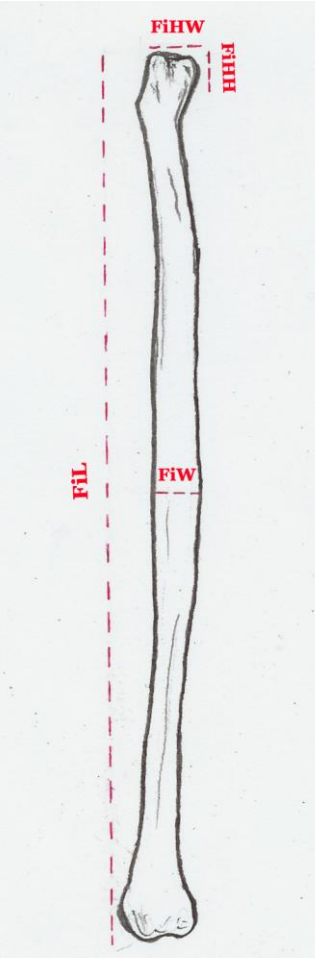

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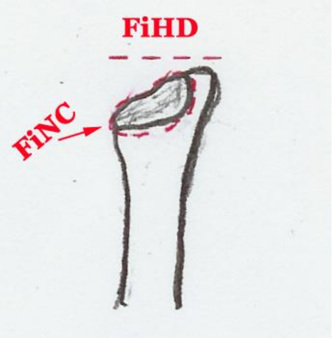

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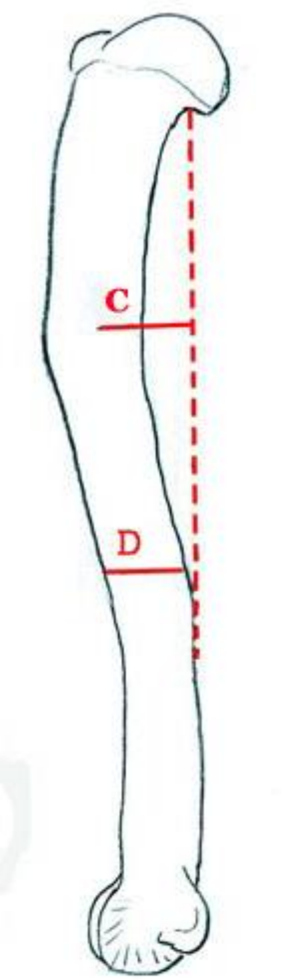

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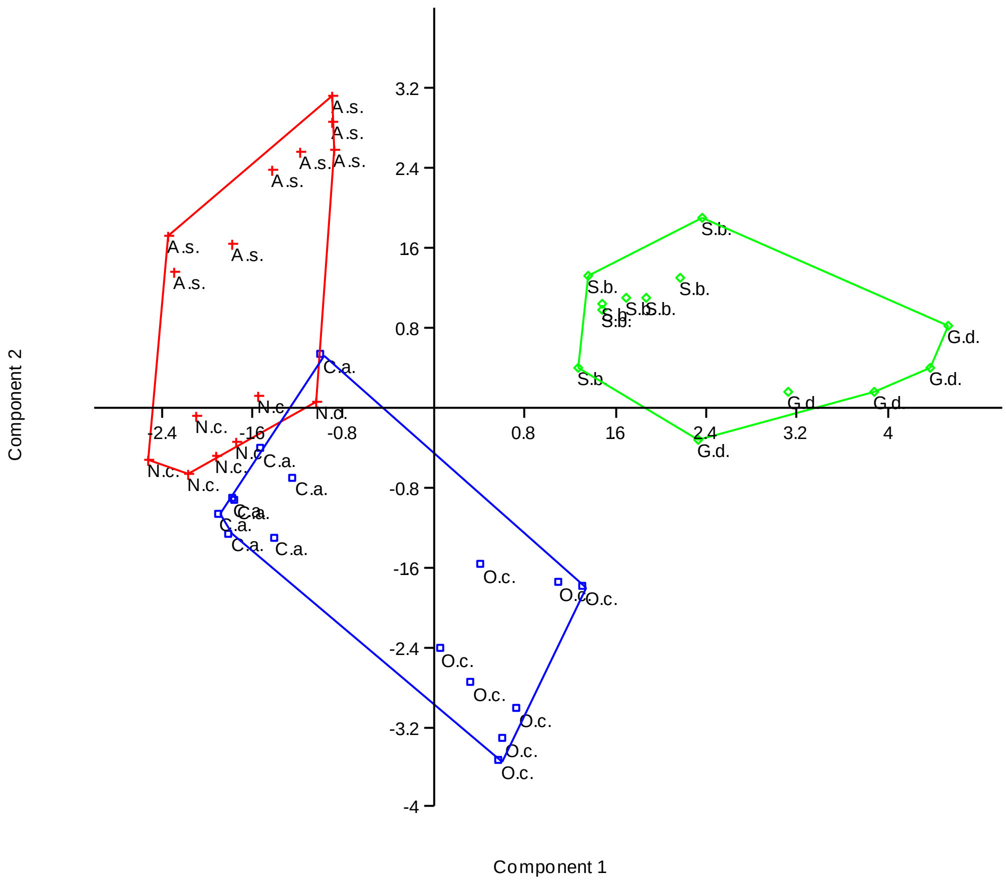
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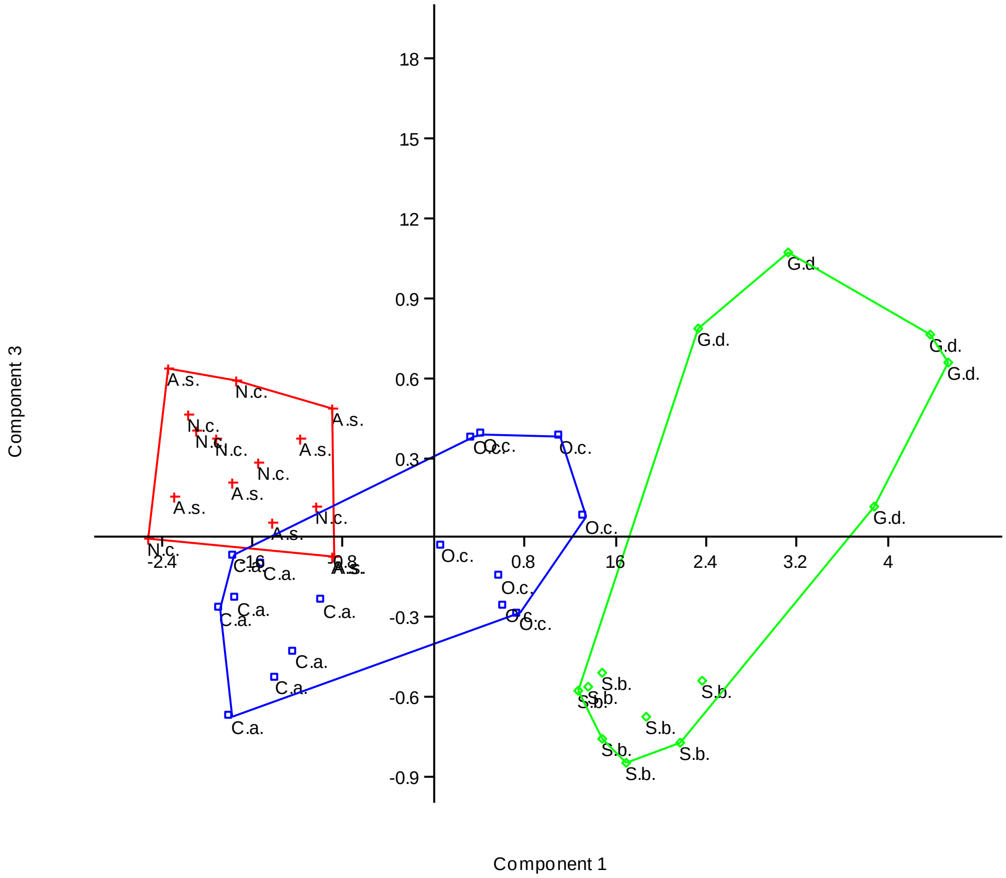
O.c.
S.b.
G.d.

Figure 25



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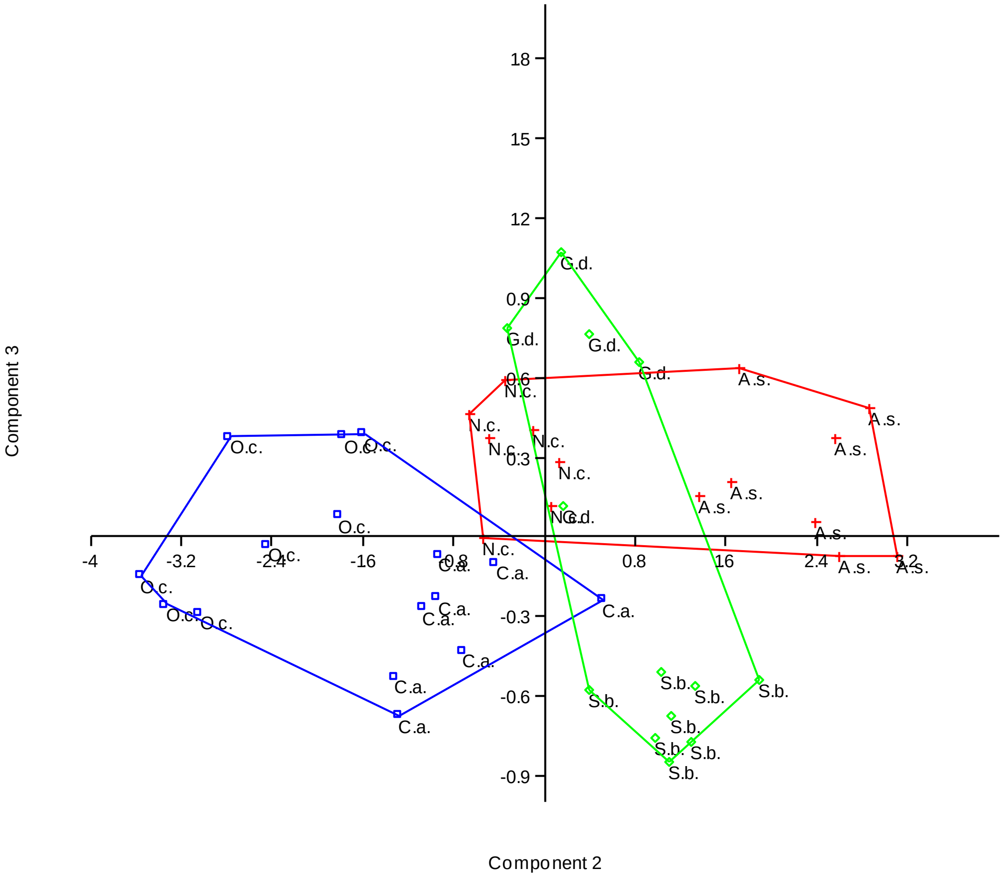
N.c.
O.c.
C.a.
G.d.
S.b.

Figure 26



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Component 2
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G.d.
G.d.
G.d.
G.d.
NG.d.
A.s.
A.s.
A.s.
A.s.
A.s.
A.s.
A.s.
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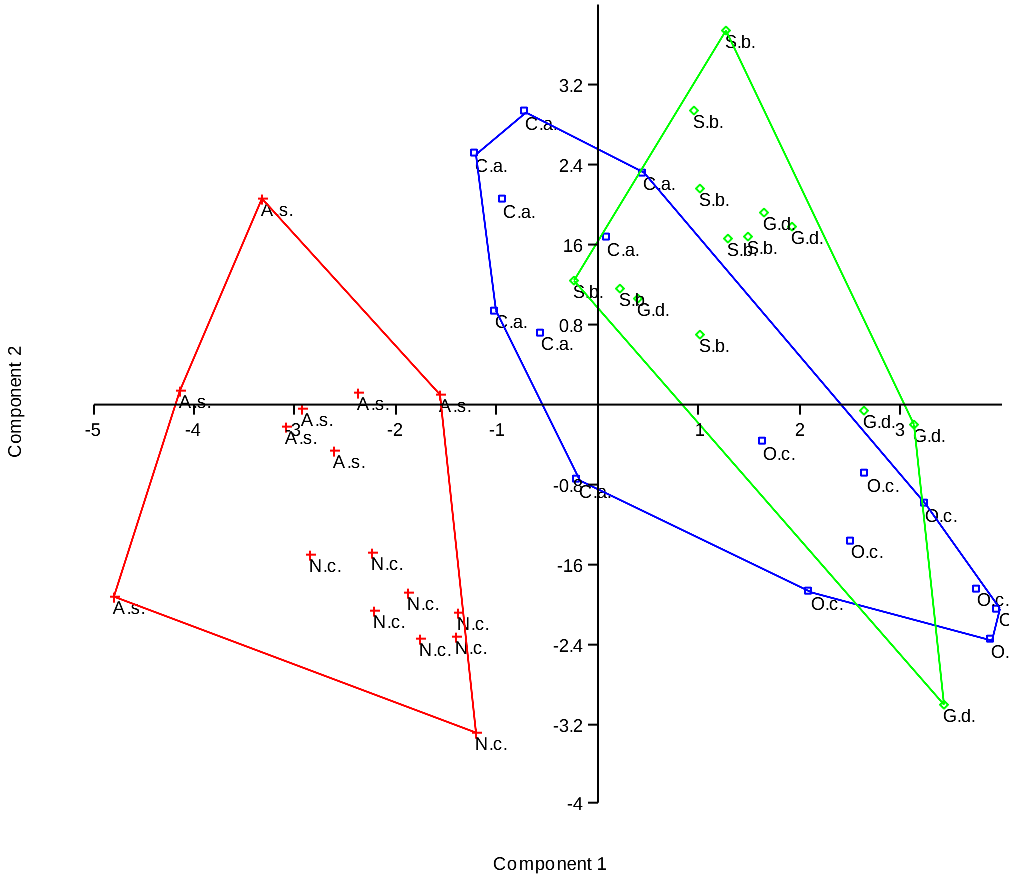
S.b.
S.b.

Figure 27



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1
2
3
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S.b.
S.b.
S.b.
S.b.
S.b.
S.b.
S.b.
G.d.
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G.d.
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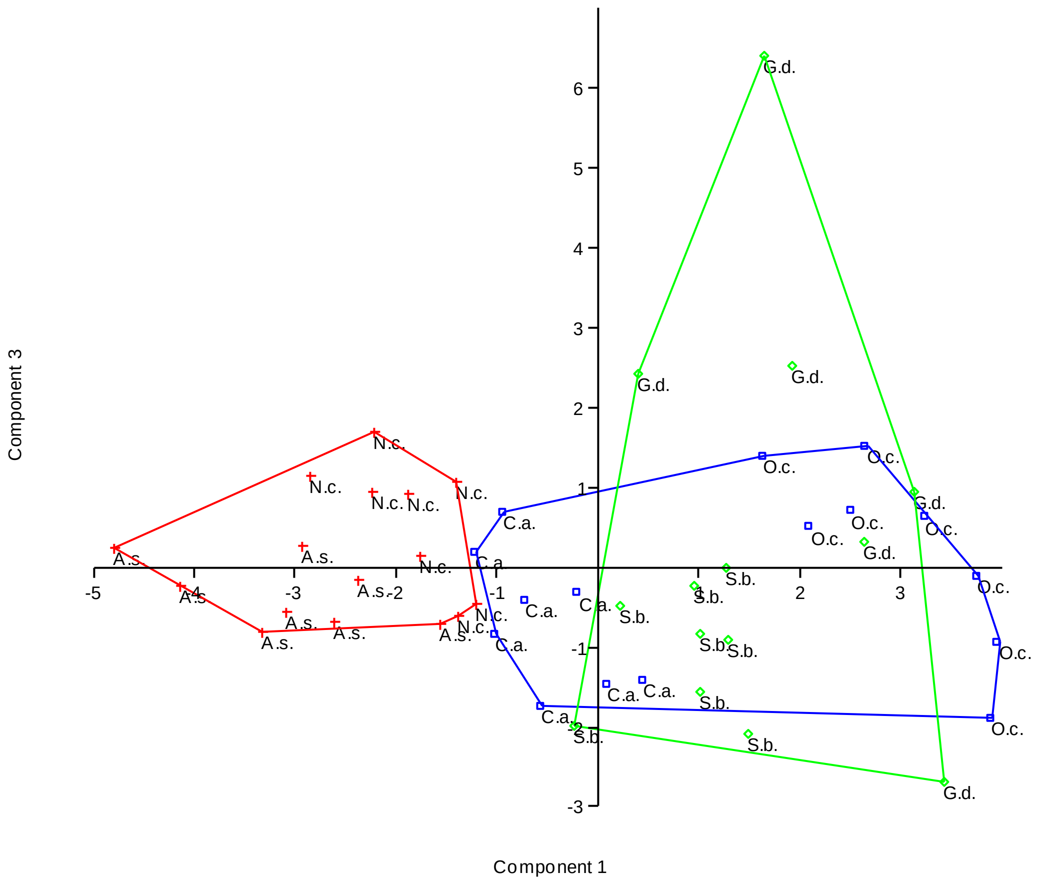
Figure 28



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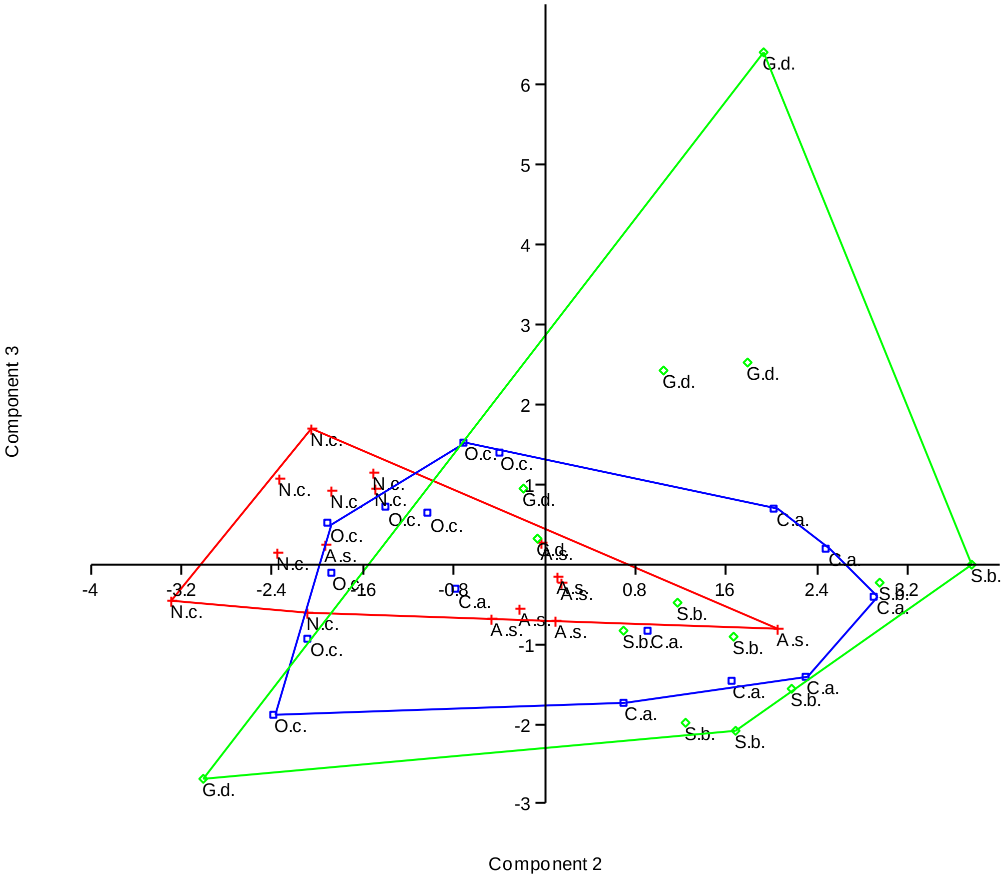
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2.4
3.2
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N.c.
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C.a.
S.b.

Figure 30

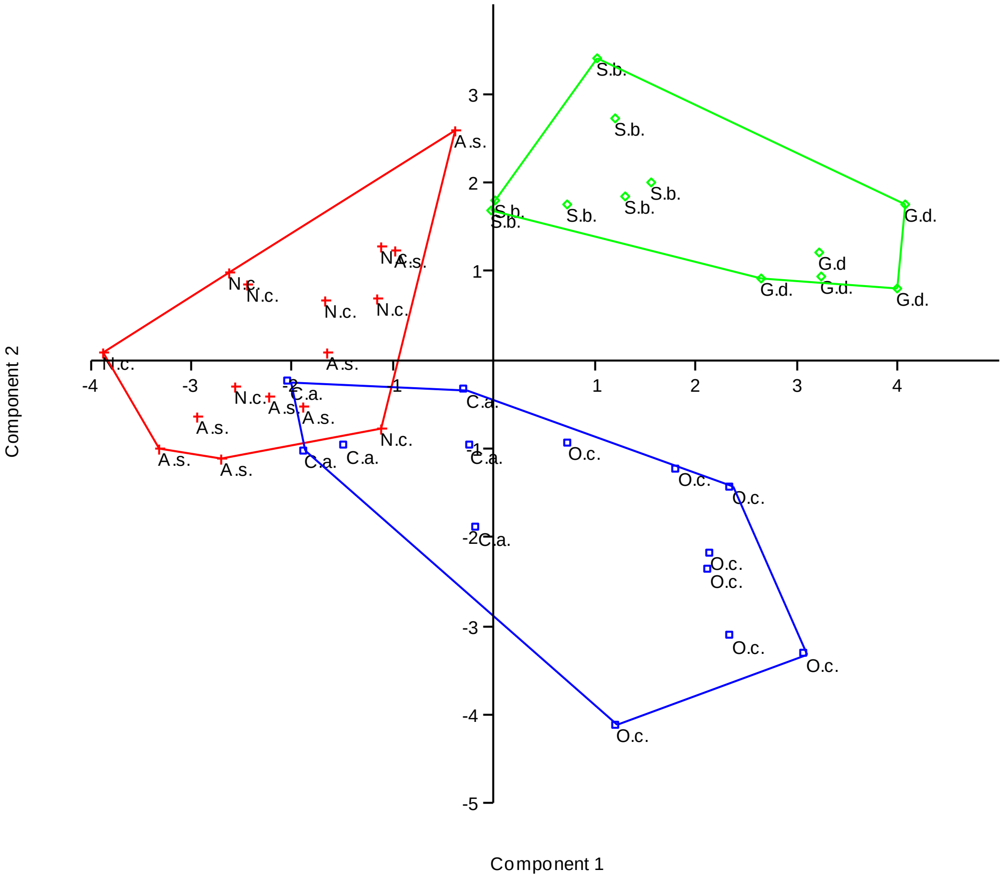
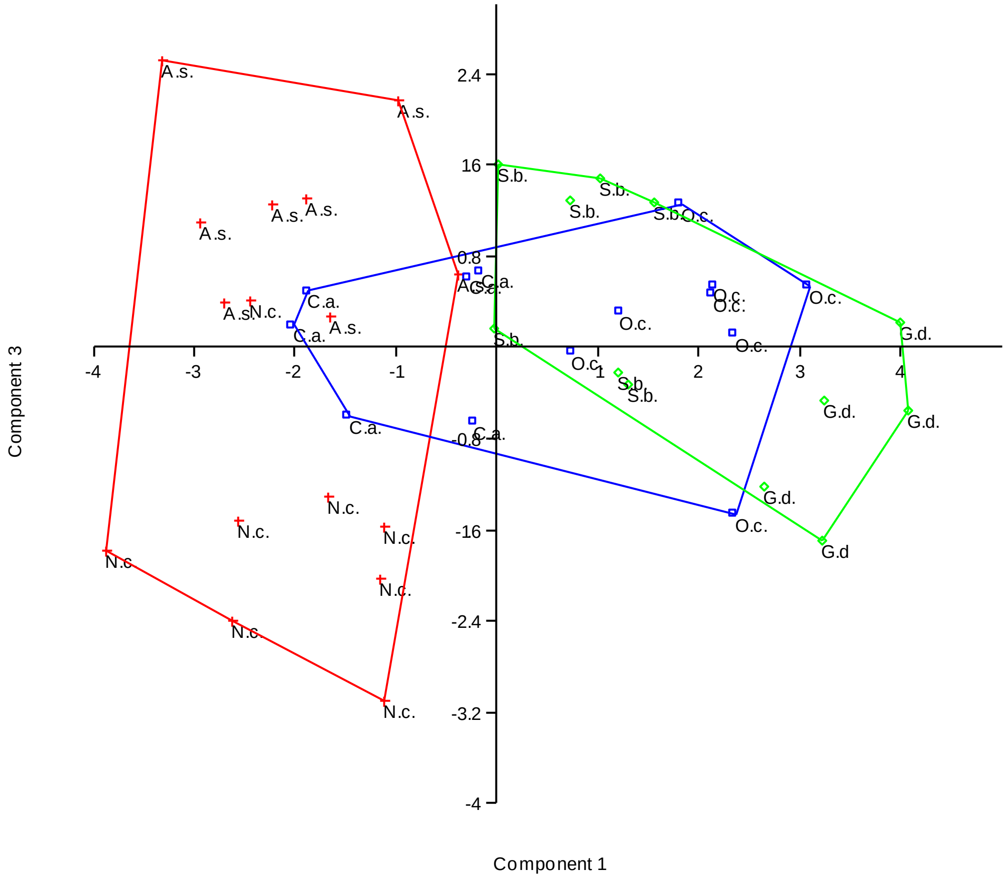


Figure 31



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4
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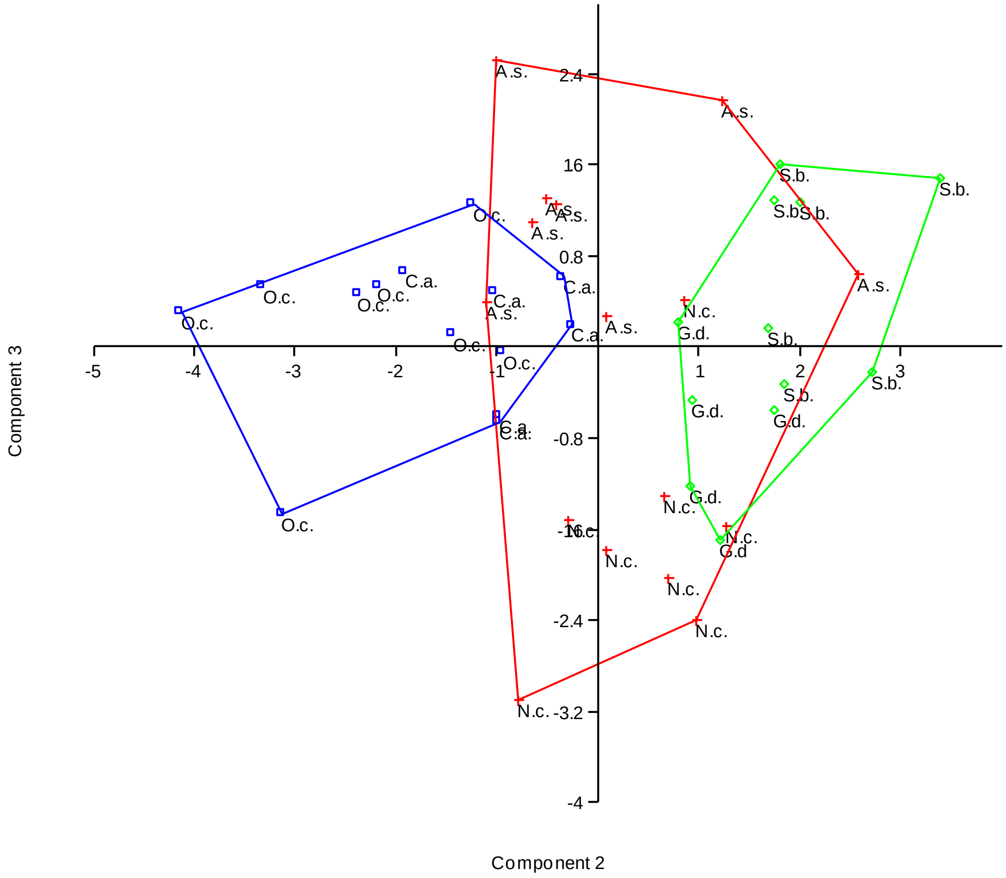
N.c.
C.a.
O.c.
S.b.
G.d.

Figure 32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O.c.
A.s.
0.8
C.a.
C.a.
A.s.
O.c.
O.c.
O.c.
C.a.
A.s.
N.c.
O.c.
A.s.
C.a.
G.d.
S.b.
O.c.
O.c.
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-4
-3
-2
-1
1
2
3
S.b.
S.b.
G.d.
G.d.
C.a.
C.a.
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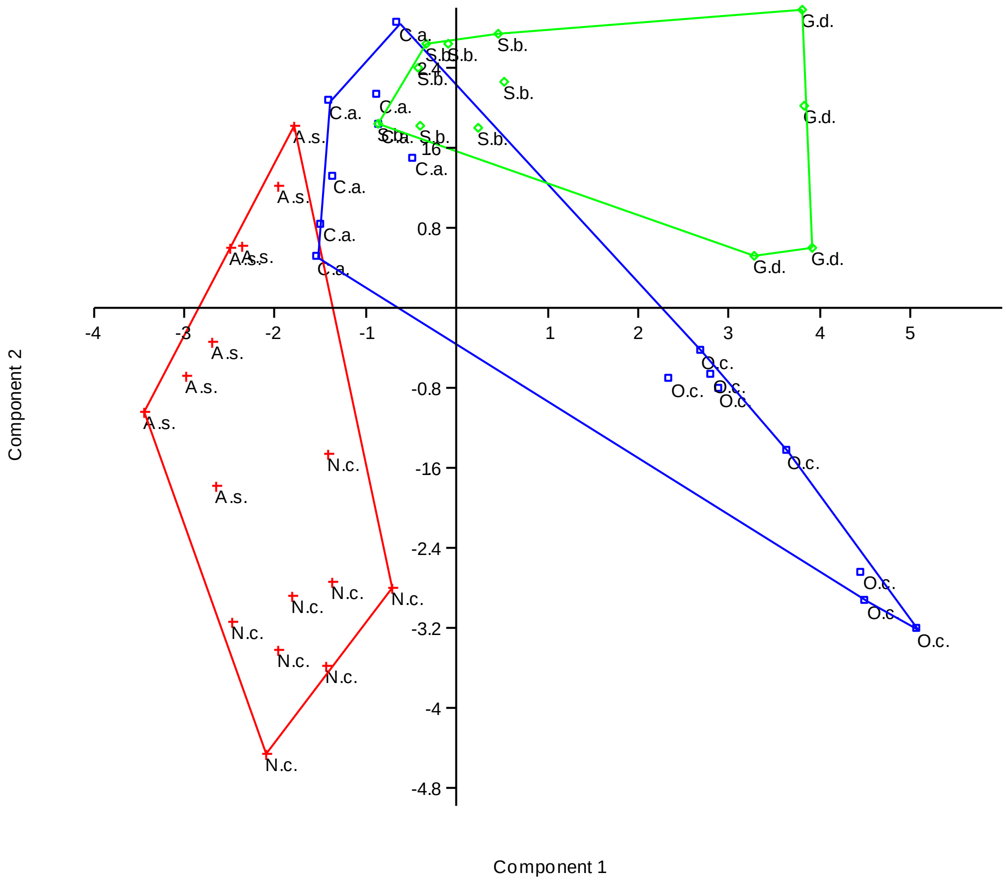
Component 3
Component 2

Figure 33



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-4.8
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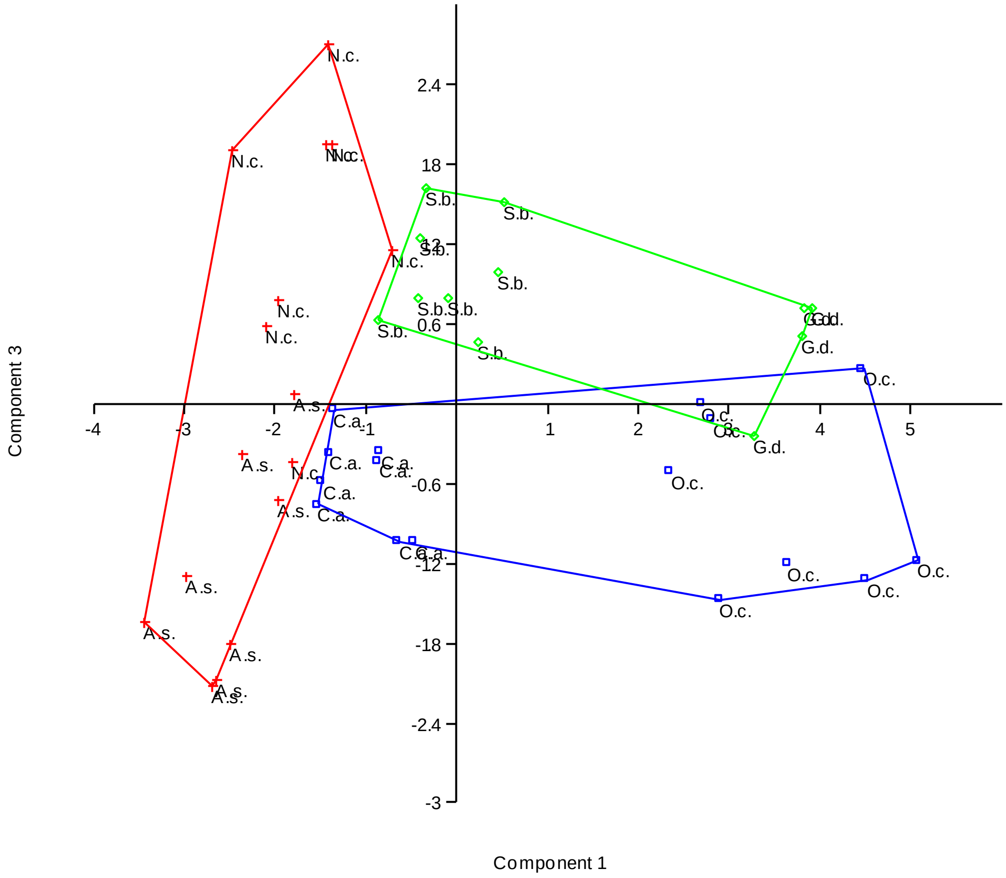
S.b.
G.d.
A.s.
N.c.
O.c.

Figure 34



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2
3
4
5
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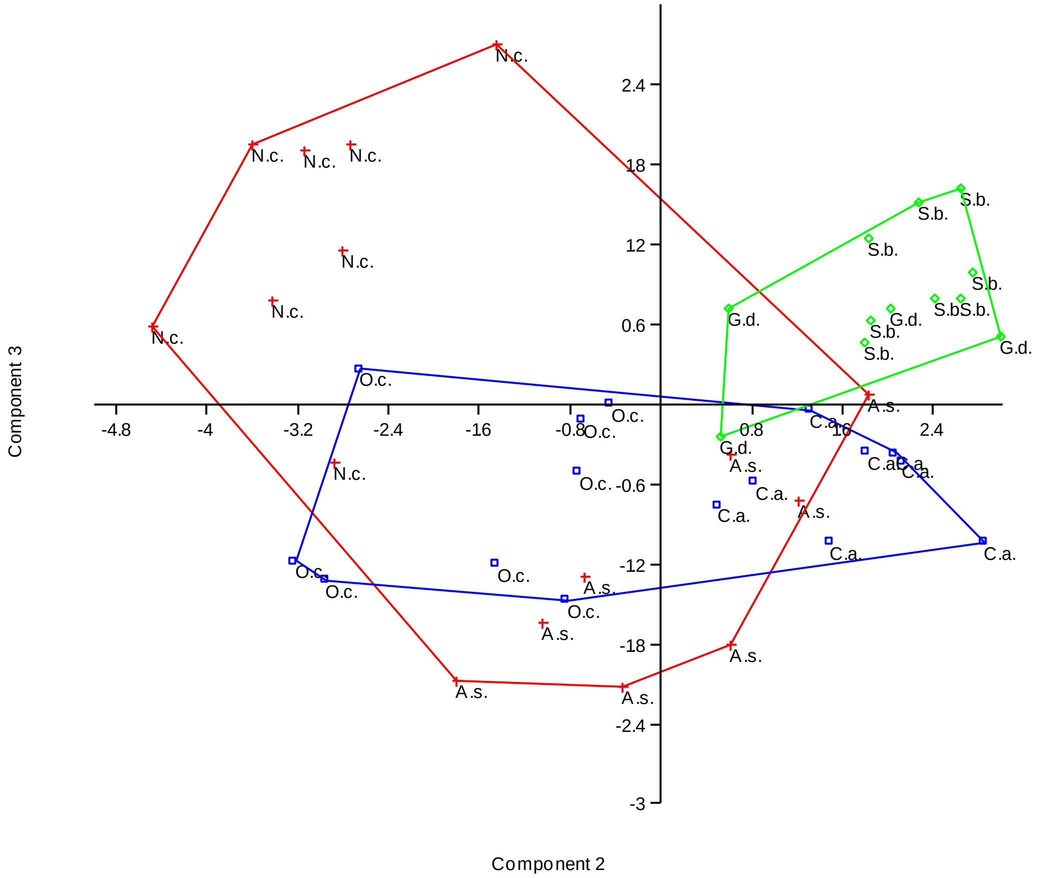
A.s.
C.a.
S.b.
G.d.
O.c.

Figure 35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-4.8
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-3.2
-2.4
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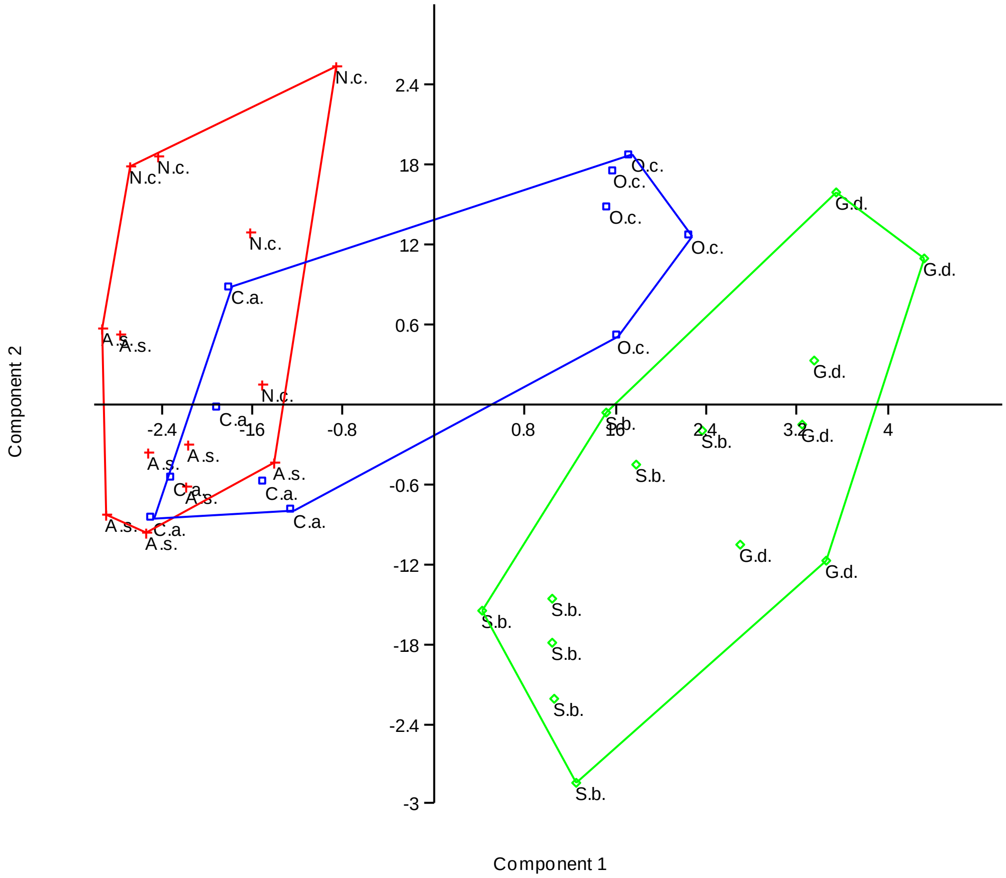
0.8
16
2.4
N.c.
O.c.
A.s.
C.a.
G.d.
S.b.

Figure 36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O.c.
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G.d.
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G.d.
C.a.
0.6
A.s.
A.s.
O.c.
G.d.
N.c.
C.a.
-2.4
-16
-0.8
0.8
S.b.
16
2.4
S.b.
3.2
G.d.
4
A.s.
A.s.
S.b.
A.s.
C.a.
A.s.
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C.a.
C.a.
A.s.
G.d.
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S.b.
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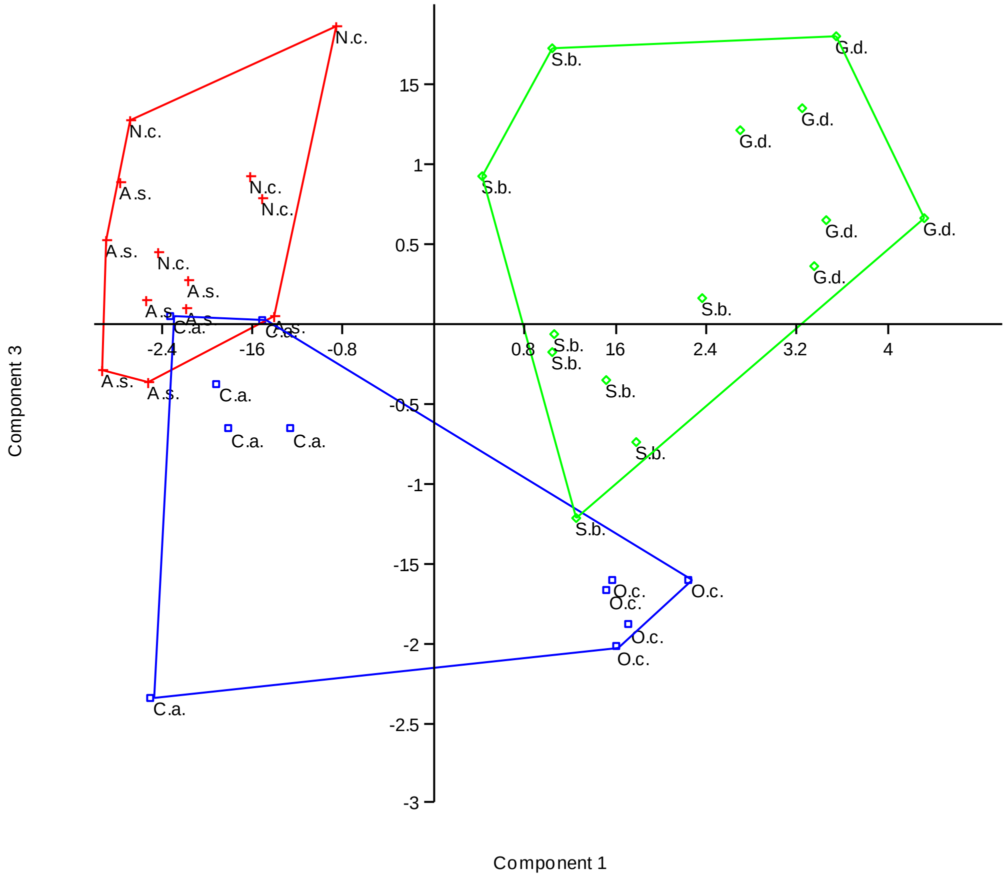
S.b.
-2.4
S.b.
-3
Component 2
Component 1

Figure 37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16
2.4
3.2
4
N.c.
A.s.
N.c.
N.c.
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N.c.
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A.s.
A.s.
C.a.
C.a.
A.s.
A.s.
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C.a.
C.a.
C.a.
C.a.
G.d.
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G.d.
G.d.
G.d.
S.b.
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S.b.
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O.c.
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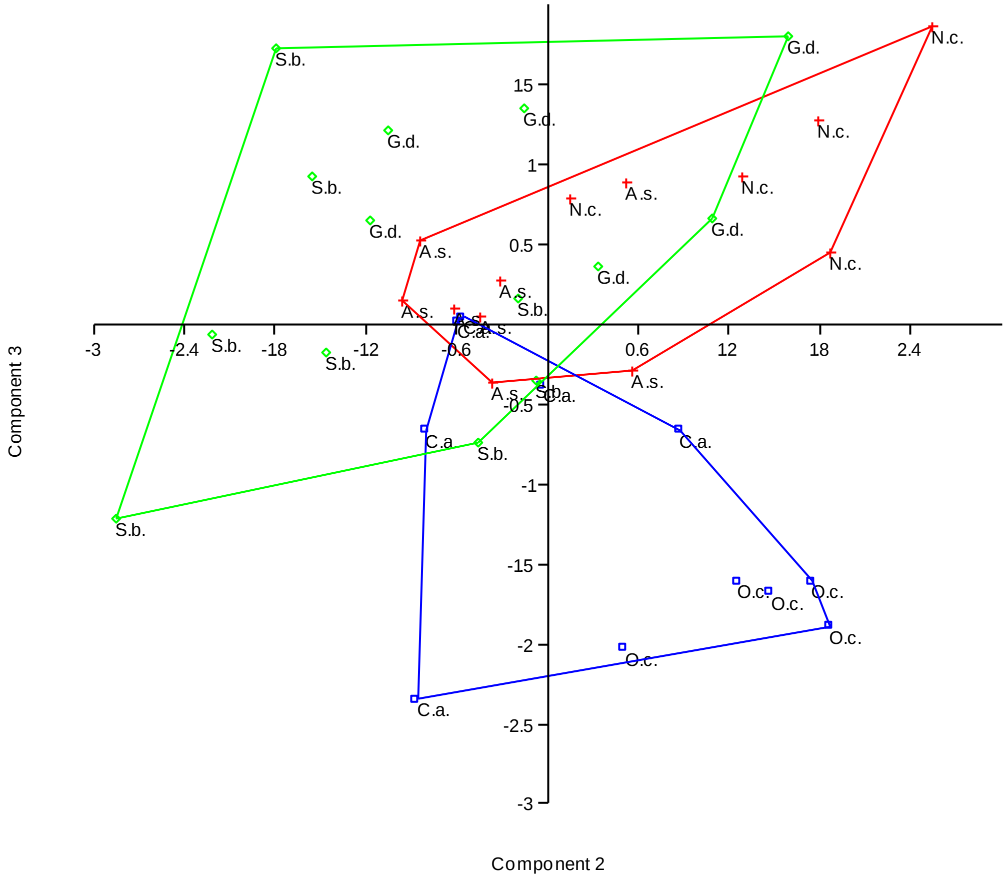
O.c.
O.c.
O.c.
Component 3
Component 1

Figure 38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N.c.
G.d.
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A.s.
C.a.
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2.4
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A.s.
A.s.
S.b.
C.a.
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O.c.
O.c.
O.c.
O.c.
-2
O.c.
C.a.
-2.5
-3
Component 3
Component 2

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Figure 7: Humeral measurements illustration, distal view.
Figure 8: Radial measurements illustration.
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Figure 13: Femoral measurements illustration.
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Figure 37: Knee PC I and PC III graph. SC – Red. G – Blue. L – Green.
Figure 38: Knee PC II and PC III graph. SC – Red. G – Blue. L – Green.

Tables

Table A

Measurement	Abbreviation
Clavicle Length	CL
Acromial End of Clavicle Width	AECW
Scapula Inferior Border Length	SIBL
Scapula Medial Border Length	SMBL
Supraspinous Fossa Height	SFH
Infraspinous Fossa Height	IFH
Protrusion of Scapular Spine	PSS
Acromian Process Length	APL
Coracoid Process Length	CPL
Glenoid Fossa Height	GFH
Glenoid Fossa Width	GFW
Glenoid Fossa Depth	GFD
Humerus Length	HL
Humeral Head Circumference	HHC
Humeral Head Height	HHH
Humeral Head Width	HHW
Humeral Head Depth	HHD
Humeral Head Height Above Greater Tubercle	HHHAGT
Greater Tubercle Height	GTH
Greater Tubercle Width	GTW
Greater Tubercle Depth	GTD
Lesser Tubercle Height	LTH
Lesser Tubercle Width	LTW
Lesser Tubercle Depth	LTD
Bicippital Groove Width	BGW
Deltoid Insertion	DI
Capitulum Height	CH
Capitulum Width	CW
Trochlea Lateral Lip Height	TLLH
Trochlear Medial Lip Height	TMLH
Capitular-Trochlear Gutter Height	CTGH
Trochlear Keel Height	TKH
Trochlear Width	TW
Lateral Humeral Epicondylar Protrusion	LHEP
Medial Humeral Epicondylar Protrusion	MHEP
Olecranon Fossa Depth	OFD
Humerus Midshaft Width	HMW

Humerus Midshaft Depth	HMD
Humerus ML Cord Length	HMLCL
Humerus AP Cord Length	HAPCL
Radius Length	RL
Radial Head Circumference	RHC
Radial Head ML Diameter	RHMLD
Radial Head AP Diameter	RHAPD
Radial Tuberosity Length	RTL
Biceps Brachii Insertion	BBI
Radial Midshaft Width	RMW
Radial Midshaft Depth	RMD
Radial AP Cord Length	RAPCL
Ulna Length	UL
Olecranon Process Height	OPH
Olecranon Process Width	OPW
Olecranon Process Depth	OPD
Trochlear Notch Surface Length	TNSL
Radial Notch Circumference	RNC
Trochlear Notch Waist Width	TNWW
Trochlear Notch Below Waist Width	TNBWW
Trochlear Notch Above Waist Width	TNAWW
Ulnar Coracoid-Olecranon Length	UCOL
Ulnar Midshaft Width	UMW
Ulnar Midshaft Depth	UMD
Ulnar AP Cord Length	UAPCL
Pelvis Length	PL
Pubis Length	PuL
Ischium Length	IsL
Ilium Length	IL
Obturator Foramen Circumference	OFC
Acetabulum Circumference	AC
Acetabular Notch Width	ANW
Acetabular Notch Entrance Width	ANEW
Acetabulum Depth	AD
Acetabulum Diameter Along Ilium	ADAI
Acetabulum Diameter Parallel to Ilium	ADPI
Femur Length	FL
Femoral Head Circumference	FHC
Femoral Head Height	FHH
Femoral Head Width	FHW
Femoral Head Depth	FHD
Femoral Neck Circumference	FNC
Femoral Neck Angle	FNA
Greater Trochanter Height	GTrH
Greater Trochanter Width	GTrW

Greater Trochanter Depth	GTrD
Lesser Trochanter Height	LTrH
Lesser Trochanter Width	LTrW
Lesser Trochanter Depth	LTrD
Third Trochanter Height	TTrH
Third Trochanter Width	TTrW
Third Trochanter Depth	TTrD
Femoral Head to Greater Trochanter Distance	FHGTD
Patellar Groove Height	PGH
Patellar Groove Proximal Width	PGPW
Patellar Groove Distal Width	PGDW
Lateral Femoral Condyle Height	LFCH
Lateral Femoral Condyle Width	LFCW
Lateral Femoral Condyle Depth	LFCD
Medial Femoral Condyle Height	MFCH
Medial Femoral Condyle Width	MFCW
Medial Femoral Condyle Depth	MFCD
Intercondyle Distance	ID
Lateral Femoral Epicondylar Protrusion	LFEP
Medial Femoral Epicondylar Protrusion	MFEP
Femoral Condyle Circumference	FCC
Femoral Epicondylar Breadth	FEB
Femoral Bicondylar Width	FBW
Femoral Midshaft Width	FMW
Femoral Midshaft Depth	FMD
Tibia Length	TL
Lateral Tibial Condyle Depth	LTCD
Lateral Tibial Condyle Width	LTCW
Medial Tibial Condyle Depth	MTCD
Medial Tibial Condyle Width	MTCW
Patellar Ligament Insertion	PLI
Tibial Midshaft Width	TMW
Tibial Midshaft Depth	TMD
Tibial ML Cord Length	TMLCL
Tibial AP Cord Length	TAPCL
Fibula Length	FiL
Fibular Head Height	FiHH
Fibular Head Width	FiHW
Fibular Head Depth	FiHD
Fibular Notch Circumference	FiNC
Fibular Midshaft Width	FiMW
Fibular Midshaft Depth	FiMD
Fibular ML Cord Length	FiMLCL
Fibular AP Cord Length	FiAPCL

Table B

Indices and Other	Abbreviation
Intermembral Index (HL+RL/FL+TL)	II
Brachial Index (RL/HL)	BI
Crural Index (TL/FL)	CI
Scapular Inferior to Medial Border Ratio (SIBL/SMBL)	SIMB
Scapular Index (SHF/IFH)	SI
Humeral Robusticity (HMW/HL)	HR
Deltoid Insertion Index (DI/HL)	DII
Capitulum Rough Surface Area (CH x CW)	CSA
Humeral ML NCMA (HMLCL/HMW)	HMLNCMA
Humeral AP NCMA (HAPCL/HMW)	HAPNCMA
Radial Robusticity (RMW/RL)	RR
Biceps Brachii Insertion Index (BBI/RL)	BBII
Radial Head Symmetry (RHMLD/RHAPD)	RHS
Radial AP NCMA (RAPCL/RMW)	RAPNCMA
Ulnar Robusticity (UMW/UL)	UR
Trochlear Index (UCOD/TNSL)	TI
Olecranon Index (OPH/UL)	OI
Ulnar AP NCMA (UAPCL/UMW)	UAPNCMA
Acetabulum Diameter Index (ADAI/ADPI)	ADI
Acetabular Depth Index (AD/AC)	ADeI
Acetabular Notch Index (ANW/ANEW)	ANI
Femoral Robusticity (FMD/FL)	FR
Greater Trochanter Ratio (GTrH/FL)	GTR
Femoral Condyle Height Ratio (LFCH/MFCH)	FCHR
Femoral Condyle Width Ratio (LFCW/MFCW)	FCWR
Femoral Condyle Depth Ratio (LFCD/MFCD)	FCDR
Bicondylar Ratio (FBW/FL)	BR
Tibial Robusticity (TMW/TL)	TR
Tibial Condyle Depth Ratio (LTCD/MTCD)	TCDR
Tibial Condyle Width Ratio (LTCW/MTCW)	TCWR
Patellar Ligament Insertion Index (PLI/TL)	PLII
Tibial ML NCMA (TMLCL/TMW)	TMLNCMA
Tibial AP NCMA (TAPCL/TMW)	TAPNCMA
Fibular Robusticity (FiMW/FiL)	FiR
Fibular ML NCMA (FiMLCL/FiMW)	FiMLNCMA
Fibular AP NCMA (FiAPCL/FiMW)	FiAPNCMA

Table C

Trait	**Slow Climber**	**Generalist**	**Leaper**	**Bonferroni Corrected *p*-values (smallest value listed) :**	***p*-value in Platyrrhines**	***p*-value in Strepsirrhines**
CL	Longest	Shorter	Shorter		< .05	**< .001**
AECW	**Smallest**	Largest	Intermediate		**< .001**	**< .001**
SIBL	**Shortest**	Longer	Longer		**< .001**	**< .01**
SMBL	**Longest**	Intermediate	Shortest		**< .001**	**< .001**
SFH	**Tallest**	Shorter	Shorter		**< .001**	**< .001**
IFH	No Relation	NR	NR		NS	**< .001**
PSS	Smallest	Intermediate	Largest		**< .01**	NS
APL	NR	NR	NR		NS	**< .01667**
CPL	Shortest	Intermediate	Longest		< .05	**< .001**
GFH	Tallest	Shorter	Shorter		NS	**< .001**
GFW	NR	NR	NR		NS	NS
GFD	NR	NR	NR		NS	< .05
HL	**Longest**	Shortest	Intermediate		**< .001**	**< .001**
HHC	Largest	Smaller	Smaller		NS	NS
HHH	Tallest	Shorter	Shorter		**< .01667**	< .05
HHW	NR	NR	NR		NS	NS
HHD	Smaller	Smaller	Deepest		NS	**< .01**
HHHAGT	**Greater**	Lesser	Lesser		**< .001**	**< .01667**
GTH	Shortest	Taller	Taller		NS	< .05
GTW	Widest	Narrower	Narrower		**< .001**	NS
GTD	NR	NR	NR		NS	NS
LTH	NR	NR	NR		NS	NS

LTW	NR	NR	NR	**< .01**	< .05
LTD	NR	NR	NR	NS	< .05
BGW	Intermediate	Narrowest	Widest	NS	NS
CH	**Tallest**	Shortest	Intermediate	**< .01**	**< .01667**
CW	**Widest**	Narrowest	Intermediate	**< .01**	**< .01**
TLLH	Shorter	Shorter	Tallest	NS	**< .001**
TMLH	Taller	Shortest	Taller	**< .01**	**< .001**
CTGH	Intermediate	Shortest	Tallest	NS	**< .01**
TKH	NR	NR	NR	**< .01**	NS
LHEP	NR	NR	NR	NS	NS
MHEP	Greater	Greater	Smallest	**< .001**	**< .01667**
OFD	Shallowest	Deeper	Deeper	NS	**< .001**
HMW	Widest	Narrower	Narrower	NS	< .05
HMD	Widest	Narrowest	Intermediate	NS	**< .001**
RL	Longer	Shortest	Longer	**< .001**	**< .001**
RHC	Larger	Larger	Smallest	NS	**< .001**
RHMLD	NR	NR	NR	**< .01667**	**< .001**
RHAPD	NR	NR	NR	**< .001**	**< .001**
RTL	Longest	Shortest	Intermediate	NS	NS
RMW	NR	NR	NR	NS	NS
RMD	Widest	Narrower	Narrower	NS	< .05
UL	Longer	Shortest	Longer	**< .001**	**< .001**
OPH	NR	NR	NR	NS	**< .001**
OPW	Widest	Intermediate	Narrowest	NS	**< .01**
OPD	Narrowest	Intermediate	Deepest	< .05	NS
TNSL	**Longest**	Shortest	Intermediate	**< .01**	**< .001**
RNC	NR	NR	NR	**< .001**	**< .01**
TNWW	**Widest**	Intermediate	Narrowest	**< .01**	**< .001**
TNBWW	**Widest**	Intermediate	Narrowest	**< .001**	< .05
TNAWW	NR	NR	NR	< .05	NS
UCOL	NR	NR	NR	**< .001**	NS

UMW	NR	NR	NR	**< .01667**	**< .01**
UMD	NR	NR	NR	NS	**< .01**
PL	Shortest	Intermediate	Longest	NS	NS
PuL	NR	NR	NR	**< .001**	NS
IsL	NR	NR	NR	**< .001**	NS
IL	NR	NR	NR	< .05	< .05
OFC	NR	NR	NR	**< .01**	NS
AC	Larger	Larger	Smallest	**< .001**	< .05
ANW	Largest	Smallest	Intermediate	**< .001**	< .05
ANEW	NR	NR	NR	**< .001**	NS
AD	NR	NR	NR	NS	< .05
ADAI	Longest	Shorter	Shorter	NS	NS
ADPI	Longest	Shorter	Shorter	NS	NS
FL	**Shortest**	Intermediate	Longest	**< .001**	**< .001**
FHC	**Largest**	Intermediate	Smallest	**< .001**	**< .001**
FHH	**Tallest**	Shorter	Shorter	**< .01**	**< .001**
FHW	**Widest**	Narrower	Narrower	**< .01**	**< .001**
FHD	Deepest	Shorter	Shorter	< .05	**< .001**
FNC	Smallest	Larger	Larger	< .05	NS
FNA	**Largest**	Intermediate	Smallest	**< .01**	**< .001**
GTrH	NR	NR	NR	**< .01**	NS
GTrW	NR	NR	NR	NS	**< .001**
GTrD	NR	NR	NR	**< .01**	NS
LTrH	NR	NR	NR	NS	NS
LTrW	Widest	Intermediate	Narrowest	NS	**< .001**
LTrD	NR	NR	NR	NS	**< .001**
TTrH	NR	NR	NR	NS	NS
TTrW	NR	NR	NR	**< .01**	NS
TTrD	Smaller	Smaller	Deepest	< .05	**< .001**
FHGTD	**Smallest**	Larger	Larger	**< .01**	**< .001**
PGH	Shorter	Shorter	Tallest	**< .001**	**< .001**

PGPW	**Widest**	Intermediate	Narrowest	< .001	< .001
PGDW	Widest	Intermediate	Narrowest	< .001	NS
LFCH	NR	NR	NR	NS	< .001
LFCW	NR	NR	NR	< .01	< .001
LFCD	Shallower	Shallower	Deepest	< .001	< .001
MFCH	Tallest	Intermediate	Shortest	< .001	NS
MFCW	Narrower	Widest	Narrower	< .001	< .01667
MFCD	NR	NR	NR	< .001	< .001
ID	Smaller	Smaller	Largest	< .01	< .01
LFEP	Greatest	Intermediate	Least	NS	< .05
MFEP	Greater	Lesser	Lesser	NS	< .001
FCC	Larger	Larger	Smallest	< .001	< .01
FEB	Widest	Intermediate	Narrowest	NS	< .001
FBW	Narrowest	Widest	Intermediate	NS	NS
FMW	NR	NR	NR	NS	NS
FMD	Narrowest	Widest	Intermediate	< .01	NS
TL	**Shortest**	Intermediate	Longest	< .001	< .001
LTCD	NR	NR	NR	NS	< .001
LTCW	NR	NR	NR	NS	< .001
MTCD	Deeper	Deeper	Narrowest	< .01	< .01
MTCW	Widest	Narrower	Narrower	NS	NS
TMW	Narrowest	Wider	Wider	NS	< .01
TMD	**Narrowest**	Deeper	Deeper	< .001	< .001
FiL	Shorter	Shorter	Longest	< .001	< .001
FiHH	Tallest	Intermediate	Shortest	NS	< .001
FiHW	NR	NR	NR	< .01	NS
FiHD	NR	NR	NR	< .001	< .001
FiNC	NR	NR	NR	< .05	NS
FiMW	NR	NR	NR	< .01	< .001
FiMD	Narrowest	Widest	Intermediate	NS	< .01667

II	**Greatest**	Lesser	Lesser	**< .001**	**< .001**
BI	Lesser	Lesser	Greatest	NS	**< .001**
CI	Lesser	Lesser	Greatest	**< .001**	**< .001**
SIMB	**Least**	Intermediate	Greatest	**< .001**	**< .001**
SI	NR	NR	NR	**< .001**	**< .01**
HR	NR	NR	NR	NS	**< .05**
DII	Intermediate	Longest	Shortest	**< .05**	**< .01**
CSA	**Greatest**	Least	Intermediate	**< .01**	**< .001**
HMLNCMA	NR	NR	NR	NS	**< .01**
HAPNCMA	NR	NR	NR	NS	NS
RR	NR	NR	NR	**< .05**	**< .05**
BBII	Longer	Longer	Shortest	**< .001**	**< .001**
RHS	Rounder	Rounder	More Oval	**< .01**	**< .01**
RAPNCMA	NR	NR	NR	NS	NS
UR	Lesser	Greatest	Lesser	**< .001**	**< .001**
TI	Lesser	Lesser	Greatest	**< .01**	**< .001**
OI	Lesser	Greatest	Lesser	**< .001**	**< .001**
UAPNCMA	Least	Intermediate	Greatest	NS	**< .05**
ADI	NR	NR	NR	NS	NS
ADeI	Shallowest	Deeper	Deeper	NS	**< .05**
ANI	Greater	Least	Greater	**< .001**	**< .01**
FR	NR	NR	NR	**< .01**	**< .01**
GTR	Largest	Intermediate	Smallest	**< .001**	NS
FCHR	**Least**	Greater	Greater	**< .001**	**< .001**
FCWR	NR	NR	NR	**< .01**	**< .001**
FCDR	**Least**	Intermediate	Greatest	**< .001**	**< .001**
BR	Larger	Larger	Smaller	**< .001**	**< .001**
TR	**Greatest**	Intermediate	Least	**< .001**	**< .001**
TCDR	NR	NR	NR	NS	**< .001**
TCWR	NR	NR	NR	NS	NS
PLII	Intermediate	Longest	Shortest	NS	NS

TMLNCMA	Least	Greater	Greater	**< .01**	NS
TAPNCMA	NR	NR	NR	NS	NS
FiR	Greater	Greater	Least	**< .001**	**< .001**
FiMLNCMA	Greatest	Intermediate	Least	NS	NS
FiAPNCMA	NR	NR	NR	NS	NS

Table D

Longest clavicle
Narrowest width of acromial end of clavicle
Longest length of medial border of the scapula
Shortest length of inferior border of the scapula
Tallest supraspinous fossa
Shortest coracoid process of scapula
Longest humerus length
Tallest humeral head
Greatest distance from Greater Tubercle to top of humeral head
Tallest height of capitulum
Widest width of capitulum
Largest area of capitulum (height x width)
Longest length of surface for Trochlear Notch
Widest width at waist of Trochlear Notch
Widest width of distal surface of Trochlear Notch
Widest width of acetabular notch
Shortest femoral length
Largest femoral head circumference
Tallest femoral head
Widest femoral head
Deepest femoral head
Largest femoral neck angle
Widest proximal width of patellar groove
Shortest tibia length
Smallest Scapular Index (SI = inferior border/medial border)
Smallest Femoral Condyle Depth Ratio (Lateral to Medial)
Smallest Femoral Condyle Height Ratio (Lateral to Medial)
Greatest Tibial Robusticity
Greatest Intermembral Index

Table E

Limb Proportions PCA Loadings			
	PC I	PC II	PC III
HL	-0.1218	0.5408	-0.7346
RL	0.1964	0.5414	0.3142
UL	0.2403	0.5041	0.4591
FL	0.4889	-0.04097	-0.3573
TL	0.5057	-0.00883	-0.1129
FiL	0.4984	0.029	-0.09292
II	-0.3818	0.3971	-0.04345

Table F

Shoulder PCA Loadings			
	PC I	PC II	PC III
AECW	0.3194	-0.04917	0.04392
APL	-0.2653	-0.2031	0.2529
GFH	-0.03575	0.441	-0.00715
GFW	-0.1768	-0.08834	-0.08734
GFD	-0.03585	0.37	0.2612
SIBL	0.1204	-0.3234	0.1471
SMBL	-0.3642	-0.01676	0.148
SFH	-0.3472	-0.03456	0.06167
SIH	-0.3126	-0.1032	0.1606
PSS	-0.00126	-0.4115	0.1016
CPL	0.1941	-0.2724	0.1499
HHH	-0.1458	0.1819	-0.3892
HHW	-0.1363	-0.01549	-0.374
GTH	0.09183	-0.2741	-0.3063
GTW	-0.2528	-0.0561	-0.1831
HHC	-0.1095	-0.1186	-0.4739
BGW	-0.1023	-0.1933	-0.2434
HHHAGT	-0.2268	0.2206	-0.05138
DI	-0.01532	0.02241	0.06271
HL	-0.3089	-0.211	0.0781
CL	-0.3301	-0.01219	0.1928

Table G

Elbow PCA Loadings			
	PC I	PC II	PC III
OFD	-0.1971	0.1447	-0.5198
CH	-0.2512	0.3443	0.09273
CW	-0.3087	0.2592	0.09473
TLLH	0.08546	0.459	-0.04915
TMLH	-0.1507	0.3814	-0.3377
LHEP	-0.156	-0.3494	-0.1632
MHEP	-0.1096	-0.3692	0.1498
RHC	-0.3254	0.1221	-0.05077
RTL	-0.1463	0.2221	0.4234
TNSL	-0.353	-0.07646	0.05602
OPW	-0.3236	-0.00702	-0.09794
OPD	0.2256	0.1431	0.04696
TNWW	-0.3375	-0.0841	0.226
TNBWW	-0.3289	-0.05412	0.2588
BBI	-0.2925	-0.1735	-0.02917
RHS	-0.146	-0.2193	-0.4806

Table H

Hip PCA Loadings			
	PC I	PC II	PC III
GTR	-0.2844	0.06872	-0.4365
FHC	-0.3019	-0.191	-0.08618
FNC	0.2337	-0.2588	0.2062
FHH	-0.2438	-0.3121	0.06471
FHW	-0.1085	-0.4052	0.2368
FHD	-0.3228	-0.13	0.1602
LTrW	-0.3585	-0.00406	0.01148
TTrD	0.2744	-0.0094	-0.152
FNA	-0.2377	-0.2059	0.0492
FHGTD	0.2382	0.196	-0.296
AC	0.07401	-0.3609	-0.2809
ADAI	0.101	-0.4026	0.01703
APAI	-0.03467	-0.2669	-0.2875
ANW	-0.3232	0.1822	-0.132
ANEW	0.04664	-0.2408	-0.6028
ANI	-0.2925	0.251	-0.1172
ADeI	0.2681	-0.1213	-0.06286

Table I

Knee PCA Loadings			
	PC I	PC II	PC III
FCC	-0.2118	0.4256	-0.4806
ID	0.1355	-0.1887	0.06363
LFEP	-0.2549	-0.468	-0.1728
MFEP	-0.2367	-0.4602	0.366
PGPW	-0.3532	0.347	0.1437
PGDW	-0.3468	-0.05446	-0.1318
PGH	0.3551	-0.1818	-0.1566
FCHR	0.359	0.2053	-0.2227
FCDR	0.3233	-0.2402	-0.3324
BR	-0.3922	0.0361	-0.08734
PLI	-0.2397	-0.3081	-0.609

Table Captions

Table A: Measurement abbreviations.
Table B: Index abbreviations.
Table C: Significance levels for measurements. Red indicates significance ($p < 0.01667$). Orange indicates approaching significance ($0.01667 < p < 0.05$). In the slow climber column, red indicates a difference between the slow climbers and the other arboreal quadrupeds which is significant. Orange indicates a difference between the slow climbers and the other arboreal quadrupeds which is approaching significance.
Table D: Summary of traits which can separate slow climbers from other arboreal quadrupeds.
Table E: Limb Proportion PCA loadings.
Table F: Shoulder PCA loadings.
Table G: Elbow PCA loadings.
Table H: Hip PCA loadings.
Table I: Knee PCA loadings.