Up in Arms: Early primate proximal ulnae show affinities with non-quadrupedal, non-primate mammalian taxa.

KRISTEN R. RAMIREZ
Anthropology, CUNY Graduate Center
NYCEP, New York Consortium in Evolutionary Primatology

Introduction

The order Primates is characterized by a set of synapomorphies including: grasping hands and feet, nails instead of claws, diagonal sequence gait, and hind limb dominated locomotion. Numerous adaptive hypotheses have been suggested to explain the historical context for the origins of the order. The ***Grasp-Leaping Hypothesis*** argues that primates are distinguished from other arboreal mammals by their acrobatic locomotion, with an ancient evolution of arboreal leaping (Szalay and Delson, 1979). Predictions of this hypothesis would include greater postcranial similarities between the earliest euprimates and arboreal leaping strepsirrhines (i.e. *Eulemur*, *Otolemur*). In contrast, both the ***Visual Predation Hypothesis*** (Cartmill, 1992) and ***Angiosperm Hypothesis*** (Sussman, 1991) argue for careful grasping of food items as important for the earliest primates. Predictions of either hypothesis would include forelimb anatomy more similar to careful climbers and predators (e.g. *Nycticebus*, *Perodicticus*).

The evolution of these competing uses for the forelimb would include changes to the proximal ulna, as the trochlea articulates with the humerus and defines the long axis of the forearm. The radius articulates with the ulna proximally at the radial notch inferior and anterio-lateral to the trochlea. More anteriorly articulated radii provide greater stability in pronation (during quadrupedalism), but limit supination. Degree of manual supination increases as the radial notch moves laterally. Supination is required for manual manipulation, and the use of the manus in obtaining and consuming foods.

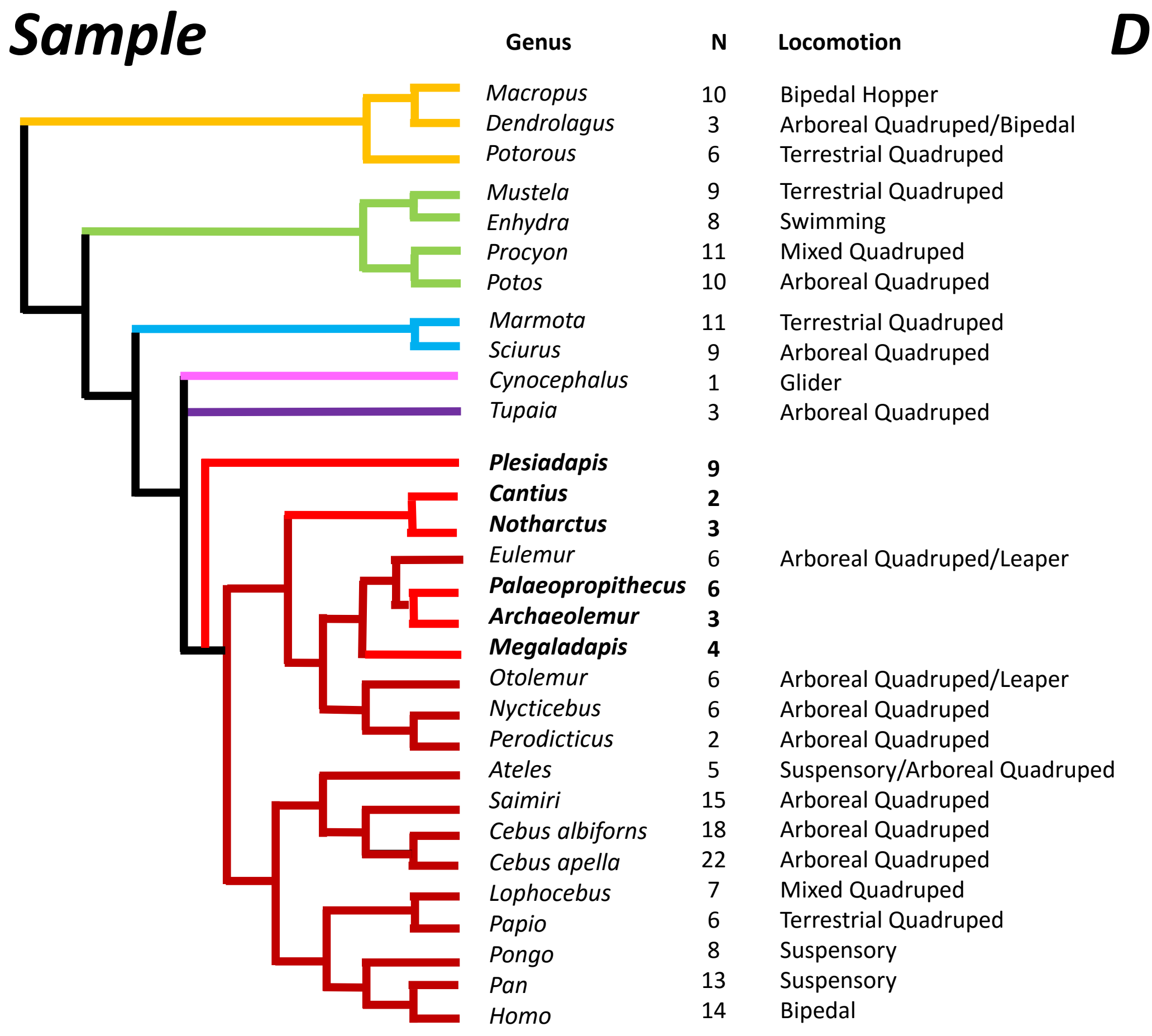
Question and Hypotheses

Can the proximal ulna evaluate competing hypotheses of early primate evolution?

- The proximal ulna will discriminate locomotor categories regardless of phylogeny.
- Fossil early primates will be more similar to extant primates than other mammalian taxa.
- Primate and non-primate manipulative taxa (e.g. *Enhydra*, *Procyon*) will have a more laterally oriented radial notch indicative of greater capacity for supination.

Materials and Methods

Sample



Genus	N	Locomotion
Macropus	10	Bipedal Hopper
Dendrolagus	3	Arboreal Quadruped/Bipedal
Potorous	6	Terrestrial Quadruped
Mustela	9	Terrestrial Quadruped
Enhydra	8	Swimming
Procyon	11	Mixed Quadruped
Potos	10	Arboreal Quadruped
Marmota	11	Terrestrial Quadruped
Sciurus	9	Arboreal Quadruped
Cynocephalus	1	Glider
Tupaia	3	Arboreal Quadruped
Plesiadapis	**9**	
Cantius	**2**	
Notharctus	**3**	
Eulemur	6	Arboreal Quadruped/Leaper
Palaeopropithecus	**6**	
Archaeolemur	**3**	
Megaladapis	**4**	
Otolemur	6	Arboreal Quadruped/Leaper
Nycticebus	6	Arboreal Quadruped
Perodicticus	2	Arboreal Quadruped
Ateles	5	Suspensory/Arboreal Quadruped
Saimiri	15	Arboreal Quadruped
Cebus albiforns	18	Arboreal Quadruped
Cebus apella	22	Arboreal Quadruped
Lophocebus	7	Mixed Quadruped
Papio	6	Terrestrial Quadruped
Pongo	8	Suspensory
Pan	13	Suspensory
Homo	14	Bipedal

Figure 1. Phylogenetic tree of sample taxa, sample size, and locomotor mode. Colors correspond to order (see Results).

Data Collection

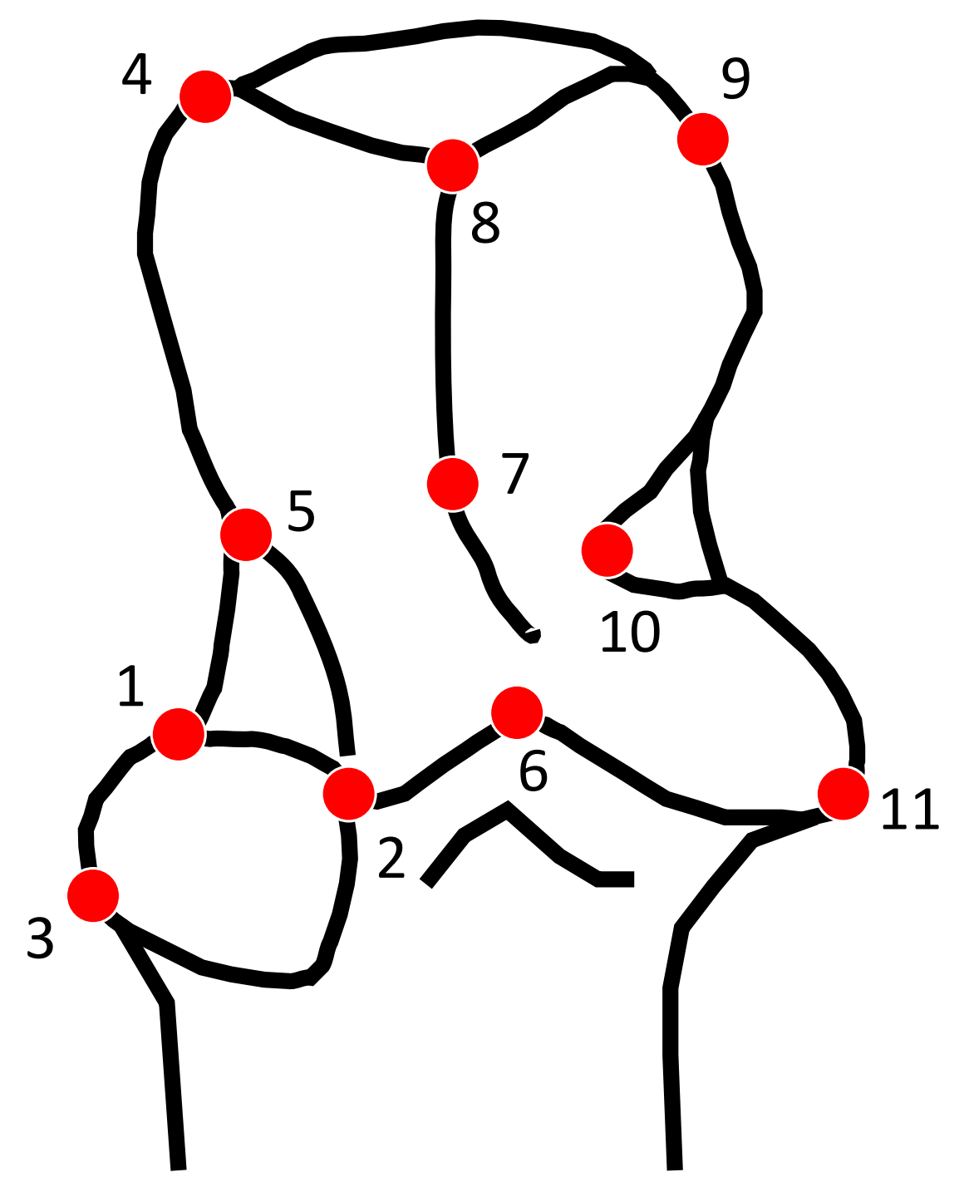


Figure 2. Landmarks on the proximal ulna collected with a microscribe.

Calculations

The x, y, z, coordinates from the raw microscribe data were used to fit a plane with landmarks 6, 7, 8 to define the long axis of the trochlear notch, and a plane fitting landmarks 1, 2, 3 to define the the radial notch. The angle between the two planes was calculated using the normal vectors for each plane, where more acute angles characterized more laterally oriented radial notches, and angles approaching 90° indicated a more anteriorly oriented radial notch.

Analyses

Morphologika 2.5 was used for the General Procrustes Analysis (GPA) and Principal Components Analysis (PCA). PC scores of extant specimens from the components that accounted for a cumulative 95% of the variation were exported to R and used to conduct a Linear Discriminant Analysis (LDA). Fossil PC scores from the same analysis were input into the LDA to predict their generic designation. UPGMA cluster analyses used genus average Procrustes values.

Acknowledgements

Funding This study was supported by the NYCEP NSF IGERT grant DGE 0333415.

Collections Special thanks to Eileen Westwig and Eleanor Hoeger, Gisselle Garcia, and Dr. Jin Meng of the Mammalogy, Anthropology, and Vertebrate Paleontology Collections at the American Museum of Natural History for access to extant and fossil specimens.

I also thank Drs. Eric Delson, Herman Pontzer, and William Harcourt-Smith for feedback on this project, Catalina Villamil, Myra Laird, and Cody Prang for helpful discussions on methodology and sample taxa, and the Human Energetics and Evolution Lab and AMNH Hominin Journal Club for comments on the poster and presentation design.

Results

Figure 3. PCA of the 3D Geometric Morphometric analysis.

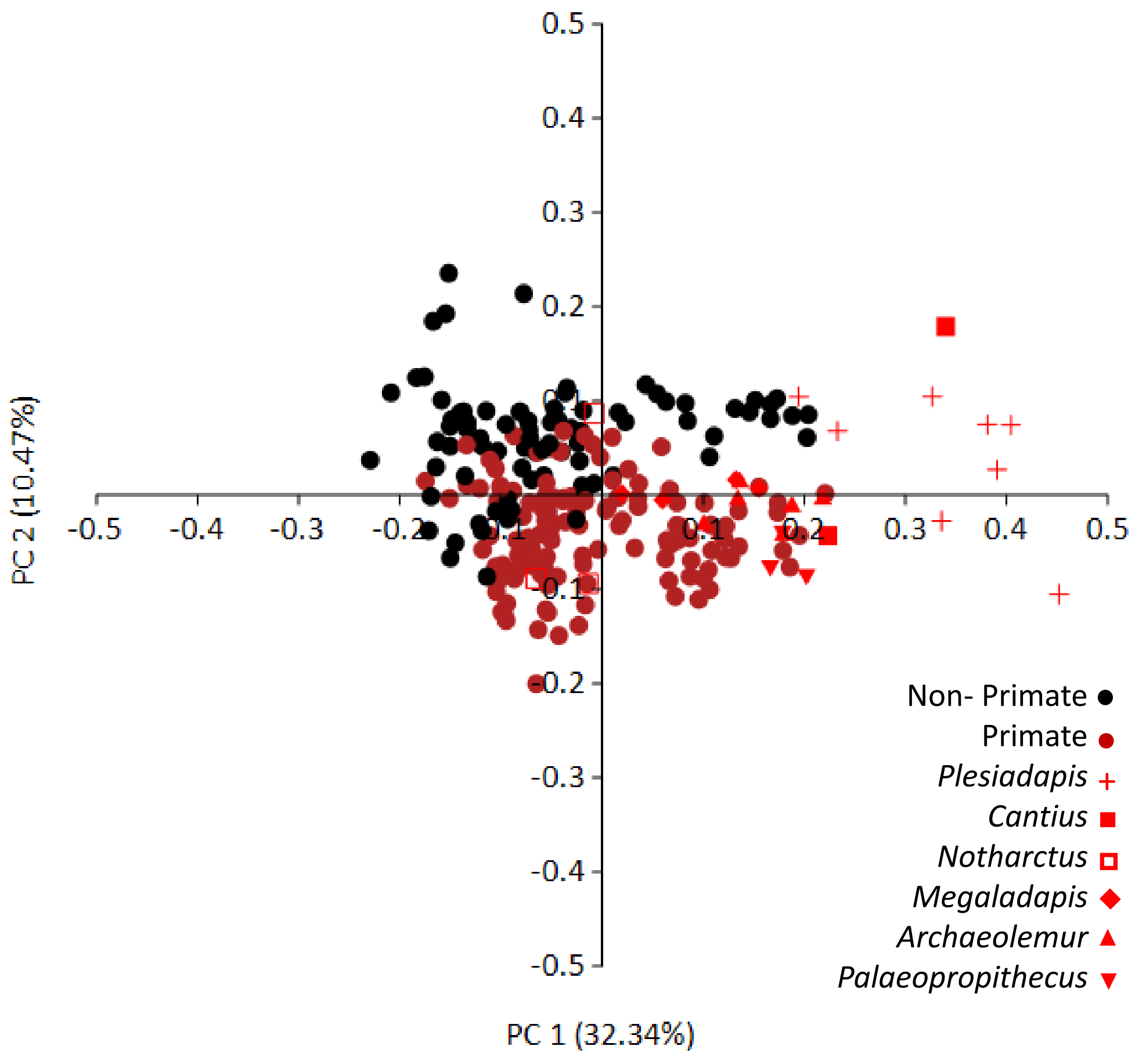


Figure 4. UPGMA pairwise cluster by average genus Procrustes shape variables.

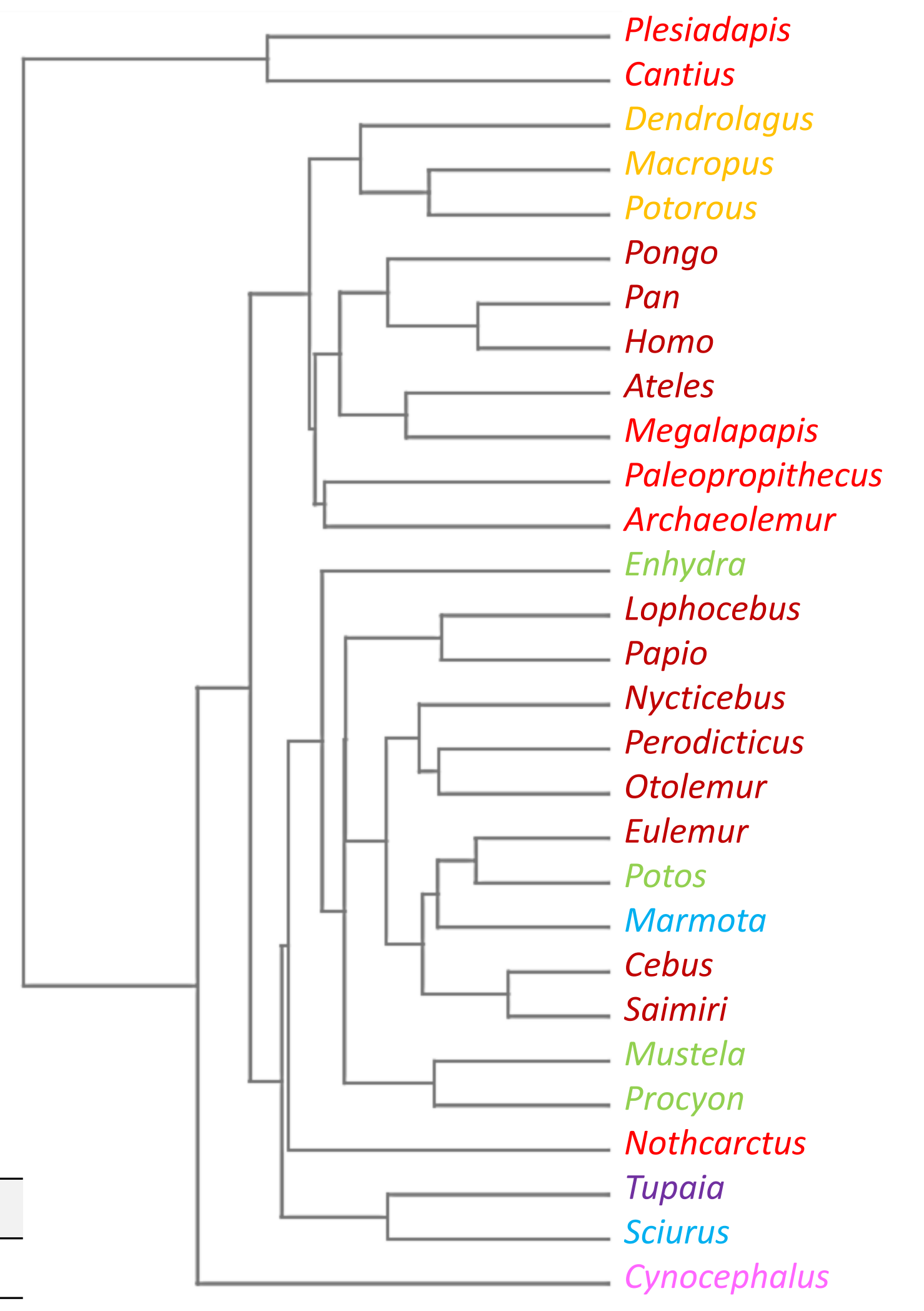
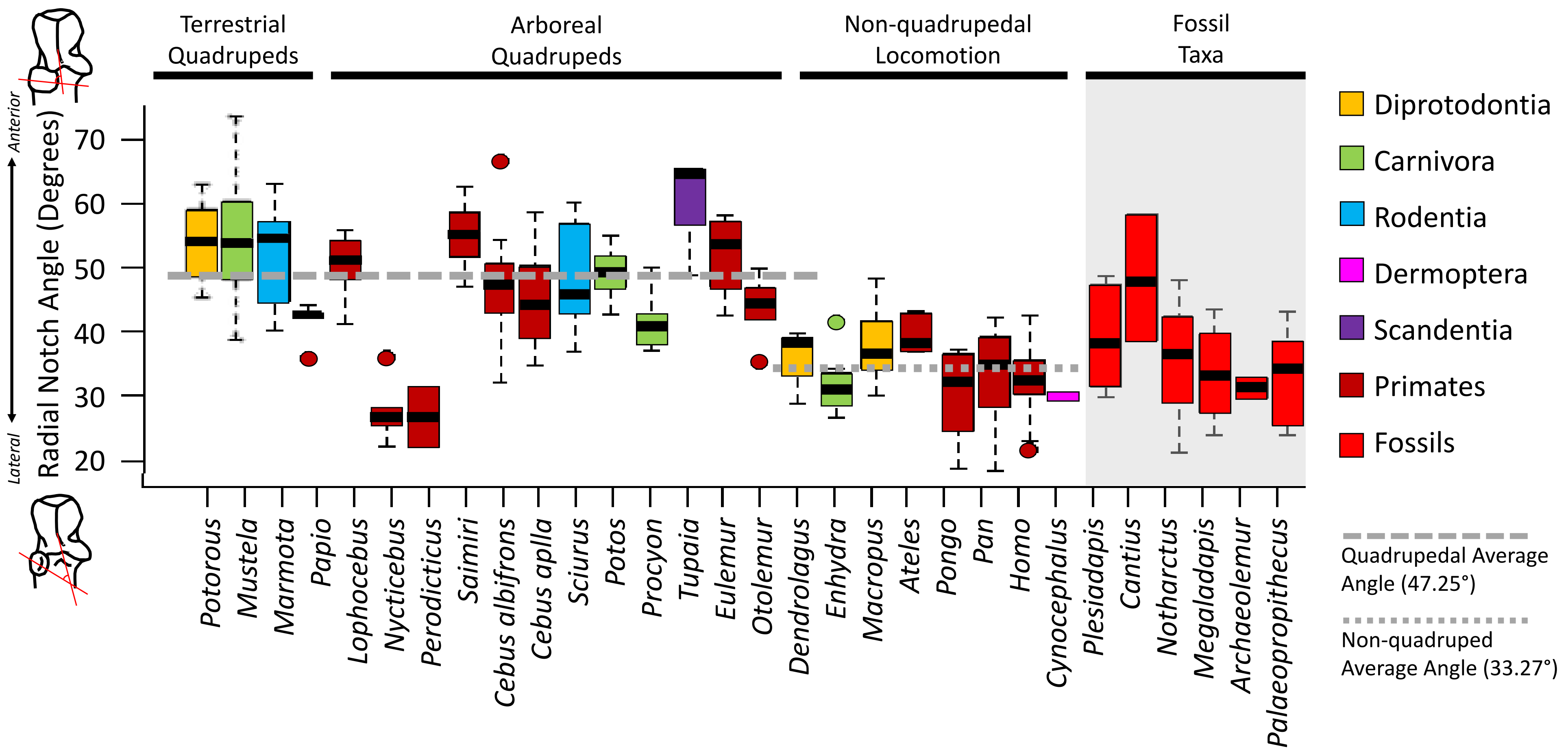


Table 1. Linear Discriminate Analyses

Extant Posterior Probability		Fossil Classification	
Group	% Correct	Genus (n)	Classification (n)
Primate	85	*Plesiadapis* (9)	*Potorous* (3), *Dendrolagus* (3), *Macropus* (3)
Non- Primate	76.5	*Cantius* (2)	*Potorous* (2)
Total	**82**	*Notharctus* (3)	*Papio* (1), *Saimiri* (1), *Marmota* (1)
		Megaladapis (4)	*Ateles* (4)
		Archaeolemur (3)	*Pan* (2), *Potorous* (1)
		Palaeopropithecus (6)	*Potorous* (2), *Macropus* (4)

Figure 5. Quadrupeds have a more anteriorly oriented radial notch than non-quadrupeds.



Discussion

The proximal ulna distinguishes primates as unique compared to other mammals. Primates and non-primates are approximately separated by PC 2 in multivariable analyses (Figure 3). Results of the linear discriminant analysis correctly classifies specimens as primates or non-primates at 82% (Table 1).

Plesiadapis and Cantius occupy a unique morphospace for mammals, and suggest a different locomotor context for primate evolution. These results indicate that *Plesiadapis* and *Cantius* may have been engaging in a unique form of locomotion not captured by this sample (Figure 3). While *Cantius* and *Notharctus* are argued to be anagenetically linked based on cranio-dental similarities, *Notharcus* is postcranially derived in the direction of extant primate arboreal quadrupeds (Table 1, Figure 4).

Within sister taxa, a more laterally oriented radial notch is associated with non-quadrupedal use of the upper limb. While primates are not specifically distinguished from other mammals in radial notch angle, the pattern of variation in the univariate analysis supports the functional hypothesis concerning the relationship between the radius, ulna, and supination (Figure 5).

References

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Sussman RW. 1991. Primate origins and the evolution of angiosperms. American Journal of Primatology 23:209-223.
Szalay FS, Delson E. 1979. Evolutionary History of the Primates. Academic Press, New York.