Environmental and dietary correlates of papionin temporal bone variation

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Introduction

The temporal bone is often considered to be an informative cranial region with respect to genetic, geographic and environmental factors. Recent studies on human temporal bone morphology have indicated that this element reflects genetic distances among human populations (Harvati and Weaver, 2006a,b; Smith et al., 2007) and hominoid species (Lockwood et al., 2004), but also indicate that other factors may play a role in determining temporal bone morphology. Because the papionins constitute a closely related primate group often argued to display similar ecological and dietary adaptations to early hominins, this group of taxa can serve as a good test case for assessing whether patterns of temporal bone variation observed in humans also characterize other primate taxa. In addition, the study of the Papionini enables the investigation of an additional factor that may influence temporal bone morphology beyond those tested for humans—diet.

Research Questions

The present study investigates the three-dimensional morphology of the temporal bone in papionin primates with the goal of:

1) assessing the degree of differentiation among taxa in temporal bone morphology, and;
2) quantifying the association between temporal bone morphology and geography, environment, and diet.

Materials and Methods

Morphological, Environmental, and Dietary Data

- 20 temporal bone landmarks following Lockwood et al. (2002) (Figure 1).
- 18 papionin species, 819 specimens (Table 1).
- Data analyzed using *Morphologika*, and output from Generalized Procrustes Analysis and Principal Components Analysis (GPA and PCA) used for further analysis.
- Shape differences expressed as a Procrustes distance matrix; size matrix calculated using absolute differences in centroid size among taxa.
- Geographic coordinates estimated using published information.
- Environmental matrices (rainfall, temperature, latitude, combined environment) calculated using data from nearby weather stations.
- Dietary matrix calculated using published data describing percentage food items (i.e., fruit, leaves, seeds, bark, etc.) ingested; values were combined into three categories describing food material properties, and a distance matrix calculated.

Analytical Methods

- Discriminant function analysis with cross-validation used to evaluate degree of differentiation among taxa.
- Correlations between centroid size and shape evaluated by regressing PC axes on centroid size, and comparing shape and size matrices using a Mantel test.
- Morphological distances (i.e., size or shape matrices) were compared to the variable of interest (e.g., geographic, environmental, or dietary matrices) using a Mantel test.
- To reduce the number of intertaxon distances in the analysis, interclade distances among taxa were averaged into five nodal values (Figure 2). Nodal values were generated for each matrix included in the analysis, and a correlation analysis was then run to examine the relationships among the variables.

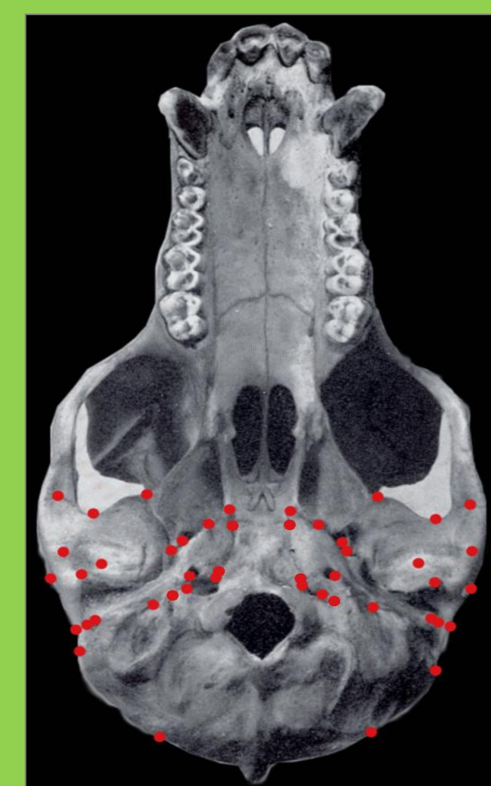

Figure 1. Temporal bone landmarks digitized in this study.
(Modified from Freedman, 1957).

Table 1. Papionin samples analyzed.

Cercocebus agilis	42
Cercocebus atys	38
Cercocebus torquatus	47
Lophocebus albigena	141
Lophopcebus aterrimus	88
Macaca fascicularis	95
Macaca mulatta	46
Macaca nemestrina	36
Macaca sylvanus	17
Mandrillus leucophaeus	33
Mandrillus sphinx	23
Papio anubis	120
Papio cynocephalus	27
Papio hamadryas	12
Papio kindae	15
Papio papio	12
Papio ursinus	52
Theropithecus gelada	21
Total	865

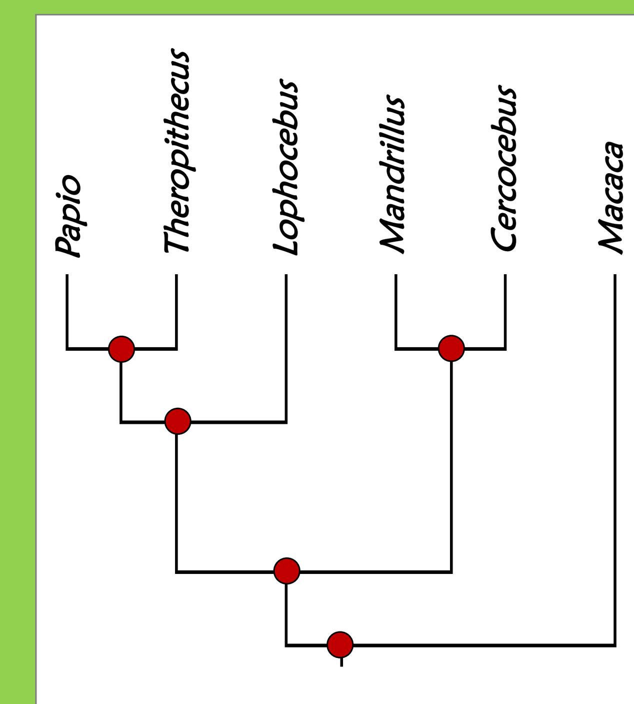

Figure 2. Phylogenetic tree showing the genera used to calculate the five nodal values.

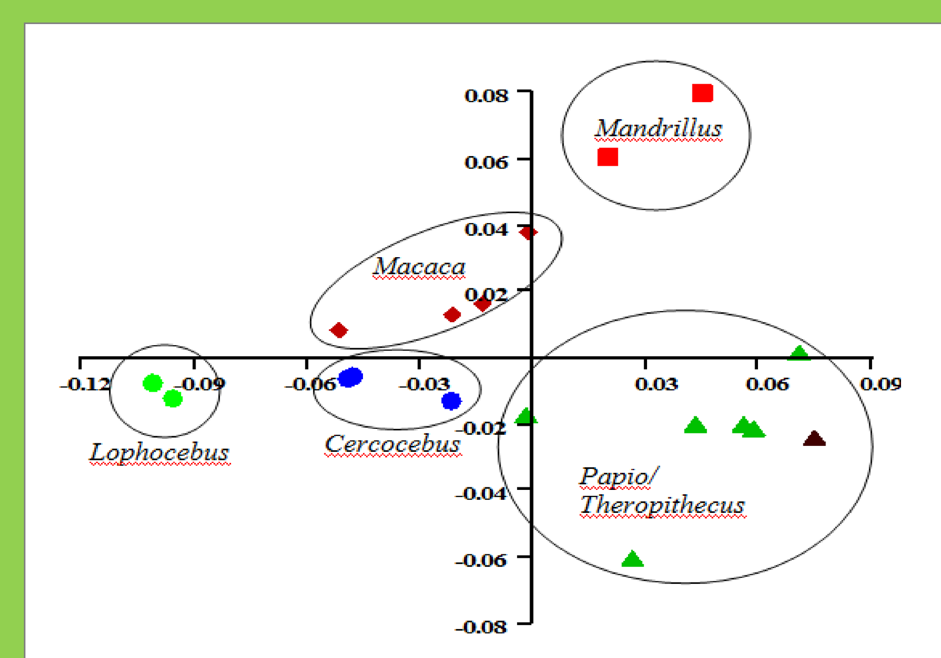

Figure 3. PC graph showing the first two PC axes. PC 1 (X-axis) represents 43% of the variation and separates smaller and larger taxa. PC 2 (Y-axis) represents 16% of the variation.

Table 2. Classification results of the discriminant function analysis. Values shown are percentage individuals correctly assigned to taxon.

	Shape + Size		Shape Only	
	Females	Males	Females	Males
M. fascicularis	80	80	80	84
M. nemestrina	88	90	81	85
M. mulatta	72	88	68	71
M. sylvanus	100	75	100	75
P. ursinus	100	80	100	68
P. papio	-	91	-	91
P. anubis	84	72	52	64
P. cynocephalus	44	56	22	33
P. kindae	50	75	50	63
P. hamadryas	-	90	-	70
L. aterrimus	88	92	64	76
L. albigena	96	100	72	96
T. gelada	100	100	100	100
M. sphinx	25	85	13	77
M. leucophaeus	76	94	88	81
C. agilis	88	92	88	88
C. atys	96	73	87	60
C. torquatus	57	84	71	84
Mean	78	84	71	76

Table 3. Significant ($p<0.05$) correlation coefficients (r) from matrix comparisons.

		Shape vs. Size	Geography	Temperature	Rainfall	Environment	Diet
Both Sexes	Shape	0.279	-	-	-	-	-
	Size	-	-	-	-	-	0.234
Males	Shape	0.219	-	-	-	-	-
	Size	-	-	-	0.167	-	0.314
Females	Shape	0.223	-	-	-	-	-
	Size	-	-	-	0.238	0.239	-
Papio	Shape	-	0.504	0.564	-	-	-
	Size	-	-	-	-	-	-
Macaca	Shape	-	-	0.852	0.849	0.845	-
	Size	-	-	-	-	-	-

Table 4. Results of the Pearson's correlation analysis of the nodal values. Statistically significant correlations are outlined.

	Shape (both sexes)	Male shape	Female shape
Size (both sexes)	0.941	n/a	n/a
Male size	n/a	0.913	n/a
Female size	n/a	n/a	0.678
Geography	-0.261	-0.334	-0.244
Latitude	0.077	-0.147	0.194
Temperature (monthly)	-0.203	-0.363	-0.077
Temperature (range)	-0.215	-0.312	-0.176
Rainfall	-0.096	-0.194	-0.124
Environment	-0.059	-0.457	0.461
Diet	-0.619	-0.747	-0.208

Results

Discriminant Function Analysis

- PCA of group means shows clear separation among taxa and grouping of species in the same genus (Figure 3). PC 1 separates taxa according to size.
- Cross-validation results show very high rates of correct classification (Table 2). Males were correctly classified more frequently than females; classification rates were slightly lower when PCs correlated with size were excluded.
- 100% correct classification for *T. gelada*; also high levels of classification for *L. albigena*, *C. agilis*, *M. sylvanus*, and *P. ursinus*.
- Low levels of classification for *P. cynocephalus*, *P. kindae*, and *M. sphinx*.

Matrix Comparisons

- Significant correlations between size and shape matrices when the entire sample was analyzed, but correlations are relatively low (r= 0.219 to 0.279).
- When considering the entire sample, there are no significant correlations between any variables and shape, but some significant correlations between size and rainfall, environment, and diet (Table 3).
- Separate analyses for the genera *Papio* and *Macaca* found significant correlations between shape and geography, temperature, rainfall, and environment.

Nodal Value Correlations

- Highly significant correlation between size and shape (Table 4)(r=0.9405, p=0.017); however, correlation driven by males, since no correlation between size and shape when females only are examined.
- No other significant correlations between shape or size and the environmental variables.

Interpretation and Conclusions

- Papionin species can be reliably distinguished from one another on the basis of their temporal bone morphology. These findings support the use of temporal bone morphology for taxonomic assignment of papionin specimens of unknown taxon, and may be particularly applicable to investigations regarding fossil papionin specimens.
- There was a stronger relationship between environmental variables and temporal bone morphology among papionins than has been found for humans, in which shape is not correlated with any environmental variables.
- Correlations between temporal bone shape and geographic distance were present within genera, supporting the idea of an isolation by distance model for temporal bone shape as seen in humans.
- As suggested by previous research, size plays an important role in papionin cranial variation, particularly among clades, and this study suggests that papionin temporal bone size may also be related to environmental factors.
- However, when an independent contrasts approach was simulated and the nodal values on a phylogenetic tree examined, there are no correlations among shape or size and environment, therefore suggesting that the effects of environment may be limited to lower taxonomic levels (i.e., among species of a single genus).

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