Scaling relationships in the anthropoid temporomandibular joint

C.E. Terhune, *Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University.*

INTRODUCTION

Many aspects of masticatory variation have been linked to changes in body size (e.g., Freedman, 1962; Bouvier, 1986a,b; Ravosa, 2000; Daegling, 2001; Singleton, 2005). For example, analyses of mandibular scaling across primate size classes indicate a positively allometric relationship between body or cranial size and mandibular dimensions that corresponds to a relationship between size and the mechanical resistance of food objects (Hylander, 1985; Bouvier, 1986a,b; Ravosa, 1996, 2000). It is largely unclear, however, how aspects of temporomandibular joint (TMJ) morphology scale with size, although the scaling data suggest that some aspects of TMJ size are likely to scale with positive allometry against body or cranial size.

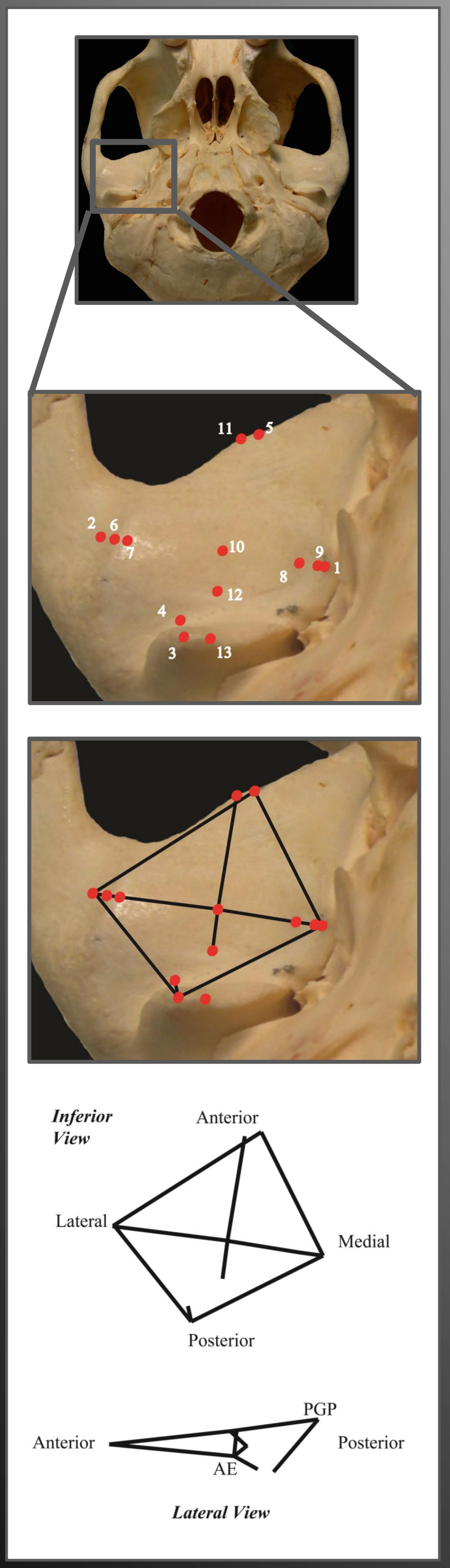
Several previous analyses have addressed how aspects of the TMJ (primarily the mandibular condyle) scale in relation to size (Smith et al., 1983; Bouvier 1986a,b, Vinyard, 1999), with somewhat conflicting results. Smith et al. (1983) found that anthropoid condylar dimensions (length, width, area) scale with slight positive allometry, while Bouvier (1986a,b) found that the same dimensions scaled with isometry. Vinyard (1999) examined the scaling patterns of mandibular condyle and glenoid dimensions in strepsirrhines, and found that most dimensions scaled with positive allometry.

This poster presents a further analysis of scaling relationships in the TMJ, including aspects of both glenoid and mandibular condyle size and shape, in an effort to evaluate these inconsistencies.

METHODS

Samples included 3D coordinate data describing mandibular fossa and condylar shape in 48 anthropoid taxa (Figures 1 and 2). These coordinate data were used to calculate linear measurements describing the TMJ (see variables listed in Table 1). These measurements were regressed against body mass (Smith and Jungers, 1997; Fleagle, 1999) and a cranial geometric mean of six variables (asterionic breadth, porionic breadth, basioccipital length, cranial height, cranial length, orbital width). Ordinary least squares (LS) and reduced major axis (RMA) regression equations were both used. An independent contrasts analysis (Felsenstein, 1985) was also conducted to account for phylogenetic covariance in the sample. Data points included in the analyses were means (by sex) for each species. Data were analyzed separately for males and females, as well as by taxonomic group. All data were log transformed prior to analysis.

The data were further analyzed using geometric morphometric methods, so that shape variation could be visualized and compared among taxonomic groups. Covariance between size and shape was evaluated by regressing the first five PC axes (85-95% of the variation in each sample) on centroid size. Independent contrasts were also used to correct for the lack of phylogenetic independence of the PC scores among closely related taxa. Shape variation along axes that covaried with centroid size was described for each taxonomic group using wireframe diagrams (Figure 2).



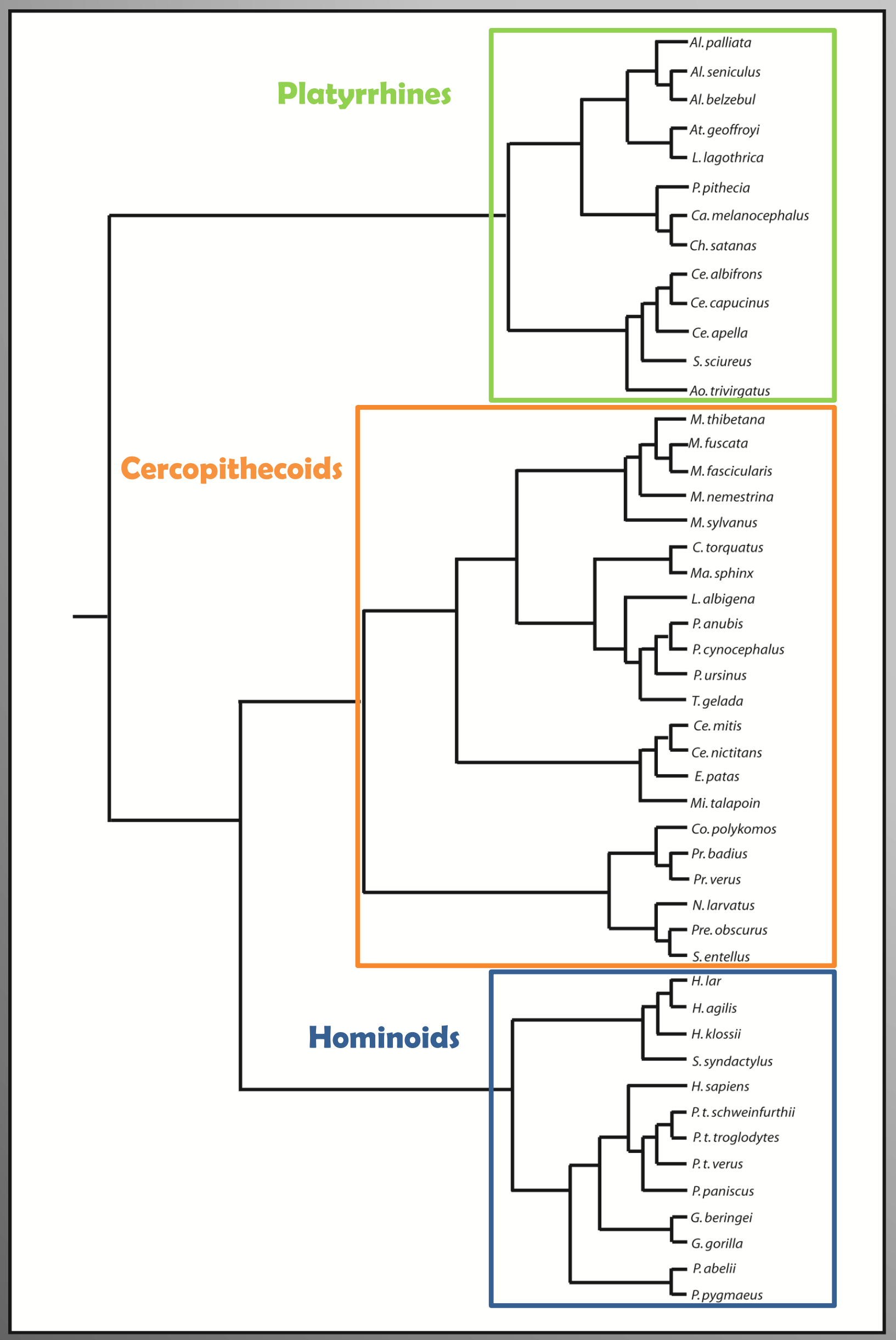
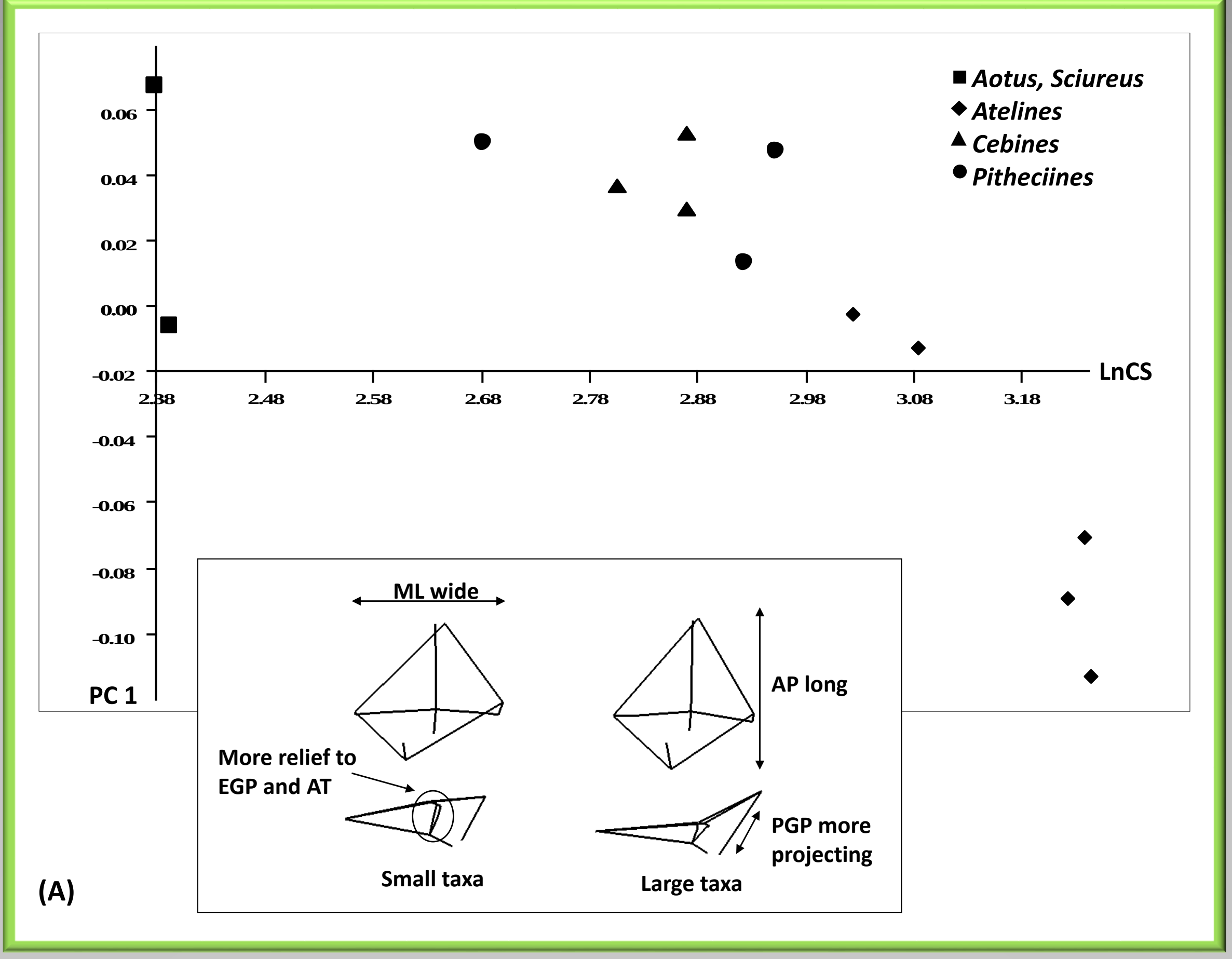
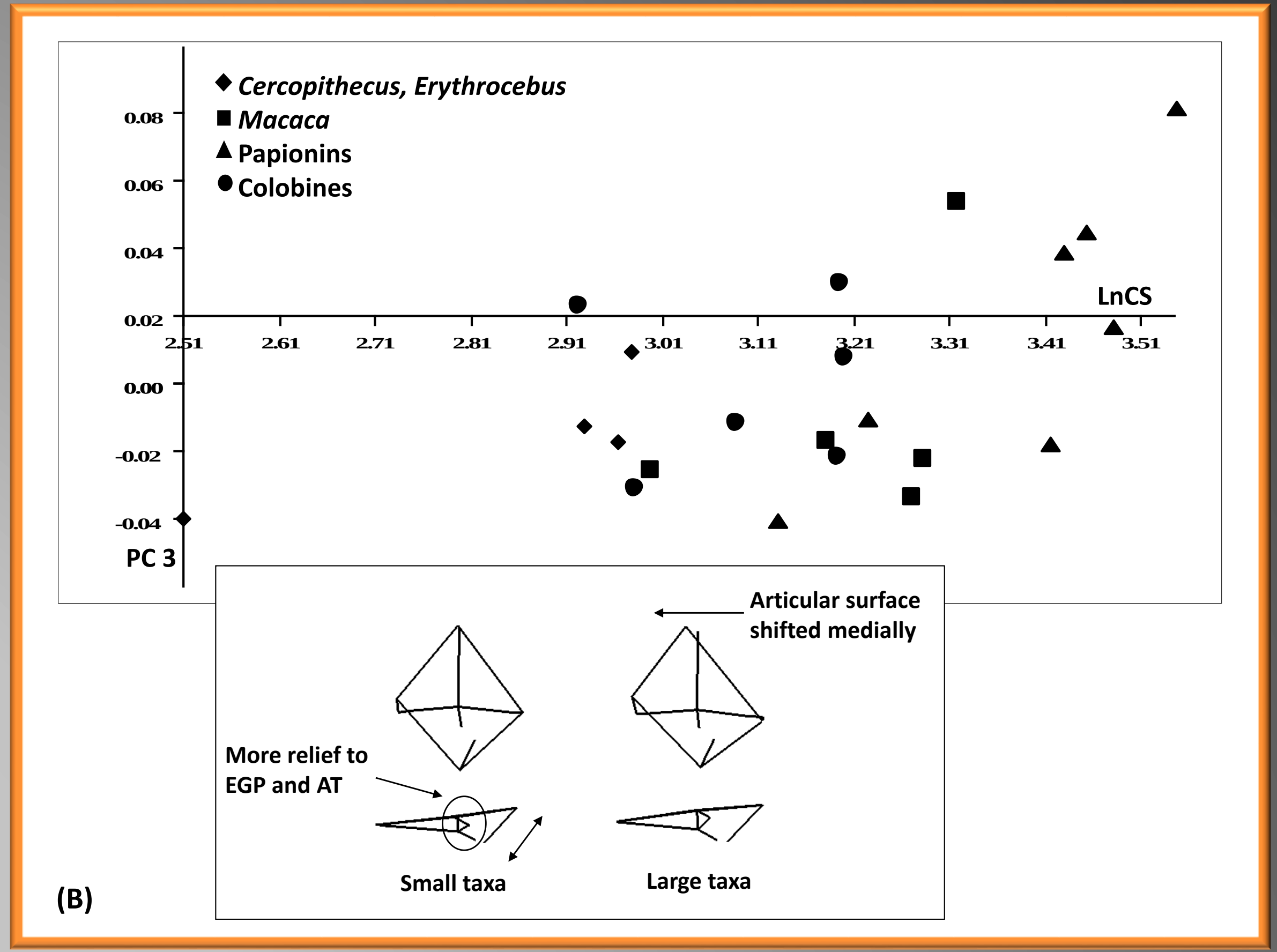


Figure 1 (Left). Inferior views of a *Papio anubis* glenoid showing landmarks and wireframe diagrams used in this study. Features indicated on the lateral view wireframe are the articular eminence (AE) and postglenoid process (PGP).

Figure 2 (Above). Phylogenetic tree used in the independent contrasts analyses showing detail of evolutionary relationships among the 48 taxa included in this analysis.





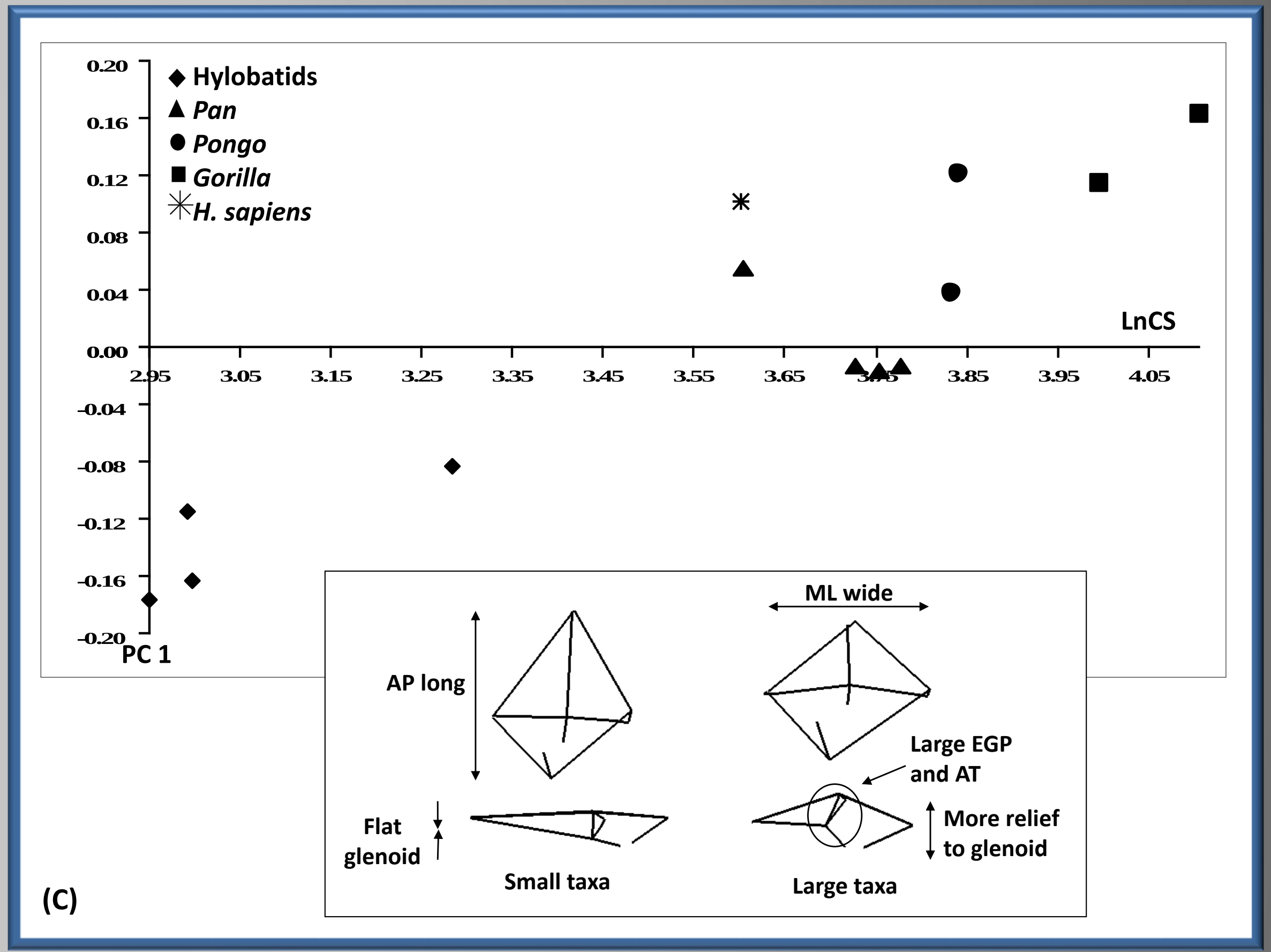


Figure 3. PC results for the platyrrhine sample (A), the cercopithecoid sample (B), and the hominoid sample (C). Axes shown are centroid size vs. PC 1 for platyrrhines and hominoids, and centroid size vs. PC 3 for cercopithecoids. Females only were included in these analyses to minimize the effects of sexual dimorphism. Wireframe diagrams show shape variation between the small and large taxa for each group.

RESULTS

Univariate analyses

- Results of the univariate regressions for both cranial and body size (Table 1) indicate that the TMJ primarily scales with positive allometry.
- Articular tubercle, entoglenoid process, and postglenoid process height all tended to scale with positive allometry in platyrrhines and cercopithecoids, but scaled with isometry in hominoids.
- Glenoid and preglenoid plane length both scaled with positive allometry in cercopithecoids and platyrrhines, but not in hominoids.
- In all taxa, condylar width, length, and area, as well as glenoid width and area, scaled with strong positive allometry, particularly against cranial size.

Geometric morphometric analyses

- Regression of the PC scores on centroid size (Table 2) indicated a strong correlation between glenoid shape and PC 1 for all groups, except cercopithecoids, in which centroid size and PC 3 were significantly correlated. However, most of these correlations disappeared when independent contrasts were used.
- Few significant correlations between centroid size and condylar shape were found, and of those correlations that were significant, the r-squared values were relatively low.
- In platyrrhines (Figure 3), smaller bodied taxa tended to have AP shorter and ML wider glenoids, with a small postglenoid process and large entoglenoid process and articular tubercle. Larger bodied platyrrhines had AP long and ML narrow glenoids, with a large postglenoid process and small entoglenoid process and articular tubercle.
- Very little size related shape variation was found in the cercopithecoids (Figure 4).
- Hominoids showed the strongest relationship between size and glenoid shape, with marked differences in glenoid morphology among smaller and larger bodied taxa (Figure 5). Small taxa tend to have a very flat glenoid, which is AP long and ML narrow. Larger bodied taxa have a raised articular eminence, a larger postglenoid and entoglenoid process, and large articular tubercle, with an AP short and ML wide glenoid.

Table 1. Results of the RMA regression analyses of TMJ measurements against cranial geometric mean and body mass using independent contrasts . Highlighted values indicate slopes that are significantly greater than expected for isometry (positive allometry) or not significantly different from isometry. No slopes were negatively allometric when independent contrasts were used. NSR= no significant relationship.

	Positive Allometry	vs. Cranial Geometric Mean					vs. Body Mass			
	Isometry	All Taxa	Platy	Cercopith	Hominoid		All Taxa	Platy	Cercopith	Hominoid
Females	Articular Tubercle Ht (to FH)	1.88	NSR	2.30	NSR		0.47	NSR	0.50	NSR
	Entoglenoid H (to FH)	2.16	NSR	2.12	NSR		0.54	0.52	0.46	NSR
	Glenoid Length	1.40	1.41	1.54	NSR		0.35	0.38	0.33	0.36
	Glenoid Width	1.54	1.24	1.73	1.56		0.38	0.34	0.37	0.46
	Glenoid Area (Ellipse)	2.90	2.64	3.23	2.75		0.73	0.72	0.70	0.80
	Postglenoid Process Ht (to FH)	2.10	NSR	2.42	NSR		0.52	NSR	0.52	NSR
	Preglenoid Plane Length	1.32	1.29	1.57	NSR		0.33	0.35	0.34	NSR
	Condyle Width	1.64	1.36	1.93	1.71		0.41	0.37	0.42	0.50
	Condyle Length	1.53	1.34	1.75	1.56		0.38	0.37	0.38	0.45
	Condyle Area	3.15	2.68	3.66	3.25		0.79	0.73	0.79	0.95
Males	Articular Tubercle Ht (to FH)	2.13	NSR	2.65	NSR		0.52	NSR	0.59	NSR
	Entoglenoid Ht (to FH)	2.31	2.18	2.43	NSR		0.56	0.60	0.54	NSR
	Glenoid Length	1.48	1.56	1.51	1.32		0.36	0.43	0.34	0.37
	Glenoid Width	1.61	1.34	1.77	1.57		0.39	0.37	0.40	0.44
	Glenoid Area (Ellipse)	3.06	2.88	3.25	2.87		0.74	0.79	0.73	0.80
	Postglenoid Process Ht (to FH)	2.26	NSR	2.61	2.35		0.55	0.55	0.58	NSR
	Preglenoid Plane Length	1.42	1.48	1.54	1.23		0.34	0.41	0.34	NSR
	Condyle Width	1.66	1.53	1.78	1.63		0.40	0.42	0.40	0.45
	Condyle Length	1.60	1.54	1.68	1.59		0.39	0.42	0.38	0.44
	Condyle Area	3.25	3.05	3.44	3.21		0.79	0.84	0.77	0.89

Table 2. Results for the regression of PC scores against centroid size for the glenoid and mandibular condyle. Numbers presented are r-squared values; shaded values are statistically significant at p<0.0125.

		Glenoid		Glenoid Contrasts		Condyle		Condyle Contrasts	
		F	M	F	M	F	M	F	M
PC 1	All Taxa	0.42	0.35	0.13	0.07	0.00	0.03	0.02	0.00
	Platyrrhine	0.50	0.68	0.12	0.30	0.16	0.22	0.00	0.02
	Cercopithecoid	0.11	0.01	0.01	0.15	0.11	0.03	0.04	0.01
	Hominoid	0.80	0.80	0.49	0.34	0.15	0.12	0.18	0.14
PC 2	All Taxa	0.11	0.10	0.02	0.12	0.01	0.00	0.05	0.02
	Platyrrhine	0.23	0.04	0.13	0.08	0.04	0.37	0.00	0.09
	Cercopithecoid	0.14	0.00	0.06	0.18	0.03	0.08	0.26	0.39
	Hominoid	0.00	0.04	0.09	0.06	0.03	0.15	0.01	0.01
PC 3	All Taxa	0.00	0.04	0.03	0.01	0.13	0.08	0.08	0.04
	Platyrrhine	0.03	0.02	0.07	0.01	0.07	0.01	0.01	0.03
	Cercopithecoid	0.31	0.55	0.20	0.41	0.29	0.00	0.27	0.02
	Hominoid	0.01	0.00	0.00	0.15	0.39	0.42	0.19	0.16

CONCLUSIONS

This study evaluated the extent to which the bony morphology of the TMJ scales in relation to body and cranial size. Results of the univariate regression analyses indicate that **features of the TMJ generally scale with positive allometry against size**. There was also considerable variation in the extent to which specific features within the TMJ scaled with positive or negative allometry or isometry. These findings may suggest specific functional differences in the role of the TMJ, and particularly the role of the various processes during mastication and the extent to which preglenoid plane and glenoid length are correlated with relative gape across size classes of primates.

Regression of the principal component axes representing shape on centroid size further suggest that **glenoid shape tends to have a strong relationship with size in hominoids and platyrrhines, but less so in cercopithecoids**. Thus, at least in comparison to other taxonomic groups, cercopithecoids tend to have more uniform glenoid morphology across body sizes. Furthermore, **the pattern of shape change with size in platyrrhines, cercopithecoids, and hominoids differs substantially**. In platyrrhines and hominoids, opposite size-related shape changes from small to large bodied taxa were observed, which suggest important differences in TMJ function that are likely associated with the amount of translation of the mandibular condyle during jaw opening and closing movements.

These findings highlight several issues that will need to be addressed in subsequent phylogenetic and dietary analyses of TMJ variation. In particular, attempts to control for body size differences within the sample may be difficult given the amount of allometric variation demonstrated here. Phylogenetically, these analyses suggest that all of the taxonomic groups examined may not vary in the same ways. The inconsistency in the pattern of scaling relationships among platyrrhines, cercopithecoids, and hominoids may indicate underlying adaptive strategies present in each of these groups that may influence phylogenetic patterns.

ACKNOWLEDGMENTS

Thanks to Bill Kimbel, Mark Spencer, Gary Schwartz, and the late Charlie Lockwood for their assistance with this research. Funding was provided by the National Science Foundation (DDIG), the Leakey Foundation, and the School of Human Evolution and Social Change at Arizona State University.

REFERENCES

Bouvier M. 1986a. A biomechanical analysis of mandibular scaling in Old World monkeys. Am J Phys Anthropol 69:473-482.
Bouvier M. 1986b. Biomechanical scaling of mandibular dimensions in New World monkeys. Int J Prim 7:551-567.
Daegling DJ. 2001. Biomechanical scaling of the hominoid mandibular symphysis. J Morphol 250:12-23.
Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1-15.
Fleagle J. 1999. Primate Adaptation and Evolution. 2nd Ed. New York: Academic Press.
Freedman L. 1962. Growth of muzzle length relative to calvaria length in Papio. Growth 26:117-128.
Hylander WL. 1985. Mandibular function and biomechanical stress and scaling. Am Zool 25:315-330.
Ravosa MJ. 1996. Jaw morphology and function in living and fossil Old World monkeys. Int J Prim 17:909-932.
Ravosa MJ. 2000. Size and scaling in the mandible of living and extinct apes. Folia Primatol (Basel) 71:305-22.
Singleton M. 2005. Functional shape variation in the cercopithecine masticatory complex. Patterns In: Slice DE, editor. Modern Morphometrics in Physical Anthropology. Kluwer New York: Academic/ Plenum Publishers, p 319-348.
Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523-559.
Smith RJ, Petersen CE, Gipe DP. 1983. Size and shape of the mandibular condyle in primates. J Morphol 177:59-68.
Vinyard C. 1999. Temporomandibular Joint Morphology and Function in Strepsirrhine and Eocene Primates. Ph.D. Dissertation, Northwestern University.