

Morphology of the enamel-dentine junction in sections of anthropoid primate maxillary molars

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Abstract

The shape of the enamel-dentine junction (EDJ) in primate molars is regarded as a potential indicator of phylogenetic relatedness because it may be morphologically more conservative than the outer enamel surface (OES), and it may preserve vestigial features (e.g., cusps, accessory ridges, and remnants of cingula) that are not manifest at the OES. Qualitative accounts of dentine-horn morphology occasionally appear in character analyses, but little has been done to quantify EDJ shape in a broad taxonomic sample. In this study, we examine homologous planar sections of maxillary molars to investigate whether measurements describing EDJ morphology reliably group extant anthropoid taxa, and we extend this technique to a small sample of fossil catarrhine molars to assess the utility of these measurements in the classification of fossil teeth. Although certain aspects of the EDJ are variable within a taxon, a taxon-specific cross-sectional EDJ configuration predominates. A discriminant function analysis classified extant taxa successfully, suggesting that EDJ shape may be a reliable indicator of phyletic affinity. When considered in conjunction with aspects of molar morphology, such as developmental features and enamel thickness, EDJ shape may be a useful tool for the taxonomic assessment of fossil molars.

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Introduction

The development of enamel and dentine, enamel thickness, and the morphology of the enamel-dentine junction (EDJ) are frequently cited in studies of the phylogenetic relationships of primate species. Studies of hominoid evolution in particular have made use of these dental characters (e.g., Miller, 1918; Jolly, 1970; Simons and Pilbeam, 1972; Simons, 1976; Dean

and Wood, 1981; Kay, 1981; Martin, 1981, 1983, 1985; Grine and Martin, 1988; Andrews and Martin, 1991; Martin and Andrews, 1993; Dean, 2000; Schwartz, 2000; Chaimanee et al., 2003; Smith et al., 2003, 2004, 2005, 2006). One aspect of tooth morphology thought to be indicative of phylogenetic relatedness is the morphology of the EDJ (Kraus, 1952; Korenhof, 1960, 1961; Sakai and Hanamura, 1971; Corruccini, 1987; Schwartz et al., 1998; Olejniczak et al., 2004).

Kraus (1952) reported that differences in morphology between the outer enamel surface (OES) and the EDJ prohibited the precise prediction of the topography of one surface from the other, with the exception of a few nonmetrical traits (e.g., the number of major cusps). Based on a study of enamel-cap “endocasts,” Korenhof (1961) observed that the

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EDJ demonstrates a “greater measure of primitiveness” compared to the enamel surface; the EDJ may preserve vestigial cusps, ridges, and cingula that are not apparent at the OES. Based on the lack of topographic correspondence between the OES and EDJ (Kraus, 1952), and due to its potential evolutionary conservatism, Korenhof (1961) suggested that the EDJ may be more useful than the OES for assessing phylogenetic relationships. Sakai and colleagues (e.g., Sakai et al., 1965; Sakai and Hanamura, 1971, 1973a,b) published a series of studies on EDJ topography in the Japanese dentition, documenting the existence and frequency of cusps and ridges on the EDJ and the OES of each tooth position. In the concluding installment of their series, Sakai and Hanamura (1973b: 102) stated that “characters on the dentinoenamel junction show phylogenetically more primitive or conservative conditions in relation to the exterior surface of the enamel layer,” concurring with the conclusions of both Korenhof (1961) and Kraus (1952), and indicating that EDJ morphology may be valuable for phylogenetic studies.

Corruccini (1987) later employed dentine surfaces produced by enamel demineralization in a comparison of OES and EDJ topography among primates and other mammals, demonstrating that morphology present at the EDJ is not necessarily present at the enamel surface (e.g., paracristids in the EDJ of humans and pitheciin primates that do not appear in the OES), lending support to Korenhof’s (1961) finding that the EDJ preserves vestigial features not manifested at the OES. Moreover, Corruccini (1987) noted that EDJ morphology may be useful for the resolution of taxonomic uncertainties. Schwartz et al. (1998) also found that the topography of the EDJ and OES are not consistently correlated in fossil hominid molars with reference to the Carabelli feature, wherein some teeth have EDJ cingula without substantial expression at the enamel surface (and vice versa), leading them to caution against using EDJ morphology as the sole variable in phylogenetic analyses. While Schwartz et al. (1998) suggested that EDJ morphology alone is probably not sufficient for fine taxonomic resolution, Korenhof’s (1961) results indicate that EDJ shape may have more discriminatory power when considered among a broader range of more distantly related taxa, and when several aspects of EDJ morphology are considered simultaneously.

The combination of short dentine horns relative to tooth height and thick molar enamel has been suggested to be a key development during hominoid evolution, with implications for phylogenetic and biogeographic hypotheses regarding late Miocene fossil hominoid taxa (Heizmann and Begun, 2001). EDJ-shape characters, such as the height of the dentine horns as they relate to enamel thickness and shape (e.g., dentine penetration), have also been qualitatively assessed and coded for parsimony analyses (Begun et al., 1997). In an attempt to quantify EDJ shape, Olejniczak et al. (2004) examined differences in the positions of EDJ landmarks among the upper molars of different anthropoid taxa via geometric morphometric analyses. Results indicate that significant differences in EDJ shape exist among taxa at superfamilial, subfamilial, generic, and specific levels, suggesting that the shape of the EDJ may be an effective

indicator of phylogenetic propinquity (Olejniczak et al., 2004). Having previously found significant differences in mean shape based on a geometric morphometric analysis of the landmarks depicted in Fig. 1, we here turn our attention to the “discovery of characters” (sensu Zelditch et al., 2000) within the previously described morphometric forms in order to assess whether unique, quantifiable characters describe and discriminate particular taxa.

The study presented here explores two facets of EDJ shape critical to its use in taxonomic and phylogenetic studies: (1) variation in cross-sectional EDJ shape at the species level and (2) the efficacy of cross-sectional EDJ shape in predicting

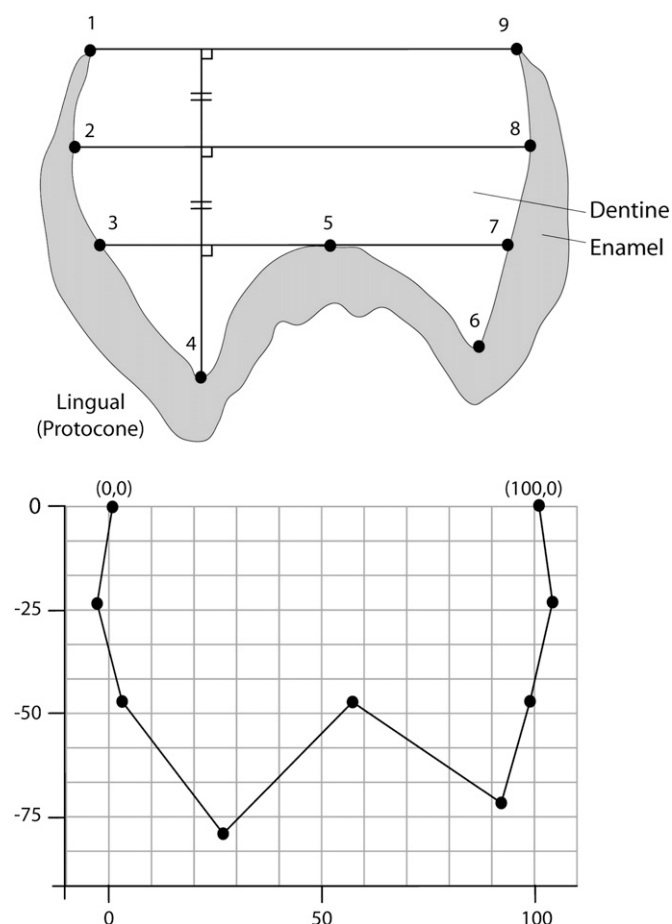


Fig. 1. Top: Cross section through the mesial cusps of a maxillary molar; lingual is to the left. Landmarks are defined as follows: (1) tip of the lingual enamel cervix; (2) lingual intersection of the EDJ and a line parallel to the cervical diameter and bisecting the length between the cervical diameter and landmark 5; (3) lingual intersection of the EDJ and a line parallel to the cervical diameter and running through landmark 5; (4) tip of protocone dentine horn; (5) lowest point of the EDJ between the protocone and paracone cusp tips; (6) tip of paracone dentine horn; (7) buccal intersection of the EDJ and a line parallel to the cervical diameter and running through landmark 5; (8) buccal intersection of the EDJ and a line parallel to the cervical diameter and bisecting the length between the cervical diameter and landmark 5; (9) tip of the buccal enamel cervix. Bottom: Landmark 1 was made to lie at (0, 0) and landmark 9 at (100, 0) in every specimen examined in order to account for differences in tooth size; the relative positions of the other landmarks in two-dimensional Cartesian space were recorded (reproduced and modified following Olejniczak et al., 2004; Smith et al., 2006).

taxonomic assignments. For the purpose of this analysis, EDJ shape is quantified in terms of scaled linear measurements rather than a geometric morphometric approach using two-dimensional coordinate locations. Linear measures are more easily translated into morphological characters, and the locations at which they are measured are more likely to be available in worn and broken fossil specimens than an entire cross-sectional plane. We also compare the EDJ shape of a small sample of fossil catarrhine molars to those of extant anthropoid taxa to assess the utility of EDJ shape in discerning the taxonomic affinities of fossil molars.

Materials and methods

Maxillary molars of multiple species from each of the three extant anthropoid superfamilies were examined, as were a small number of molars from fossil catarrhine taxa, for a total sample size of $n = 141$ (Table 1). Each molar had been sectioned in a coronal plane through the mesial cusps for previous studies of enamel thickness (Martin, 1983, 1985; Andrews and Martin, 1991; Ulhaas et al., 1999; Martin et al., 2003; Grine et al., 2005), so an approximately homologous plane of section in which the EDJ is clearly visible was available for each specimen (Fig. 1). Although the present study is based on linear distances, landmarks were used in order to generate these lines. Specific details regarding the methods data acquisition and definitions of landmark positions are given in Olejniczak et al. (2004), and they are only briefly recounted here.

Nine distance measurements describing EDJ shape were calculated for each molar (Fig. 1). These measurements describe the relative height and width of various aspects of the cross-sectional dentine component of the molar crown and are defined in Table 2. The mean and coefficient of variation (CV) of each distance measurement for each taxon with a sample size larger than three was also recorded. Sokal and Rohlf (1995) noted that the CV, even when corrected for small sample sizes, is an ineffective measure of variation when sample sizes are as small as they are for many species in this study. Lacking a more appropriate measure of variation for small samples, we use caution in our interpretation of the CV among those taxa that are represented by only a few molars.

In order to assess intrataxonomic variation in EDJ shape, the comparatively large sample of *Papio ursinus* molars (Table 1) was employed. The sample was chosen because it represents the only species in this study for which sufficiently large samples of first, second, and third molars were available in order to perform statistical analyses comparing molars from different positions within a species. Each of the nine distance measurements in the *Papio* sample was compared with a Kruskal–Wallis test, using tooth position as the grouping variable; when significant differences were found, Conover's (1999) post hoc test was employed to determine which molar was significantly different from the others.

In order to test whether the nine distances were capable of correctly assigning molars from extant taxa to the correct (known) phylogenetic group, the measurements were subjected to direct (i.e., simultaneous) discriminant function

Table 1
Composition of the study sample

Taxon	M ¹	M ²	M ³	Total	Accession #
Ceboidea					
Aotinae					
<i>Aotus trivergatus</i>	2	1		3	
Atelinae					
<i>Ateles paniscus</i>	2	2	2	6	
Pitheciinae					
<i>Cacajao calvus</i>		1		1	
<i>Chiropotes satanus</i>		1		1	
<i>Pithecia pithecia</i>	2			2	
Cercopithecoidea					
Colobinae					
<i>Colobus polykomos</i>		14		14	
<i>Ptilocolobus badius</i>		8		8	
<i>Procolobus verus</i>		2		2	
Cercopithecinae					
<i>Cercopithecus campbelli</i>		24		24	
<i>Cercopithecus diana</i>		2		2	
<i>Cercopithecus erythrotis</i>		1		1	
<i>Cercopithecus nictitans</i>		4		4	
<i>Macaca nemistrina</i>	1			1	
<i>Papio ursinus</i>	10	11	9	30	
Hominoidea					
Gorillinae					
<i>Gorilla gorilla</i>	3	3	3	9	
Homininae					
<i>Homo sapiens</i>	3	1	3	7	
<i>Pan troglodytes</i>	3	3	1	7	
Ponginae					
<i>Pongo pygmaeus</i>	2	4	3	9	
Fossil molars					
<i>Australopithecus africanus</i>	1			1	Stw-402
<i>Dryopithecus laietanus</i>	1			1	IPS-68
<i>Griphopithecus alpani</i>		1		1	BP-29
<i>Griphopithecus darwini</i>		1		1	BP-37
<i>Laccopithecus robustus</i>	1			1	Unaccessioned (IVPP)
<i>Oreopithecus bambolii</i>	1			1	BM-11565
<i>Pliopithecus antiquus</i>		1		1	2094b
<i>Proconsul africanus</i>	1			1	M-14085
<i>Sivapithecus sivalensis</i>	2			2	M-13365, M-13366
Total sample	35	85	21	141	

analysis (DFA) at the superfamilial level. We made no initial assumption about the group affiliation of any molar, so the probability of each molar belonging to any taxonomic group was equal. Because the sample is not drawn at random from

Table 2
Distance measurements recorded in this study

Variable name	Interlandmark distances ¹	Definition
D1	6x–4x	Width between the tips of the dentine horns
D2	5x–1x	Width of lingual cusp
D3	9x–5x	Width of buccal cusp
D4	7x–3x	Width at cusp base
D5	8x–2x	Width at midline
D6	(4y–5y)/4y	Height of lingual horn
D7	(6y–5y)/6y	Height of buccal horn
D8	4y	Lingual height
D9	6y	Buccal height

¹ For example, “6x” is the x-coordinate of landmark 6.

the various species among the order Primates (the sample represents taxa that were deliberately chosen for previous enamel-thickness studies), and because sample size is not randomly distributed among species (e.g., the number of *Pongo* molars is greater than the number of *Cacajao* molars), we believe that group sample sizes should not be reflected in classification (for a discussion of prior probabilities, see Tabachnick and Fidell, 2000). All statistical tests were performed using SPSS software (v12.0.1, SPSS Science, Inc.). Taxonomic assignments were made following Groves (2001), Wood and Richmond (2000), Andrews (1992), and Fleagle (1999).

The probability of each fossil molar belonging to any of the extant superfamilies was assessed by a second DFA treating each fossil molar as an ungrouped case; subfamily relationships among extant and fossil taxa are not known with certainty, so we performed only a single superfamily-level DFA. We recognize that *Proconsul*, *Oreopithecus*, *Pliopithecus*, and *Laccopithecus* may belong to extinct superfamilies (Proconsuloidea, Oreopithecoidea, and Pliopithecoidea; e.g., Harrison, 1987), but when visualized as a plot of the discriminant functions, DFA results may point to similarities between a particular fossil molar and an extant superfamily. It must also be noted that, with sample sizes of one or two fossils in each case, DFA results may be contingent on a statistical outlier for a fossil taxon, so interpretation of the discriminant function analysis must be made with caution.

Due to limitations inherent in DFA when small samples of ungrouped cases are included (Tabachnick and Fidell, 2000), we also created plots depicting the range of values recorded for each superfamily for each of the nine measurements to augment interpretation of the data. Values recorded for fossil molars may then be compared to the extant ranges, and similarities noted on the basis of individual measurements.

Results

Variation in EDJ shape

The average shape of the EDJ for each taxon examined in this study is presented in Fig. 2. The mean and coefficient of variation (CV) are reported in Table 3 for each measurement of each species represented by more than three specimens. The CV is typically greatest in measurements D5, D6, and D7. *Ateles paniscus* molars, which have the largest CVs in this sample, are highly variable for these measurements. The other species show more uniform shape patterns across individuals. These uniform shape patterns appear to be taxon-specific. That is to say, despite variation in the location of EDJ landmarks within a species, the overall shape can still distinguish a molar as belonging to a particular species. Figure 3 depicts the EDJ shape of each molar of three taxa included in this study, showing the least uniform (*Pongo*) and the most uniform (*Colobus*) in terms of cross-sectional EDJ shape. These results generally agree with our previous findings, which demonstrated that species-specific landmark configurations describe each taxon (Olejniczak et al., 2004).

Kruskal–Wallis tests performed on the *Papio ursinus* sample show that first molars are significantly different than the other two molars in terms of the location of the midocclusal basin (landmark 5) and the relative buccal placement of landmark 7 (Fig. 4). These differences in landmark locations cause a relative asymmetry in cusp width in first molars [manifested as significantly different distances D2 ($\chi^2 = 13.19$, $p < 0.01$) and D3 ($\chi^2 = 13.19$, $p < 0.01$)]. The relatively shallow placement of landmark 5 also causes the two relative dentine-horn-tip heights (distances D6 [$\chi^2 = 15.55$, $p < 0.01$] and D7 [$\chi^2 = 12.36$, $p < 0.01$]) to be significantly different between the first molar and the other two molar positions.

Extant superfamily-level classification

The DFA at the superfamily level had two significant discriminant functions, with a combined χ^2 (6) = 194.07 ($p < 0.01$). After removal of the first function, there was still a strong association between groups and predictors— χ^2 (2) = 21.30 ($p < 0.01$). The two discriminant functions accounted for 94.9% and 5.1%, respectively, of the between-group variation. As shown in Fig. 5, the first discriminant function separates cercopithecoids from ceboids and hominoids. The second discriminant function discriminates ceboids from hominoids, although hominoids overlap somewhat with both of the other groups.

The DFA's loading matrix (Table 4) suggests that the best predictors for distinguishing cercopithecoids from the other two groups (first function) are the relative width between the tips of the dentine horns (D1) and the relative width of the molar at the cusp base (D4). Cercopithecoids have more closely spaced dentine cusp tips (D1) and narrower molars at the cusp base than do the other superfamilies.

Ceboids are discriminated from hominoids on the second function by the following variables: (1) ceboids have relatively wider molars at the cusp base (D4); (2) ceboids have relatively lower buccal cusps (D9); (3) ceboids have relatively taller lingual cusps (D8); (4) ceboids have relatively wider molars at the midline between the bicervical diameter and the height of the dentine horn (D5); (5) ceboids have relatively taller lingual dentine horns relative to tooth height (D6); and (6) ceboids have relatively taller buccal dentine horns relative to tooth height (D7).

The classification results of the superfamily-level DFA are provided in Table 5. Overall, 93.9% of molars were correctly classified by superfamily using the nine EDJ distance measurements. Two ceboid molars were misclassified as hominoid molars, two hominoid molars were misclassified as ceboid molars, one hominoid molar was misclassified as a cercopithecoid molar, and two cercopithecoid molars were misclassified as hominoid molars.

Classification of fossil molars

A second DFA was performed at the superfamilial level with fossil molars treated as unclassified cases. This DFA had two significant discriminant functions, with a combined χ^2

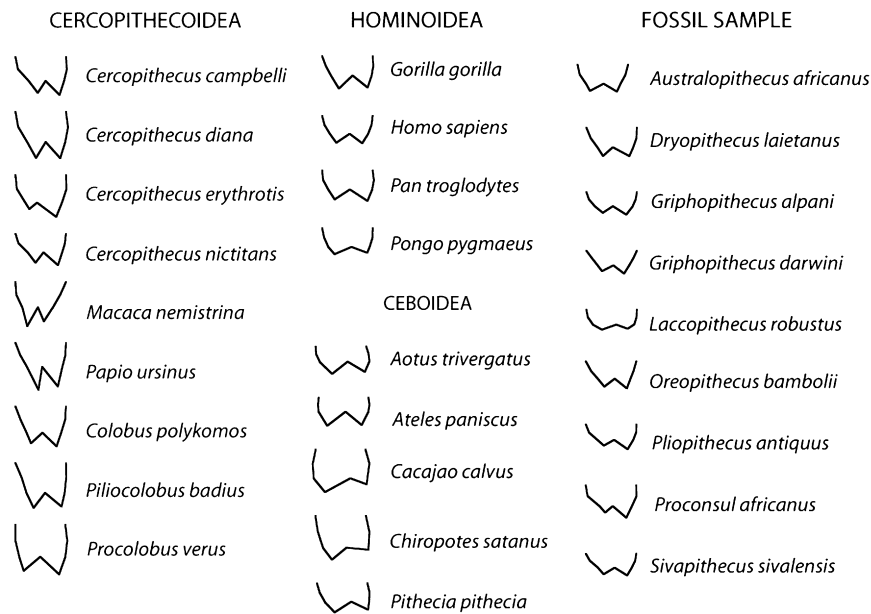


Fig. 2. Schematic diagrams of the average maxillary cross-sectional EDJ shape for each species included in this analysis, based on the nine landmarks measured by Olejniczak et al. (2004). Diagrams are as defined in Fig. 1 (lingual is to the left; the bicervical diameter in each diagram is standardized to 100 units in length). The average shape is taken to be the average (x, y) coordinate of each landmark for each species.

(6) = 194.06 ($p < 0.01$). After removal of the first function, there was still a strong association between groups and predictors [$\chi^2(2) = 21.23$, $p < 0.01$]. The two discriminant functions accounted for 94.9% and 5.1%, respectively, of the between-group variation. Results of this DFA were similar to those of the superfamily-level DFA of extant taxa because the only change was the addition of a few ungrouped cases. The same variables correlated with the discriminant functions in the original superfamilial analysis were correlated with the two discriminant functions in this analysis (the first discriminant function is most highly correlated with D1, D2, and D3, and the second discriminant function is most highly correlated with the remaining predictors, D4–D9).

Figure 6 depicts the two discriminant functions. *Laccopithecus* falls within the hominoid range due to the fact that this molar has relatively broadly spaced dentine horns and relatively symmetrical cusps, as is the case for many hominoid and ceboid taxa (see Fig. 2). *Proconsul* falls within the cercopithecoid range, largely because this molar has relatively closely spaced dentine horns (D1) and strong cuspal-width asymmetry (D2 and D3) (see Fig. 2). The remaining taxa fall into an area on the first discriminant function that is roughly between the hominoid and cercopithecoid range. On the second discriminant function, all of the fossils fall into the lower half of the plot with Colobinae, *Homo*, and *Pongo* because these molars all share the following features: (1) relatively narrow molars at the cusp base (D4); (2) relatively tall buccal cusps (D9); (3) relatively short lingual cusps (D8); (4) relatively narrow molars at the midline between bicervical diameter and the height of the dentine horn (D5); (5) relatively short lingual dentine horns relative to tooth height (D6); and (6) relatively short buccal dentine horns relative to tooth height (D7). These features are in contrast to Cercopithecinae, Aotinae, Atelinae, and *Pan*, which

have the opposite conditions and occupy the positive end of the second discriminant function in Fig. 6.

The fossil data for each distance measurement are plotted with the ranges of the extant superfamilies in Fig. 7. The foremost result apparent by examining these plots is that there is considerable overlap among the extant superfamilies for each variable. This overlap prohibits the definitive recognition of an affiliation between a fossil molar and any particular extant superfamily based on a single variable, and it demonstrates that greater taxonomic resolution is achieved through simultaneous consideration of many variables than by looking at each variable separately (compare the overlap of ranges in Fig. 7, for instance, with the discrimination of superfamilies in Fig. 5).

Discussion

Any character that is said to be indicative of phyletic affiliation should not be so variable that intraspecific variation overwhelms interspecific variation. The results of the present study demonstrate that EDJ-shape variation does not mask taxon-specific patterns in EDJ landmark configurations, and that there is little intertaxonomic overlap, even between closely related species (Fig. 2; see also Olejniczak et al., 2004). When species were combined into higher taxa, however, variation was substantial among individual EDJ distance measurements (e.g., among superfamilies; see Fig. 7).

Metameric variation (slight differences in shape between M^1 , M^2 , and M^3) may contribute to the variation in combined tooth-position samples from a single species (e.g., Hlusko, 2002). Metameric variation has been documented in other dental variables among hominoid primates (e.g., Smith et al., 2005). Differences between maxillary third and first/second molars have also been identified in *Homo sapiens* dentitions (Smith

Table 3
Mean and coefficient of variation (CV) for measurements of genera represented by six or more specimens

Taxon	n	D1		D2		D3		D4		D5		D6		D7		D8		D9	
		Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
<i>Ateles</i>	6	69.32	8.73	53.90	18.02	46.10	21.07	100.30	4.23	23.11	40.01	23.11	40.01	21.88	33.95	46.29	23.61	45.06	21.70
<i>Cercopithecus</i>	31	43.99	9.06	58.59	7.54	41.41	10.68	70.15	7.05	19.42	22.64	19.42	22.64	22.99	21.35	58.41	15.56	61.98	15.19
<i>Colobus</i>	14	50.73	8.06	53.46	5.08	46.54	5.84	68.63	6.15	17.19	16.85	17.19	16.85	22.39	14.94	60.15	6.08	65.34	4.25
<i>Gorilla</i>	9	56.81	7.94	60.28	7.21	39.72	10.94	80.50	4.32	21.42	10.94	21.42	10.94	19.68	19.80	53.06	9.97	51.32	7.04
<i>Homo</i>	7	51.36	12.29	54.51	6.10	45.49	7.31	75.83	3.68	14.63	30.42	14.63	30.42	15.50	20.25	44.07	20.10	44.93	14.32
<i>Pan</i>	7	64.98	13.64	54.96	8.85	45.04	10.81	87.22	10.32	16.30	17.09	16.30	17.09	18.77	36.72	47.34	17.11	49.81	22.94
<i>Papio</i>	30	38.44	14.75	52.84	7.41	47.16	8.31	70.14	4.50	89.70	4.92	48.81	11.62	44.75	12.67	76.64	11.82	71.27	14.35
<i>Ptilocolobus</i>	8	55.47	11.00	58.56	4.69	41.44	6.62	75.64	6.21	24.65	9.11	24.65	9.11	22.38	9.15	73.31	9.12	71.04	8.33
<i>Pongo</i>	9	64.71	6.30	58.25	7.38	41.75	10.29	81.72	6.62	11.88	25.50	11.88	25.50	9.56	33.46	42.60	13.82	40.28	14.48
<i>Procolobus</i>	12	70.85	16.13	49.66	14.82	50.34	14.62	92.70	17.18	23.01	30.24	23.01	30.24	28.42	12.49	75.48	15.19	80.88	1.19

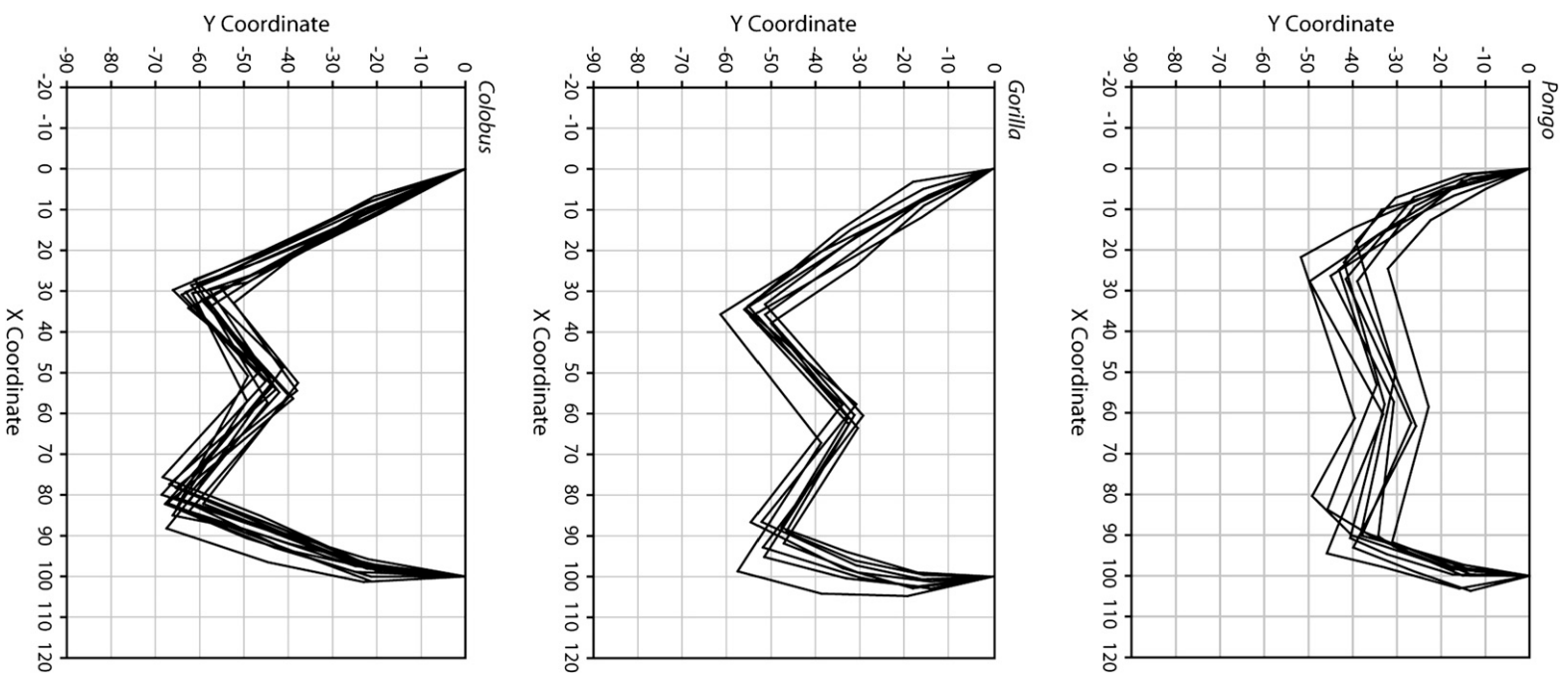


Fig. 3. Plots demonstrating variability in EDJ shape of three representative taxa; definitions of landmarks and orientation are as in Fig. 1. Each plot shows the individual EDJ-shape outline of the entire sample of the taxon represented. While there is variability in the location of some landmarks, molars from a given genus display a taxon-specific arrangement of landmarks.

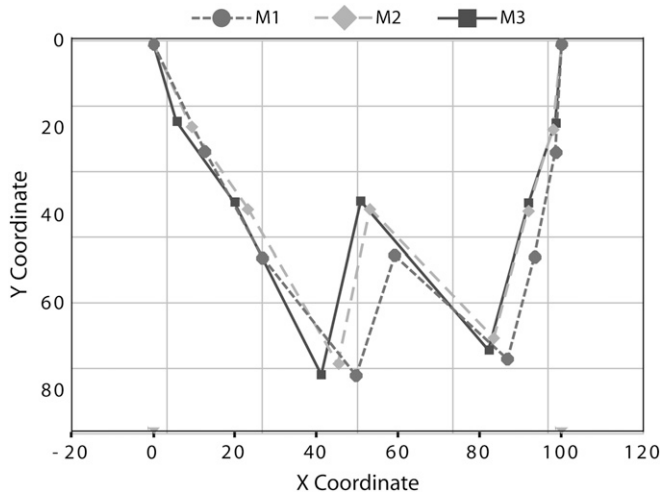


Fig. 4. Plot depicting the average cross-sectional EDJ shape in *Papio ursinus* first, second, and third molars. First molars are significantly different from second and third molars based on the relatively shallow midocclusal basin and the relatively buccal placement of the buccal shoulder of the molar.

et al., 2006). The analysis of *Papio ursinus* molars from all three maxillary molar positions demonstrates that EDJ morphology is, as is the case in human molars (Smith et al., 2006), somewhat dependent on molar position (Fig. 4), particularly with reference to the height of the midocclusal basin. First molars tend to have shallower midocclusal basins than second or third molars. First molars are also more asymmetrical than second or third molars, with dentine-horn tips and the midocclusal basin placed buccally relative to the width of the tooth. Nonetheless, compared with other species averages presented in Fig. 2, the *Papio* molars from each position share a unique cross-sectional shape that is consistent within the species and different from other taxa. This finding is strengthened by the EDJ-shape plots in Fig. 3, which show shape consistencies across taxa despite combining molars from different positions.

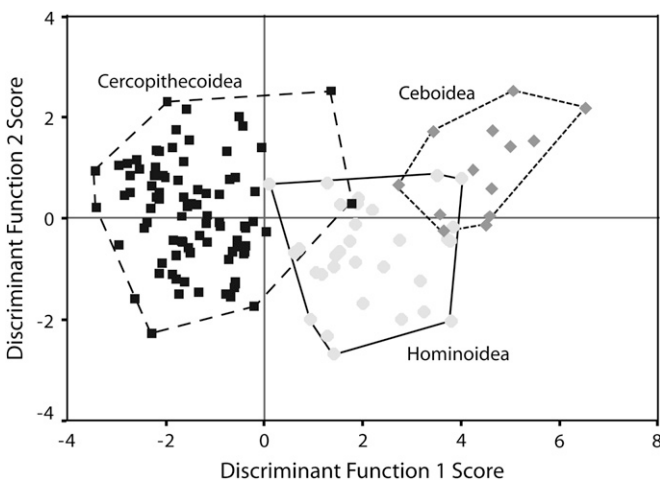


Fig. 5. Plot depicting scores on two discriminant functions resulting from a DFA at the superfamily level of extant taxa. Overall, 93.9% of molars were classified correctly. Cercopithecoidea and ceboidea have completely non-overlapping ranges, while hominoids occupy a central position overlapping somewhat with the other two superfamilies.

Table 4
DFA pooled within-group correlations

	Function 1	Function 2
D1	0.521	-0.039
D2	0.105	0.149
D3	-0.105	-0.149
D4	0.623	0.608
D5	0.312	0.415
D6	0.033	0.548
D7	-0.056	0.376
D8	-0.379	0.712
D9	-0.498	0.656

Regarding the other taxa, variation in the height of the dentine horns (D6, D7) is, perhaps, partially explained by variation in the degree of obliquity from the ideal coronal plane in the molar sections examined. Martin (1983) and Smith et al. (2004) reported that deviations from an ideal plane passing through the tips of the enamel cusps and the tips of the dentine horns will exaggerate the area of enamel in cross section, and reduce the area of dentine, in part because the full height of the dentine horn is not visible in an oblique plane. It is unclear why D5 (the relative width of the molar at half of the distance between the bicervical diameter and a parallel line passing through the lowest point of midocclusal enamel) is also relatively variable. We stress that individual measurements of EDJ shape are not sufficient for the classification of extant or fossil molars, but that several measures examined simultaneously can be used for classification. This is congruent with our previous finding (Olejniczak et al., 2004) that individual EDJ-shape landmarks are variable within a taxon, but when many landmarks are considered together, taxonomic discrimination is possible.

The ability of EDJ distance measurements to discriminate taxa lends support to Korenhof's original findings (1960, 1961). The level of classificatory success achieved from the superfamily-level analysis suggests that there is a component of phylogenetic conservatism (sensu Korenhof, 1961) manifest in cross-sectional EDJ shape. This suggests that EDJ shape is a suitable character for the taxonomic assessment of fossil molars and that it is relevant in examining the phylogenetic relationships of fossil taxa.

We recognize that small samples prohibit a rigorous study of the EDJ shape of the fossil molars examined here, and analyses based on such limited data are necessarily tentative. Moreover, although little evidence of variation due to metameric variation was found, larger samples may demonstrate that molar position does influence EDJ-shape metrics. Nonetheless, a few of the

Table 5
Classification results of the superfamily-level DFA

	Ceboidea	Cercopithecoidea	Hominoidea	Total molars
Ceboidea	10	0	3	13
Cercopithecoidea	0	84	2	86
Hominoidea	2	1	29	32

Notes: Overall, 93.9% of cases were correctly classified. Columns represent the taxon into which molars were misclassified.

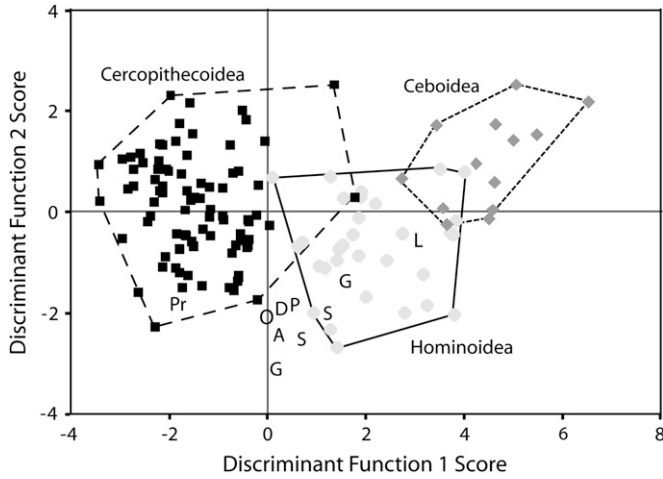


Fig. 6. Plot depicting the range of scores for each superfamily and each fossil molar on the first two discriminant functions resulting from a DFA at the superfamily level. Outlines representing the total area occupied by all individuals of one superfamily are drawn. Fossils are labeled as follows: Pr = *Proconsul*; O = *Oreopithecus*; D = *Dryopithecus*; G = *Griphopithecus*; L = *Laccopithecus*; S = *Sivapithecus*; A = *Australopithecus*; P = *Pliopithecus*.

fossil molars fall outside the extant hominoid range and so are worthy of discussion. *Proconsul africanus*, for instance, falls squarely within the range established by cercopithecoid molars. The single *Proconsul* molar shares with the cercopithecoids examined here a prominent dentine lingual cingulum and closely approximated dentine horns. This configuration is especially reminiscent of the condition in *Cercopithecus nictitans* (e.g., compare the EDJ outlines of these taxa in Fig. 2). However, because other aspects of molar morphology show wide variation in *Proconsul* (e.g., enamel thickness; Andrews and Martin, 1991; Beynon et al., 1998), it is unclear whether this cercopithecoid-like morphology is that of an aberrant individual molar, represents an EDJ configuration unique to *Proconsul africanus*, or is representative of the entire genus *Proconsul*. Molar sections from other *Proconsul* species (*P. heseloni* and *P. nyanzae*) do not appear to show this EDJ configuration (see Fig. 4 of Beynon et al., 1998).

Similar to the *Proconsul africanus* molar, the *Oreopithecus* molar also falls closer to the cercopithecoid centroid than to the hominoid centroid (Fig. 6). The *Oreopithecus* molar shows tall and narrow dentine horns and recalls the overall

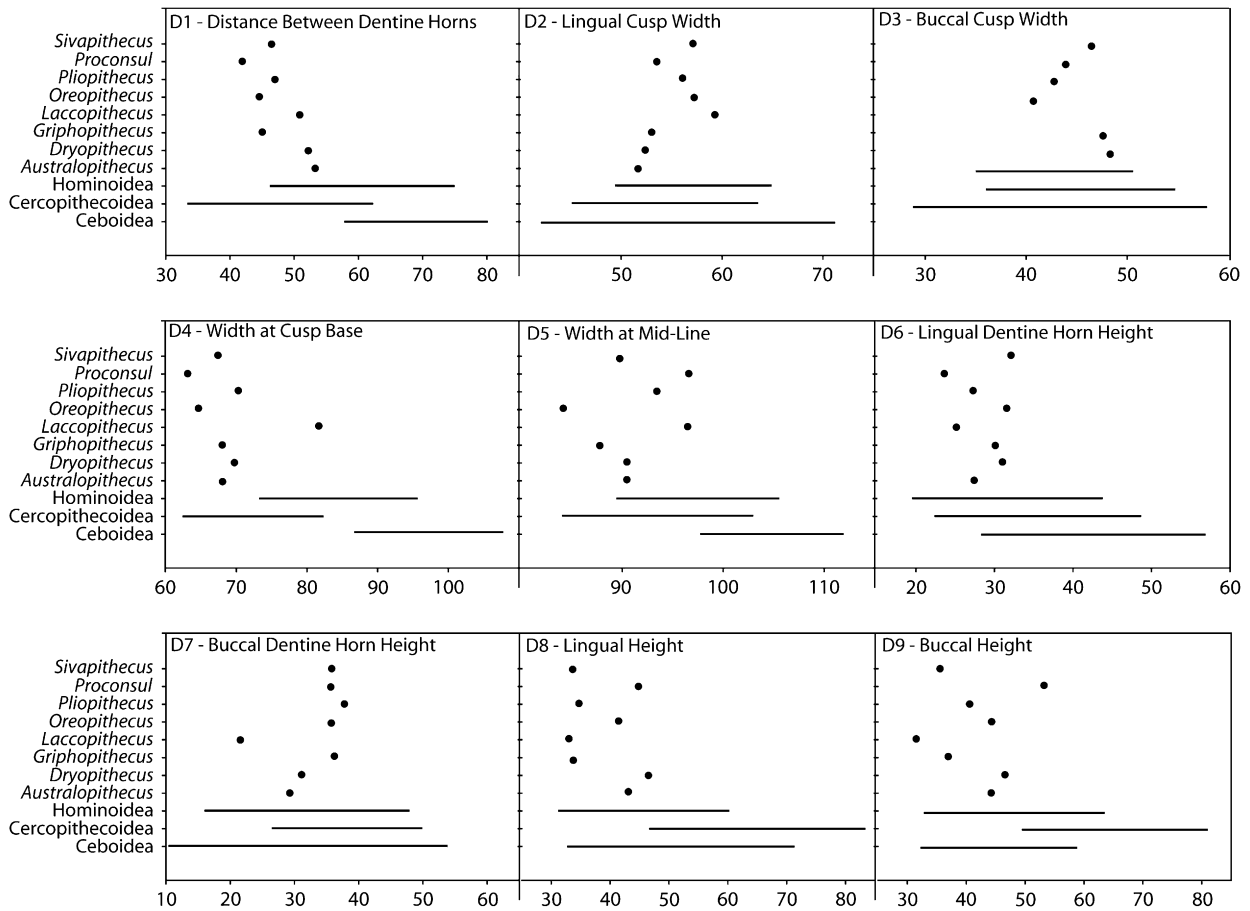


Fig. 7. Plots depicting variation of the nine distance measurements in extant and fossil taxa. In each case, the x-axis represents the distance measurements as defined in Table 2, which are given in terms of the standardized length of the bicervical diameter (=100 units). Bars for Ceboidea, Cercopithecoidea, and Hominoidea represent the entire range of data for these superfamilies. Points for the fossil taxa represent the single molar measured or in the case of *Griphopithecus* and *Sivapithecus*, the mean of the two molars measured. Overlapping ranges among the extant taxa prohibit definitive statements about the closest affinity to an extant superfamily of fossil molars, reinforcing the notion that many measurements must be considered simultaneously for maximum taxonomic discrimination (e.g., DFA analyses).

morphology of colobines (Fig. 2), perhaps representing convergent molar design among folivores.

Heizmann and Begun (2001) noted that *Griphopithecus* molars have relatively short dentine horns (see also Fig. 2), and *Griphopithecus* also has relatively thick molar enamel (Martin, 1983; Smith et al., 2003), a condition also apparent in *Sivapithecus* and *Pongo*. Other primate taxa with relatively short dentine horns (*Pliopithecus*, *Laccopithecus*, Pitheciinae) have relatively thin molar enamel. This combination of characters supports the idea that the earliest Eurasian hominoids (i.e., *Griphopithecus*) may have passed the unique combination of thick molar enamel and short dentine horns on to later Eurasian taxa (e.g., *Pongo*, *Sivapithecus*, *Gigantopithecus*), as proposed by Heizmann and Begun (2001).

The *Australopithecus africanus* molar (Stw 402) is characterized by relatively short dentine horns (Fig. 2), falling in the negative range of the second discriminant function along with *Pongo*, *Homo*, African apes, and colobines (Fig. 6). The first discriminant function did not effectively separate the *Australopithecus* molar from those of cercopithecoids or hominoids, suggesting that, like many of the other fossil molars examined here, this molar shows an intermediate morphology between cercopithecoids and hominoids in terms of relative cusp-width asymmetry and the proximity of the two mesial dentine-horn tips. In a previous analysis (Olejniczak et al., 2004), we found that the two extant African ape genera could not be discriminated based upon cross-sectional EDJ shape, but that *Homo* was distinct from the African ape form. We therefore expected that the *Australopithecus* molar would be distinguishable from the African apes and fall closer to the *Homo* cross-sectional EDJ morphotype, but it appears that this *Australopithecus* molar is not aligned with any of the hominoid genera in particular.

While cross-sectional EDJ shape appears to be a good discriminator of extant taxa at the superfamily level, related characters should also be considered. The thickness of molar enamel may be related to EDJ shape, as the combination of these characters is responsible for patterns of tooth wear. The initiation of enamel and dentine secretion begins along the future EDJ in dental development, so developmental variables may also be correlated with EDJ shape. Future research in this area should concentrate on the relationship of EDJ shape to these other dental variables (e.g., Schwartz et al., 1998). Future research will also benefit from improved imaging techniques, such as synchrotron and laboratory micro-computed tomography, which allow for the EDJ to be accurately visualized without the destruction of valuable fossils and museum specimens (e.g., Kono, 2004; Tafforeau, 2004; Olejniczak and Grine, 2005, 2006; Olejniczak, 2006). Tomographic studies of molars will also allow for the mesiodistal dimension of molars to be measured, rather than all data being reduced to a single plane; the inclusion of a third dimension may substantially increase taxonomic resolution.

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