

Quantification of dentine shape in anthropoid primates

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Summary. The external shape and thickness of the enamel component of primate molars have been employed extensively in phylogenetic studies of primate relationships. The dentine component of the molar crown also has been suggested to be indicative of phylogenetic relationships, but few studies have quantified dentine morphology in order to evaluate this possibility. To explore the utility of dentine shape as an indicator of phylogenetic affinity, a two-dimensional geometric morphometric analysis (EDMA-II) was performed using nine homologous landmarks on a sample of sectioned maxillary molars of extant ceboid, cercopithecoïd, and hominoid primates. Results indicate that dentine shape (the configuration of the enamel-dentine junction, or EDJ) can distinguish taxa at every taxonomic level examined, including superfamilies, subfamilies, and closely related genera and species. This supports the idea that dentine morphology may be useful for phylogenetic studies. It is further suggested that the morphology of the EDJ may be more conservative than enamel morphology, and perhaps better-suited to phylogenetic studies. Among the samples studied, cercopithecoïd primates have a unique dentine shape, and it is suggested that the development of bilophodont molars may be related to the distinctive EDJ configuration in cercopithecoïds.

Key words: Dentine – Enamel-dentine junction – EDJ – EDMA II – Dental evolution – Bilophodont molars

Introduction

The enamel character complex (enamel thickness, developmental aspects of enamel growth, and morphology of the enamel-dentine junction) has emerged as a key component of debates surrounding hominoid phylogenetic relationships (e.g., Martin 1985; Begun et al. 1997; Schwartz 2000). Enamel thickness has routinely been quantified in a standard plane of section, following Martin (1983, 1985), and aspects of enamel development have also been quantified (e.g., Beynon et al. 1998; Smith et al. 2003). The morphology of the enamel-dentine junction (EDJ), however, is typically qualitatively assessed and coded in cladistic analyses (e.g., Begun et al. 1997). Dentine morphology has recently been suggested to be a key character for understanding hominoid migration patterns (Heizmann and Begun 2001), but to date there has been no attempt to quantify this character.

Based on a study of “endocasts” of primate enamel caps from which the dentine had been removed through natural processes, Korenhof (1960, 1961) wrote that the EDJ demonstrates a “greater measure of primitiveness” compared to the enamel surface. Korenhof (1960, 1961) described the evolutionary “stages” through which the primate dentition had developed; importantly, he noted that the dentine surface was almost always more conservative, maintaining an ancestral morphology relative to the modified enamel surface.

In light of Korenhof’s (1960, 1961) findings and the importance of EDJ morphology in recent studies of primate relationships, we attempted to quantify differences in EDJ morphology among extant primates. The goal of the present study was to establish a framework from which to

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explore EDJ shape differences in future studies of phylogenetic relationships, and to provide a means by which to quantify these shape differences.

Materials and Methods

The study sample consisted of maxillary molars of species representing the three extant superfamilies of anthropoid primates; Table 1 displays the sample size for each taxon under consideration. Enamel thickness for each of the samples has been reported elsewhere (hominoids: Martin 1985; cercopithecoids: Ulhaas et al. 1999; ceboids: Martin et al. 2003), so each of the molars had previously been sectioned in a coronal plane through the mesial cusps following the protocol established by Martin (1983, 1985). Figure 1 depicts the morphology of a typical molar cross-section, in which the EDJ (Fig. 1, dashed line) can clearly be distinguished. Each section was photographed, facilitating the identification of homologous landmarks; nine landmarks were identified along the EDJ on each section (Fig. 1). Two-dimensional Cartesian coordinates (x, y) of each landmark were recorded using a digitizing tablet and SigmaScan software (Jandel Scientific).

Euclidean distance matrix analysis (EDMA-II) was used to compare interlandmark distances among the samples. The EDMA-II method requires that specimens are uniformly scaled in order to account for size differences (Lele and Cole 1996). Lele and Cole (1996) recommend that the choice of an *a priori* scaling factor should be based on biological grounds. In the present study, the distance between *landmark 1* and *landmark 9* (i. e., cervical diameter) was chosen as the scaling factor. Martin (1983) posited that the cervical diameter was a suitable choice as a scalar in enamel thickness studies, and Schwartz (2000) argued

that the cervical diameter accounts for tooth size differences among hominoid primates. Grine (2002) found that cervical diameter correlates significantly with dentine area, which is known to have an isometric relationship with both body and tooth size among a wide range of primates (Shellis et al. 1998). Thus, for the purposes of minimizing the confounding effects of tooth size differences between taxa in the present study, *landmark 1* was always considered the origin (0, 0), and the x -axis was taken to run horizontally through *landmark 9*, at point (0, 100) (Fig. 1).

EDMA-II entails the calculation of the mean distance between pairs of landmarks in order to determine whether interlandmark distances (and therefore shape) differ between two samples. A detailed description of EDMA-II methodology is given in Lele and Cole (1996). The null hypothesis in each comparison conducted in the present study was that none of the samples had a different EDJ shape (i. e., no difference in interlandmark distances).

The software package WinEDMA, v1.0.1 beta (Cole 2002), was used to perform all comparisons; WinEDMA software uses bootstrap resampling to obtain significance values relating to the mean form (the average landmark positions) of the taxa in question. In the present study, each analysis was bootstrapped 100 times. WinEDMA elicits two critical pieces of information in order to explore shape differences: first, the Z statistic and its 10% confidence interval indicate whether there is a significant difference in the overall shape of two samples being compared; if the confidence intervals do not contain zero, then the forms are considered to be different and the null hypothesis of equal shapes is rejected (Lele and Cole 1996). Second, WinEDMA produces a shape difference matrix, wherein each difference in interlandmark distance between the two samples being compared

Table 1. Samples Included in This Study

Taxon	M ¹	M ²	M ³	Total
Ceboidea				
<i>Aotus trivirgatus</i>	2	1	0	3
<i>Ateles paniscus</i>	2	2	2	6
<i>Cacajao calvus</i>	0	1	0	1
<i>Chiropotes satanus</i>	0	1	0	1
<i>Pithecia pithecia</i>	2	0	0	2
Cercopithecoidea				
Colobinae				
<i>Colobus polykomos</i>	0	14	0	14
<i>Ptilocolobus badius</i>	0	8	0	8
<i>Procolobus verus</i>	0	2	0	2
Cercopithecinae				
<i>Cercopithecus campbelli</i>	0	24	0	24
<i>Cercopithecus diana</i>	0	2	0	2
<i>Cercopithecus erythrotis</i>	0	1	0	1
<i>Cercopithecus nictitans</i>	0	4	0	4
<i>Papio ursinus</i>	0	7	0	7
Hominoidea				
<i>Gorilla gorilla</i>	3	3	3	9
<i>Homo sapiens</i>	3	1	3	7
<i>Pan troglodytes</i>	3	3	1	7
<i>Pongo pygmaeus</i>	2	4	3	9
Total Sample =	17	78	12	107

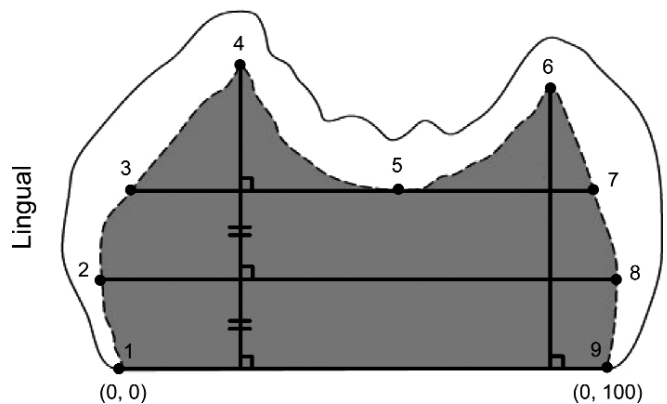


Fig. 1. Cross-section through the mesial cusps of a maxillary molar. Dashed line is the EDJ. Landmarks are defined as follows: 1) tip of the lingual enamel cervix; 2) lingual intersection of the EDJ and a line parallel to the cervical diameter and bisecting the length between the cervical diameter and *landmark 5*; 3) lingual intersection of the EDJ and a line parallel to the cervical diameter and running through *landmark 5*; 4) protocone dentine cusp tip; 5) lowest point of the EDJ between the protocone and paracone cusp tips; 6) paracone dentine cusp tip; 7) buccal intersection of the EDJ and a line parallel to the cervical diameter and bisecting the length between the cervical diameter and *landmark 5*; 8) buccal intersection of the EDJ and a line parallel to the cervical diameter; 9) tip of the buccal enamel cervix. *Landmark 1* was made to lie at (0, 0) and *landmark 9* at (0, 100) in every specimen examined in order to account for differences in tooth size.

Table 2. Results of Shape Comparisons; H_0 : there is no difference in mean shape.

Taxa Compared	Z	10% C.I.		Reject H_0 ?
		Lower	Upper	
Ceboidea v. Cercopithecoidea	0.265	0.231	0.290	Yes
Ceboidea v. Hominoidea	0.164	0.132	0.198	Yes
Cercopithecoidea v. Hominoidea	0.201	0.179	0.218	Yes
Colobinae v. Cercopithecinae	0.110	0.089	0.139	Yes
<i>Procolobus</i> vs. <i>Colobus</i>	0.244	0.203	0.335	Yes
<i>Colobus</i> vs. <i>Piliocolobus</i>	-0.140	-0.171	-0.114	Yes
<i>Procolobus</i> vs. <i>Piliocolobus</i>	0.204	0.161	0.303	Yes
<i>Homo</i> vs. <i>Gorilla</i>	-0.099	-0.078	-0.141	Yes
<i>Cercopithecus</i> v. <i>Papio</i>	-0.186	-0.160	-0.221	Yes
<i>Gorilla</i> vs. <i>Pan</i>	0.080	-0.134	0.125	No
<i>Pongo</i> vs. <i>Gorilla</i>	-0.167	-0.187	-0.147	Yes
<i>Homo</i> vs. <i>Pan</i>	-0.138	-0.172	-0.102	Yes
<i>Pongo</i> vs. <i>Homo</i>	0.129	0.107	0.151	Yes
<i>Pongo</i> vs. <i>Pan</i>	-0.097	-0.141	-0.068	Yes
<i>C. diana</i> vs. <i>C. nictitans</i>	0.241	0.205	0.280	Yes
<i>C. campbelli</i> vs. <i>C. nictitans</i>	0.115	0.087	0.148	Yes
<i>C. diana</i> vs. <i>C. campbelli</i>	0.151	0.115	0.206	Yes

is estimated, along with a 10% confidence interval; if the confidence interval does not contain zero, then that interlandmark distance is significantly different between the two samples (Lele and Cole 1996). The shape difference matrix thus allows for individual interlandmark distances to be examined in order to understand the direction of the change in distance between the two samples being compared (e.g., greater distance between a pair of landmarks in sample 1 than in sample 2, or *vice versa*) without regard to whether the overall forms are significantly different.

Shape comparisons were conducted at the following taxonomic levels in order to explore changes in dentine shape in anthropoid evolution: 1. Superfamily (Ceboidea vs. Cercopithecoidea, Ceboidea vs. Hominoidea, Cercopithecoidea vs. Hominoidea); 2. Subfamily (Cercopithecinae vs. Colobinae); 3. Genus (compared 3 colobine genera, compared two cercopithecine genera, and compared four hominoid genera). 4. Species (compared 3 species within genus *Cercopithecus*).

Results

Table 2 lists the results of the Z-statistic analysis for all of the comparisons (a complete set of shape difference matrices and statistics is available from the author of correspondence). Comparisons among the three superfamilies were all statistically significant. A plot of the average (x, y) coordinates within each superfamily (Fig. 2 a), however, indicates that cercopithecoids have the most distinct shape, with relatively tall dentine cusps (*landmarks 4* and *6*) and with the protocone dentine tip (*landmark 4*) nearer to the midline of the tooth than is the case in the more symmetrical ceboid and hominoid average shapes. In each of the superfamilies the midpoint of the midoc-

clusal basin (*landmark 5*) is located towards the buccal side of the tooth (at ~55–60 on the x-axis; Fig. 2 a), such that the lingual side of the tooth accounts for a greater percentage of the entire width of the molar crown.

The comparison between the Old World monkey subfamilies Colobinae and Cercopithecinae demonstrated significant differences in dentine shape. Figure 2 b depicts the average dentine shape of colobine and cercopithecine molars, with the average ceboid shape included in order to represent the probable ancestral condition. Both colobine and cercopithecine molars have taller dentine cusp tips than ceboids. The cercopithecine molars, however, have a more centrally placed protocone dentine tip (*landmark 4*) than the colobines. Additionally, the cercopithecines have a slightly lower mid-occlusal basin (*landmark 5*) than the colobines, rendering their dentinal inter-cuspal furrow relatively narrow and deep compared to both the ceboids and the colobines.

The three colobine genera were statistically distinguishable based on dentine shape (Fig. 2 c). *Procolobus* molars are distinctively symmetrical relative to those of *Colobus* and *Piliocolobus*, both of which demonstrate a more medial placement of the protocone dentine tip (*landmark 4*). The two cercopithecine genera, *Papio* and *Cercopithecus*, were statistically significantly different in dentine shape. Figure 2 d depicts, however, that the difference between these two genera is primarily accounted for by a difference in the height of the dentine cusp tips (*landmarks 4* and *6*). *Papio* molars have tall dentine cusps compared to *Cercopithecus* molars, and consequently the *Papio* molars have a relatively deeper dentinal inter-cuspal furrow. The molars of both *Papio* and *Cercopithecus* are characterized by a lingual dentine tip (*landmark 4*) that is placed medially, near to the midocclusal basin (*landmark 5*), causing the dentine shape to be asymmetrical.

Among the hominoid genera, the only dyad that could not be distinguished based on dentine shape was *Gorilla* and *Pan*. Figure 2 e depicts the average dentine shape of each hominoid genus. Although *Pongo* and *Homo* molars were significantly different from one another, the way in which they differ from molars of *Pan/Gorilla* was similar. *Pongo* and *Homo* molars were found to have *landmarks 6, 7, and 8* located more medially than in *Pan* and *Gorilla*. As reported by Martin (1983), *Pongo* molars have shorter dentine tips (*landmarks 4* and *6*) than the other hominoids, creating a broad and shallow dentinal inter-cuspal furrow; *Homo*, *Pan*, and *Gorilla* molars each have taller dentine tips and more medially placed lingual dentine tips (*landmark 4*).

Comparisons between the molars of three species within the genus *Cercopithecus* were statistically significant. Figure 2 f, however, demonstrates that these differences were largely based on the height of the tooth relative to the cervical diameter. *Landmark 2* and *landmark 8* were in approximately the same position in all three taxa, but *landmarks 3-6* were higher in molars of *Cercopithecus campbelli* than in *Cercopithecus nictitans*, and higher still in *Cercopithecus diana*.

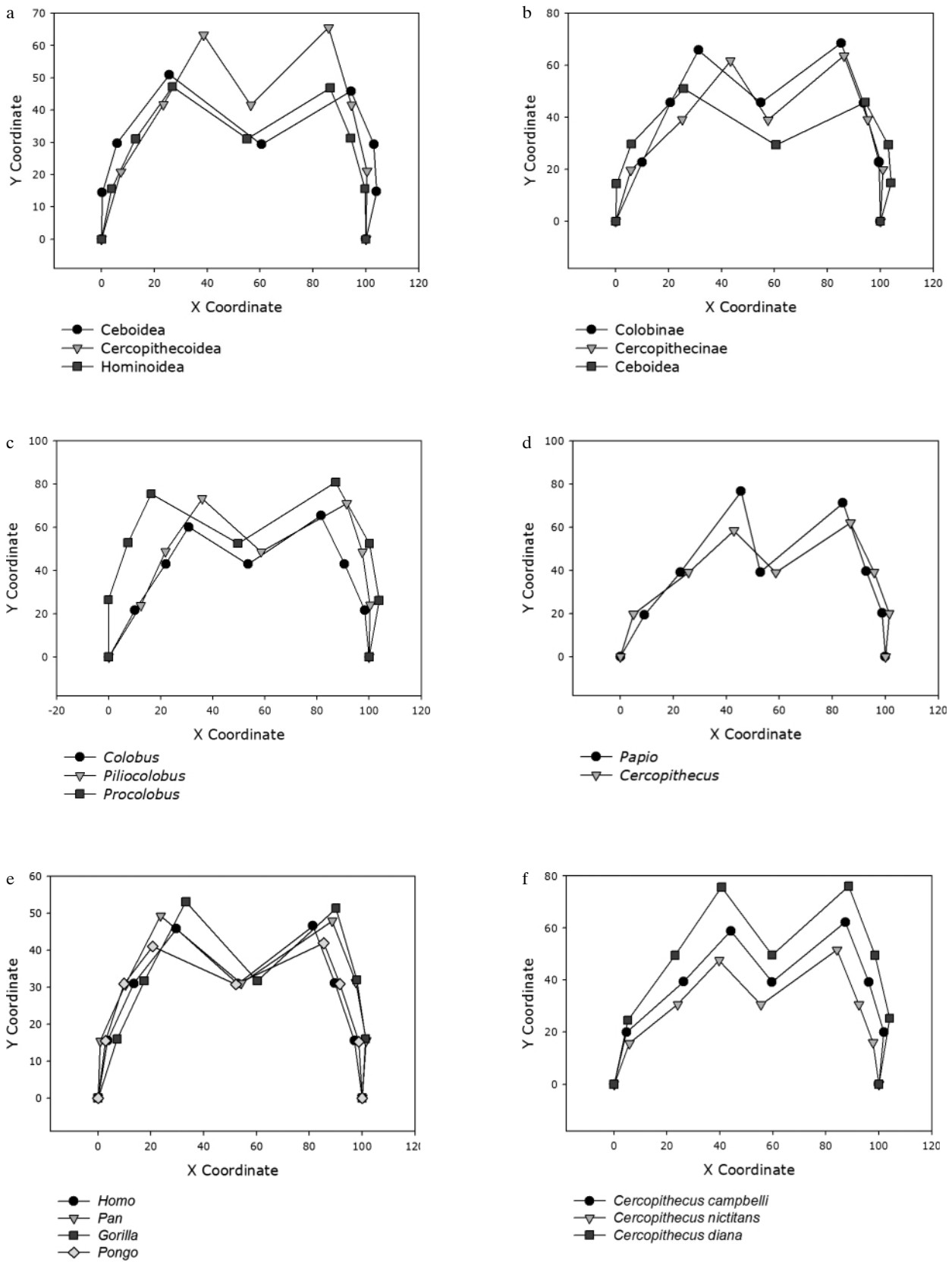


Fig. 2. The average dentine shape landmark coordinates for the comparisons explored in this study. *a)* anthropoid superfamilies; *b)* colobines, cercopithecines, and ceboids; *c)* three colobine genera; *d)* two cercopithecoid genera; *e)* four hominoid genera; *f)* three *Cercopithecus* species.

Discussion

Taxonomic Comparisons. Our results indicate that comparisons of dentine shape can distinguish taxa at levels from the superfamily to the species. The significance of the comparisons among three species within the genus *Cercopithecus* should be treated with caution, however, because the differences stem from tooth height relative to tooth width, rather than on differences in specific landmark configurations. The three *Cercopithecus* species exhibit those traits that distinguish cercopithecines from colobines (centrally placed dentine protocone tip and low midocclusal basin, creating a deep and narrow dentinal inter-cuspal furrow), but they appear to be a gradient of inter-cuspal furrow), but they appear to be a gradient of different molar heights rather than distinct shapes. A different choice of landmark analysis, perhaps one that does not require a scalar to be chosen *a priori*, may not have found these three species to be significantly different (discussed in Rohlf 2000).

Development of Bilophodont Molars. Cercopithecoids demonstrate a unique dentine morphology, characterized by tall dentine tips that are close together (Fig. 2 a). The approximation of lingual and buccal cusps results in a relatively deep and narrow dentinal inter-cuspal furrow. The evolution of bilophodont molars, a quintessential cercopithecoid trait, may be partially explained in terms of this unique dentine configuration. If the relative amount of occlusal enamel on a basic anthropoid molar (the configuration seen in ceboids and hominoids; Fig. 3 a) stays constant while the cusp tips move closer together and become taller, then the enamel will “fill in” the inter-cuspal furrow (Fig. 3 b), creating a ridge (i. e., a loph) connecting the two cusp tips.

If this is the case, then the enamel in the inter-cuspal furrow should be thickest in the midline of the tooth, where the enamel has been most severely compressed into a narrower space. In fact, Ulhaas et al. (1999, Tab. 2) report that among cercopithecoids, the midocclusal enamel is thicker than the enamel lateral to it on either side (Fig. 3 b, dashed lines in the occlusal enamel; Fig. 3d). In contrast, among the hominoid maxillary molars studied by Martin (1983: Appendix A, measurements *h*, *i*, and *j*), there is no tendency for the midocclusal enamel to be thicker, and it is often thinner than the enamel lateral to it. Among ceboids (Martin et al. 2003) the midocclusal enamel is mostly the same thickness or thinner than enamel measured lateral to it, and only occasionally it is slightly thicker. The development of bilophodont molars in cercopithecoids may thus be facilitated by a change in the configuration of the EDJ, rather than of the enamel itself.

Among cercopithecoids, cercopithecine molars exhibit the greatest migration of the protocone towards the midline, the deepest dentinal inter-cuspal furrow, and thus the greatest compression of occlusal enamel into the inter-cuspal furrow. Measurements of (enamel) cusp proximity have been used to identify functional implications (e. g., Kay 1978; Kay and Covert 1984), close cusps being indicative of frugivory. Nonetheless, the origin of cercopithecoid bilophodont molars has always been assumed to be related to the development of folivory (Delson 1975; Andrews 1981), providing greater shearing capacity to slice leaves. Other functional analyses, however, demonstrate that cercopithecoid bilophodonty is related to increasing grinding surfaces and developing wedge-like cusp slopes in order to facilitate the fracture of seeds and

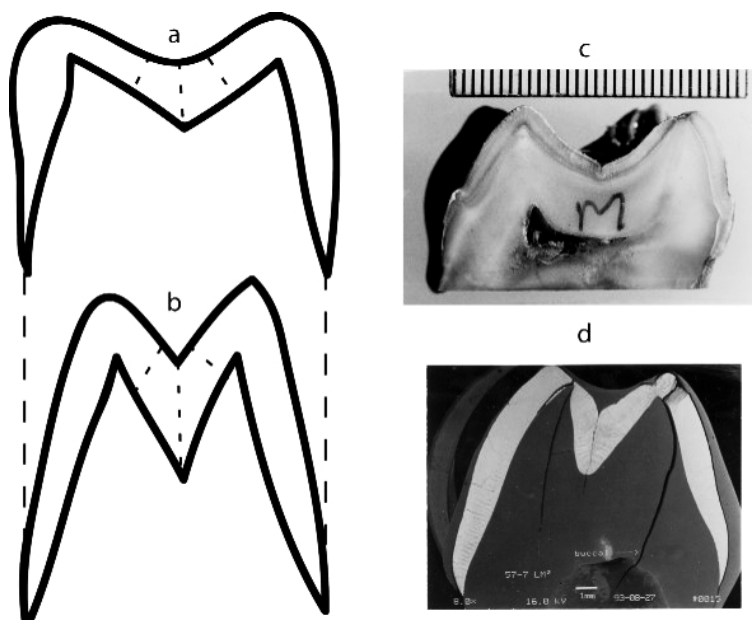


Fig. 3. *a* and *b* demonstrate the effects of changing the shape of a hominoid or ceboid molar cross-section (*a*) to increase the height of the dentine horns and bring them closer together as in cercopithecoids (*b*). Dashed lines in the occlusal enamel demonstrate that the midline of the occlusal enamel should become thicker than the enamel lateral to it. *c* and *d* show these different molar configurations in the molars of *Gorilla* (*c*) and *Papio* (*d*).

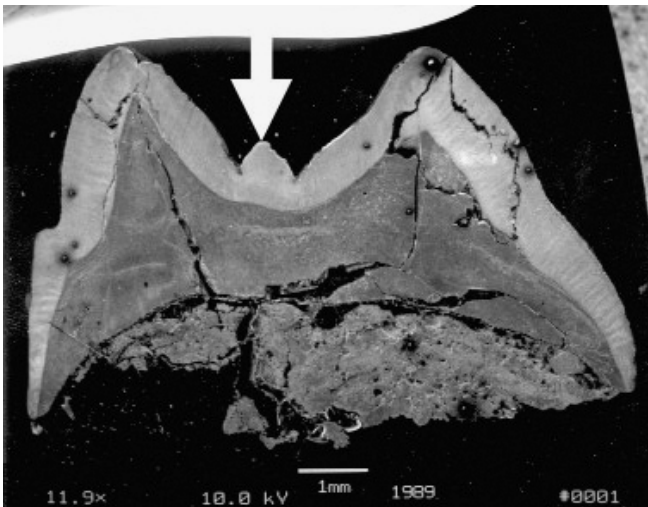


Fig. 4. Cross-section of a maxillary molar of the Miocene hominoid *Oreopithecus* (BM11565). The white arrow points to an accessory cusp (metaconule) that has no dentinal counterpart.

other hard, brittle food (Happel 1988; Lucas and Teaford 1994). Other derived cercopithecoid dental and facial features support this theory of adaptation to high occlusal forces produced during fracturing of hard fruit or seed coatings, which is consistent with the general assumption that the common ancestor of all cercopithecoids was a frugivore (Benefit 1999). The data presented above are commensurate with this hypothesis, because the greatest constriction of the inter-cuspal furrow is in the mostly frugivorous and grammivorous cercopithecines, not the largely folivorous colobines.

Enamel Surface-EDJ Correlations. There does not appear to be a predictive relationship between dentine topography (the EDJ surface) and enamel topography. Kraus (1952) studied differences in enamel and dentine shape in human molars, finding little correspondence between the enamel and dentine surfaces. This is further evidenced by maxillary molars of the Miocene hominoid *Oreopithecus*, which have a derived central enamel cusp, under which there is no corresponding dentine cusp (Fig. 4). It is nota-

ble that, in a study of maxillary molar enamel thickness distribution, Schwartz (2000) found significant differences between *Pan* and *Gorilla*, which the present study of EDJ shape has failed to do. Perhaps this indicates that while molar enamel has adapted to the different dietary regimes of these taxa, the underlying dentine shape has remained conservative (*sensu* Korenhof 1960).

In the present study, it was noticed that the molars of *Papio ursinus* variably express a “dentine cingulum” in which the lingual side of the tooth has a “shelf” of dentine near the lingual cervix (Fig. 5 a, arrow). This change in dentine surface topography is apparent among all of the *Cercopithecus* specimens, but not among the colobines or ceboids. Interestingly, the molars from species of the genus *Cercopithecus* demonstrate a concomitant change in the shape of the enamel surface, wherein the enamel essentially follows the same path as the dentine (Fig. 5 b, dashed line). In *Papio ursinus* molars, the enamel does not follow the same path as the dentine, but rather has “filled in” the indentation created by the dentine shelf, causing differences in the shapes of the dentine and enamel surfaces (Fig. 5 a, dashed line). This may indicate that *Papio ursinus* has the ancestral EDJ configuration for cercopithecines, but has changed the morphology of its enamel surface. When this is considered in light of the evidence presented in Korenhof (1960, 1961) and Kraus (1952), dentine may indeed be better suited to the study of phylogenetic relationships than enamel because it conserves ancestral morphology.

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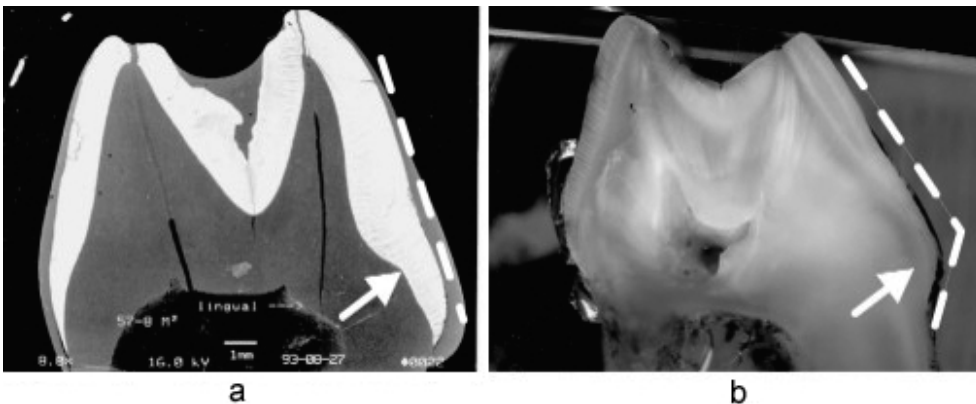


Fig. 5. White arrows point to the “dentine cingulum” expressed in *Papio* and *Cercopithecus*. In the molar of *Papio* (left), the enamel does not follow the same path as the EDJ, but instead follows a straight course from the cusp tip to near the cervix (dashed line). In the molar of *Cercopithecus* (right), the enamel follows the same course as the dentine (dashed line).

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