

Brief Communication: Contributions of Enamel-Dentine Junction Shape and Enamel Deposition to Primate Molar Crown Complexity

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ABSTRACT Molar crown morphology varies among primates from relatively simple in some taxa to more complex in others, with such variability having both functional and taxonomic significance. In addition to the primary cusps, crown surface complexity derives from the presence of crests, cuspules, and crenulations. Developmentally, this complexity results from the deposition of an enamel cap over a basement membrane (the morphology of which is preserved as the enamel-dentine junction, or EDJ, in fully formed teeth). However, the relative contribution of the enamel cap and the EDJ to molar crown complexity is poorly characterized. In this study we examine the complexity of the EDJ and enamel surface of a broad sample of primate (including fossil

hominin) lower molars through the application of micro-computed tomography and dental topographic analysis. Surface complexity of the EDJ and outer enamel surface (OES) is quantified by first mapping, and then summing, the total number of discrete surface orientation patches. We investigate the relative contribution of the EDJ and enamel cap to crown complexity by assessing the correlation in patch counts between the EDJ and OES within taxa and within individual teeth. We identify three patterns of EDJ/OES complexity which demonstrate that both crown patterning early in development and the subsequent deposition of the enamel cap contribute to overall crown complexity in primates. Am J Phys Anthropol 142:157–163, 2010. © 2010 Wiley-Liss, Inc.

The occlusal surface of primate molar crowns can be simple, possessing only the primary cusps, or it can be complex, exhibiting numerous morphological features including additional accessory cusps, cuspules, crests, and crenulations. Variation in such features and overall complexity is utilized in both primate systematics and functional morphology, but the interpretation of this variation requires an accurate understanding of its developmental origin.

Tooth crown morphology is the culmination of two phases of development. The first is the patterning phase of development when species-specific cusp patterns appear on the basement membrane (also called the *membrana praeformativa*) located between the dental papilla and overlying inner enamel epithelium. The second phase is the deposition of dentine below and enamel above this basement membrane (Butler, 1956; Kraus and Jordan, 1965; Jernvall and Jung, 2000; Jernvall and Thesleff, 2000; Cobourne and Sharpe, 2003; Tafforeau et al., 2007). The enamel-dentine junction (EDJ) of fully

formed teeth is a proxy of the first phase and the enamel cap is a proxy of the second.

Previous studies have indicated that many features of the tooth crown originate at the EDJ prior to enamel

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TABLE 1. Patch count results (mean \pm SD) for EDJ and OES for each taxon

Taxon	Sample size <i>n</i> = EDJ/ <i>n</i> = OES	Mean EDJ patch count ^a	Mean OES patch count	OES/EDJ patch count ^b
<i>Homo sapiens</i>	15/7	118 \pm 14	120 \pm 14	1.00 \pm 0.07
<i>Homo neanderthalensis</i>	26/10	145 \pm 21	135 \pm 26	0.99 \pm 0.17
<i>Paranthropus robustus</i>	11/4	102 \pm 9	98 \pm 13	0.93 \pm 0.09
<i>Australopithecus africanus</i>	11/7	116 \pm 26	117 \pm 15	1.01 \pm 0.09
<i>Pan paniscus</i>	20/4	90 \pm 12	133 \pm 49	1.50 \pm 0.49
<i>Pan troglodytes</i>	33/9	93 \pm 15	158 \pm 42	1.70 \pm 0.30
<i>Gorilla</i>	5/1	89 \pm 10	111	1.29
<i>Pongo</i>	16/8	159 \pm 39	306 \pm 48	1.73 \pm 0.27
<i>Hylobates</i>	4/2	67 \pm 12	63 \pm 12	1.06 \pm 0.07
<i>Sympalangus</i>	11/4	67 \pm 6	63 \pm 2	0.95 \pm 0.06
<i>Presbytis</i>	5/1	71 \pm 3	90	1.28
<i>Cercopithecus</i>	4/2	63 \pm 6	52 \pm 2	0.90 \pm 0.08
<i>Chiropotes</i>	6/3	79 \pm 11	193 \pm 9	2.30 \pm 0.18

^a Values in bold indicate statistically significant differences between mean EDJ and mean OES patch count below $P = 0.05$.

^b Ratio = OES patch count/EDJ patch count. Mean ratio calculated for specimens having an unworn enamel surface (*n* = OES in sample size column).

Sample details: *Homo sapiens*: National Museum of Natural History, Washington, USA; Royal Belgian Institute of Natural Sciences, Belgium; University of Liège, Belgium; *Homo neanderthalensis*: Krapina (D1, D6, D10, D77, D79, D80, D81, D86, D105, D107, 52, 53, 54, 55, 57); La Chaise-Abri Suard (5, 49); Le Moustier 1; Roc de Marsal, La Quina (Q760 H9); Scladina (4A1); El Sidrón (SD540, 755); *Paranthropus robustus*: Drimolen (DNH60B, DNH60C), Gondolin (GDA2), Swartkrans (SK104, SK1587B, SK1, SK3974, SK6, SK828, SK843, SK846A); *Australopithecus africanus*: Sterkfontein (STS9, STW145, STW213, STW296, STW309A, STW412B, STW421A, STW424, STW537, STW560E). Nonhominin primates: Royal Museum for Central Africa, Tervuren, Belgium; Museum für Naturkunde, Berlin, Germany; Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; National Museum of Natural History, Washington, USA; Senckenberg Museum, Frankfurt, Germany.

deposition. For example, Schwarz (1927: Fig. 410, p. 724) noted the correspondence between crests on the enamel surface and the EDJ in a single histological thin section of a chimpanzee lower molar. Weidenreich (1937, 1945) noted a correspondence between the EDJ and outer enamel surface (OES) in a cross-section of a *Homo erectus* molar and argued that OES features tended to have an EDJ component. Kraus and Oka (1967) examined a small sample of *Pongo*, *Gorilla*, *Pan* and modern human fetal tooth germs and noted “wrinkling” of the inner enamel epithelium prior to calcification. Korenhof's (1960, 1961, 1982) seminal studies of EDJ/OES correspondence established that external crown features often derived from the EDJ. Corruccini (1987, 1998) noted a general correspondence of features between the OES and EDJ, but with exceptions and modifications in some taxa (particularly modern humans). Finally, Skinner et al. (2008, 2009) determined that a number of discrete dental traits (e.g., accessory cusps and crests) were evident at the EDJ and that enamel deposition modifies traits, rather than eliminating or generating them.

Despite these findings the relative contribution of the EDJ and enamel cap to the developmental origin of features affecting the complexity of occlusal crown morphology remains poorly characterized. In particular, it is unclear whether patterns of development are consistent across a variety of primate taxa. In this study, we employ conventional and synchrotron micro-computed tomography to produce high-resolution images of the EDJ and OES of lower molars from a variety of primate taxa, including fossil hominins. Using dental topographic analysis, the complexity of each surface is quantified and the extent of the correlation between the EDJ and OES is assessed both within taxa and within individual teeth.

The results of our analysis indicate that patterns of EDJ/OES complexity differ among primate taxa in the degree to which crown patterning early in development and the subsequent deposition of the enamel cap contribute to overall crown complexity. These results improve

our understanding of when taxonomically and functionally relevant morphology appears during the development of the tooth germ and have implications for how the EDJ can be used as a proxy for the OES in worn teeth.

MATERIALS AND METHODS

The study sample is composed of first and second lower molars (*n* = 167) from extant and extinct hominoids as well as two Old World monkey and one New World monkey species (Table 1). Given the limited availability of unworn molars in both the fossil record and museum collections, the sample size of EDJ surfaces exceeds that of outer enamel surfaces. Individual hominin specimens and museum collections from which the sample is derived are listed in Table 1.

Micro-computed tomography and surface generation

To produce three-dimensional surface models of the EDJ and OES (when unworn), each tooth was subjected to conventional or synchrotron micro-computed tomography [scan voxel sizes ranging from 7 (e.g., for *Chiropotes* molars) to 61 microns (e.g., for *Gorilla* molars)]. To facilitate tissue segmentation, the complete image stack for each tooth was filtered using a three-dimensional median filter (kernel size of three) followed by a mean of least variance filter (kernel size of three), implemented as a computer-programmed macro. Filtering results in more homogenous tissue classes (e.g., enamel and dentine) and enhances tissue borders through the adjustment of pixels with intermediate grayscale values at air-enamel, enamel-dentine, and air-dentine interfaces (Schulze and Pearce, 1994). Filtered image stacks were segmented into enamel and dentine tissues in the Amira software package using both automated and manual processing.

After segmentation, surface models of the OES and EDJ were generated and each model was rotated to approximate anatomical position of the tooth in the occlusal plane (note: EDJ and OES models from the same tooth were rotated simultaneously as a single unit). Using Geomagic Studio (v10) the cervix region of each surface was removed in a plane parallel to the occlusal surface and immediately below the lowest point of the occlusal basin. Each surface was smoothed (relax polygons module), reduced to one hundred thousand triangles (decimate module), and converted to a text file of x , y , z coordinates. Decimating the number of triangles in each surface was not found to differentially affect the mapping of small features on either very large or very small teeth.

Dental topographic analysis

Dental topographic analysis was conducted using Surfer Manipulator software written by and available from Alistair Evans (Evans et al., 2007). The morphological features (i.e., cusps, cuspules, crests, and crenulations) on the EDJ and (if unworn) OES of each specimen were captured by mapping their differing orientations as follows. Using the x , y , z coordinates of each surface a digital elevation model was interpolated in the form of a grid. Next, regions of each surface not visible in occlusal view (e.g., undercuts located deep within enamel fissures) were removed. To standardize for differences in molar size, the grid of each digital elevation model was represented by 150 data rows (meaning that the mesio-distal dimension of each tooth was represented by the same number of rows in the grid). The orientation mapping function of the Surfer Manipulator software classifies each cell of the digital elevation model into one of eight groups (each representing 45 degrees of a circle). It then identifies patches that are composed of a minimum of six contiguous cells having the same orientation. For example, a small cusp that approximates the shape of a half sphere would have eight patches as compared with a mesio-distally oriented crest which would have two patches. The number of morphological features, or overall complexity, can thus be quantified as the orientation patch count on each surface, with molars having smooth, uncomplicated surfaces exhibiting fewer patches than molars exhibiting large numbers of accessory cusps, crests, and crenulations (see Fig. 1).

We compared the patch count at the EDJ with the patch count at the OES for each taxon. For the smaller subset of molars for which an unworn OES was present, we also compared the OES and EDJ patch counts directly as a ratio between the two surfaces (OES patch count/EDJ patch count). Our predictions were that patch count would not differ significantly between the OES and EDJ surfaces within taxa, and that there would be an approximately one-to-one ratio of OES to EDJ patch count within unworn individual molars. Similar patch counts at each surface would suggest that features form early in development (on the basement membrane/future EDJ) and remain present at the OES after enamel deposition. A decrease in complexity at the OES compared with the EDJ would indicate that enamel deposition is obscuring EDJ features, while an increase would indicate that enamel deposition is adding additional features to those present at the EDJ. Differences in average patch count were tested using the non-parametric Mann-Whitney U statistic. Statistical analyses were conducted

using SPSS 15. It is important to note that this method generates a single value of surface complexity (i.e., the patch count of each surface) and cannot address the relative contribution of the EDJ and enamel cap to individual morphological features, such as a specific cusp or crest.

RESULTS

Table 1 lists the mean patch count of the EDJ and OES for each taxon and the mean ratio of EDJ/OES intratooth patch count for molars preserving both surfaces. Figure 2 presents box and whisker plots of EDJ and OES patch count for each taxon. For the majority of taxa, patch count at the OES does not differ significantly from that at the EDJ. *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes* exhibit an increase in patch count at the OES, being most marked in *Pongo*. This increase was statistically significant ($P < 0.01$) in *Pongo* and *Pan troglodytes*. It appears that the crenulated enamel of these taxa (expressed most strongly in *Pongo*) originates at the EDJ and is accentuated, sometimes markedly, through the deposition of enamel (see also surface models of the *Pan troglodytes* and *Pongo* molars in Fig. 1). *Chiropotes* exhibits a unique pattern among the study taxa, having a relatively featureless EDJ but a markedly complex OES (the patch count at the OES is twice that at the EDJ, more than doubling after enamel deposition). Thus, the crenulated enamel of *Chiropotes* develops through enamel deposition with no EDJ contribution to the crenulation pattern.

Comparisons of patch count within individual molars (mean ratio values in Table 1) exhibit a similar pattern with *Homo*, *Paranthropus*, *Australopithecus*, *Hylobates*, *Sympalangus*, and *Cercopithecus* having a ratio around 1.0 (i.e., approximately equal patch counts at the OES and EDJ). In contrast *Pan paniscus*, *Pan troglodytes*, and *Pongo*, with mean ratios of ~1.50, 1.70, and 1.73 respectively, exhibit an increase in patch count with enamel deposition. *Chiropotes* exhibits an even greater increase in patch count with enamel deposition (mean ratio of ~2.30). *Gorilla* and *Presbytis* exhibit a slight increase of complexity with enamel deposition; however, analyses of more unworn enamel surfaces are required for these taxa.

DISCUSSION

The results of this analysis demonstrate three different patterns among the study taxa in the relative contribution of the EDJ and the enamel cap to crown complexity. In the first pattern the presence of morphological features on lower molars appears to derive primarily from the EDJ, with enamel deposition having little or no effect on the degree of complexity on the OES. This is consistent with previous analyses of discrete dental traits that also highlighted the predominant role of the EDJ in their origin and degree of expression (Korenhof, 1960, 1961, 1982; Nager, 1960; Sakai and Hanamura, 1973; Kimura et al., 1977; Corruccini, 1998; Sasaki and Kanazawa, 1999; Skinner, 2008; Skinner et al., 2008, 2009). From a developmental perspective, this indicates that many morphological features originate during the growth and folding of the basement membrane and prior to the differentiation of ameloblasts and odontoblasts and their subsequent secretion of enamel and dentine. Although not tested explicitly in this study,

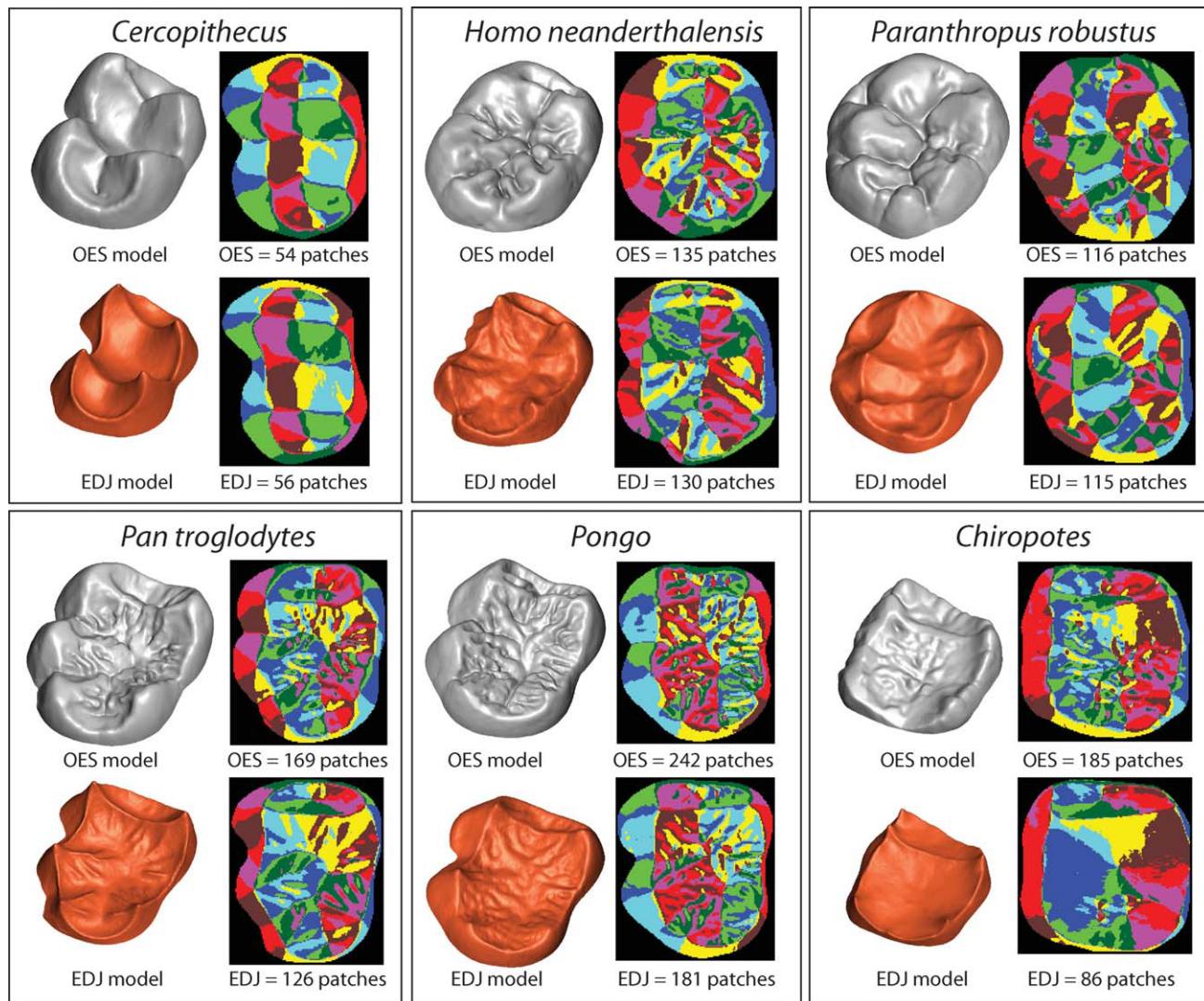


Fig. 1. Surface models and orientation patch maps of the outer enamel surface (OES) and enamel-dentine junction (EDJ) of a selected lower molar from six of the study taxa. *Cercopithecus*, *Homo neanderthalensis* (Krapina D10), and *Paranthropus robustus* (SK 3974) illustrate the most common condition in which enamel deposition neither adds or removes a significant number of features to those present at the EDJ (although these taxa differ in absolute patch count). *Pan troglodytes* and *Pongo* exhibit an increase in patch count at the OES representing an accentuation of features present at the EDJ. Unique among the study taxa is *Chiropotes satanas* which exhibits a significant increase in patch count at the OES which can only be attributed to enamel deposition.

it is noteworthy that the similarity in the number of EDJ and OES features is consistent among primates of widely disparate enamel thickness (Olejniczak et al., 2008) indicating that EDJ features can be manifest at the OES even after the deposition of a very thick enamel cap (e.g., see the *Paranthropus* molar in Fig. 1). Comparing modern humans to Neanderthals, our results support the conclusion that the latter exhibit inherently more complex occlusal morphology at the EDJ ($P < 0.01$) (Macchiarelli et al., 2006). One aspect of tooth crown morphology which is altered with enamel deposition is surface slope. Particularly in thick-enameled taxa, the slope of the dentine horns, which tend to be flat or even concave, can become convex at the OES. The effect of enamel deposition to changes in the slope of features at the OES awaits future investigation.

In the second pattern, present in *Pongo* and *Pan*, the increase in morphological features via enamel deposition is best characterized as an expansion of features already present at the EDJ. That is, while the number of features of the OES is increased, the pattern of features appears similar to that at the EDJ (see crest patterning on the *Pan* and *Pongo* molars in Fig. 1). Additional features that appear on the OES arise in areas of the EDJ that are already moderately complex (e.g., wrinkled). New features do not seem to appear in smooth, low-complexity areas outside the talonid and trigonid basins. In essence, the higher complexity areas of the EDJ are being accentuated on the OES. This increase in features at the OES is caused by the action of ameloblasts and is evidence for enamel deposition playing a role in forming the external morphology of the crown in these taxa.

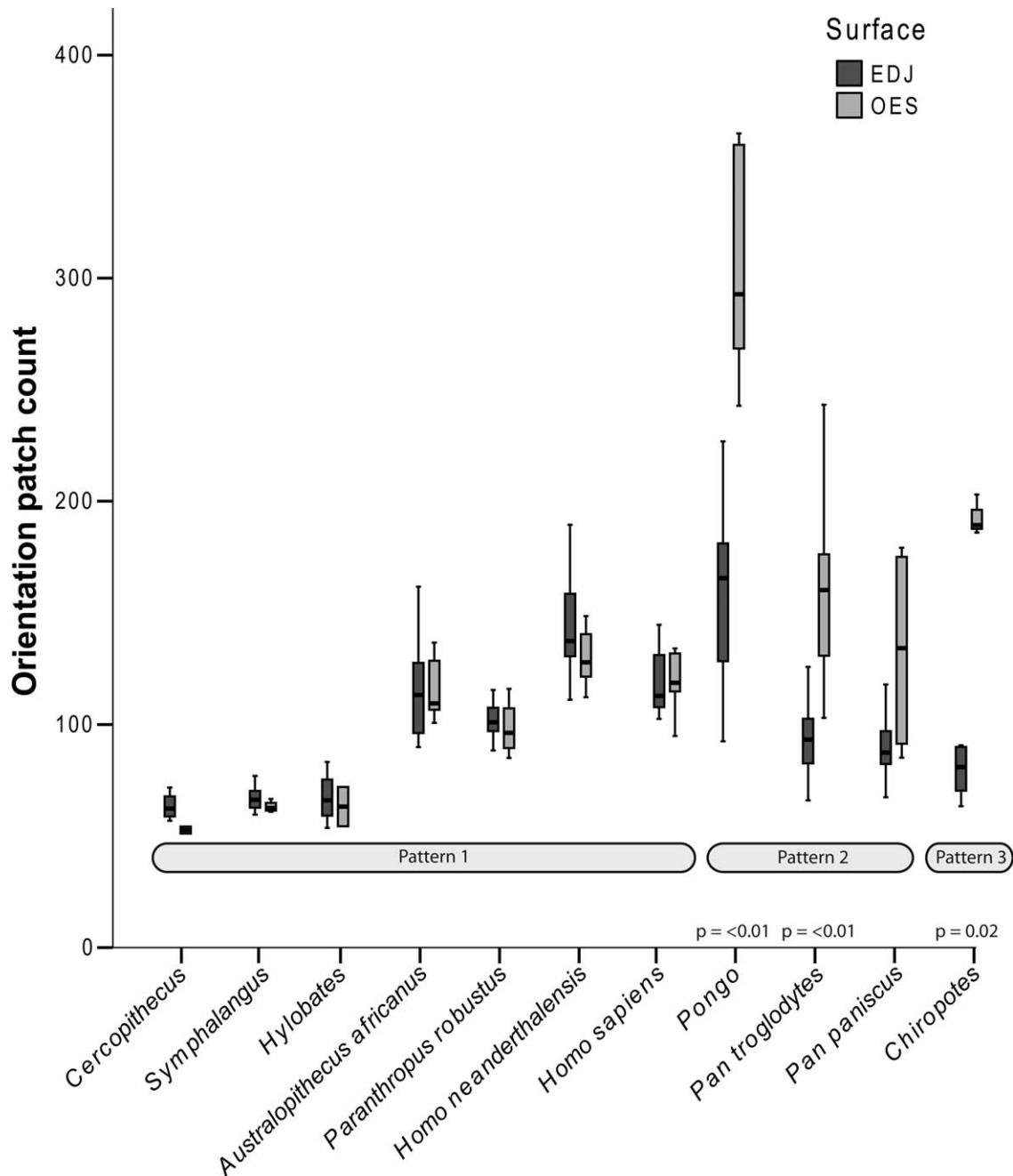


Fig. 2. Box and whisker plots of EDJ and OES patch count in each of the study taxa. Three patterns of relative patch count at the EDJ and OES are noted. The majority of taxa exhibit a similar EDJ/OES patch count (Pattern 1), while *Pongo* and *Pan* exhibit an increase in patch count with enamel deposition (Pattern 2), and *Chiropotes* exhibits a doubling of patch count at the OES (Pattern 3). Significant differences in EDJ and OES patch count (Mann-Whitney *U*) are noted. *Gorilla* and *Presbytis* are not shown due to small sample sizes for these taxa.

The third pattern, found only in *Chiropotes*, presents a crenulated OES whose complexity is independent of the EDJ. This would suggest that the convergence of the crenulated enamel of hominoids (*Pongo* and *Pan*) and that of *Chiropotes* is due to the phenotype of the enamel cap and not the EDJ. Kinzey (1992) attributed functional significance to crenulated enamel for the secondary breakdown of seed particles, and/or the gripping of hard and resilient seeds facilitating their fracture during chewing (but see below for another possible explanation).

Our results suggest that this morphology occurs via a qualitatively different developmental process in *Chiropotes* compared with *Pongo* and *Pan*.

The contribution of the EDJ to the complexity present in *Pongo* and *Pan* molars is consistent with the findings of Kraus and Oka (1967) who noted the correspondence of "wrinkles" between the EDJ of fetal molar germs and OES of fully formed molars in a small sample of hominoids. These authors suggested that "wrinkling" could derive either from rapid cell division in the epithelium

constrained within the occlusal basin or that it was "an endogenous process similar to that which results in the uplift of the future cusps" (Kraus and Oka, 1967:329). Butler (1956: 60–61) speculated that wrinkles "are produced by tensions set up in the epithelium by the relative movement of cusps, owing to unequal growth or to change in the shape of the follicle." In the context of developmental genetics of crown formation, tooth cusps develop at the places where the nondividing cells of the epithelial signaling centers, enamel knots, secrete growth factors stimulating the growth of the surrounding tissue (Jernvall et al., 1994; Jernvall and Thesleff, 2000). This nonuniform distribution of cell division may play a role in creating tension in the inner enamel epithelium resulting in the formation of ridges and crenulations. Determining whether crenulations are due to differential cell division and/or tension in the basement membrane requires further study.

Generally, there is a close match between major features of EDJ and OES morphology among primates; however, a number of authors have noted examples where there is a lack of correspondence between the EDJ and OES for particular features (e.g., Nager, 1960; Korenhof 1960, 1961; Corruccini 1987, 1998; Schwartz et al., 1998; Olejniczak et al., 2004; Skinner et al., 2008). These examples mostly relate to discrepancies at an individual level rather than as a species specific phenomenon and most of the examples come from modern humans. Although EDJ surface reconstructions from fully formed teeth cannot directly resolve the developmental basis of individual crown features, the detailed images of the EDJ surfaces of the molars in this and previous studies (Kraus and Oka, 1967; Sakai and Hanamura, 1973; Kono, 2004; Tafforeau, 2004; Skinner et al., 2008, 2009) do allow us to draw some conclusions. First, the growth of the dental follicle prior to mineralization plays the predominant role in creating the features present on the primate tooth crown (including the formation of the primary cusps, accessory cusps, and major crests). Second, the morphology of features that originate on the basement membrane can be modified, in some cases substantially, by enamel deposition. Finally, an undocumented aspect of ameloblast activity can create crenulations in the absence of associated EDJ features, as seen in the *Chiropotes* sample in this study. The latter two conclusions are important because they demonstrate that ameloblasts can be responsible for crown features. This is consistent with previous findings (e.g., Corruccini 1987, 1998) in which enamel deposition appears to be primarily responsible for the morphology of a particular cusp or crest feature. However, such instances have been poorly documented to date in terms of sample size, taxonomic breadth, and frequency within a species, and require further study.

CONCLUSIONS

The purpose of this study was to assess the contribution of the early and late phases of molar crown development (preserved in fully formed molars as the enamel-dentine junction and enamel cap, respectively) to the complexity of outer enamel surface morphology. Using dental topographic analysis to map morphological crown features we identified three patterns in the relative complexity of the EDJ and that of the OES in the primate taxa studied. In the most common pattern, there is similarity in EDJ and OES complexity

indicating that the EDJ is primarily responsible for external crown morphology, with the deposition of enamel neither adding nor removing a substantial number of features. The second pattern, present in *Pongo* and *Pan*, is an increase in complexity at the OES in which enamel deposition accentuates features present on the EDJ. Finally, a unique pattern is present in *Chiropotes* molars in which enamel deposition is solely responsible for the crenulated enamel surface.

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LITERATURE CITED

- Butler PM. 1956. The ontogeny of molar pattern. *Biol Rev* 31: 30–70.
- Cobourne MT, Sharpe PT. 2003. Tooth and jaw: molecular mechanisms of patterning in the first branchial arch. *Arch Oral Bio* 48:1–14.
- Corruccini RS. 1987. The dentinoenamel junction in primates. *Int J Primatol* 8:99–114.
- Corruccini RS. 1998. The dentino-enamel junction in primate mandibular molars. In: Lukacs JR, editor. *Human dental development, morphology, and pathology: a tribute to Albert A. Dahlberg*. Portland: University of Oregon Anthropological Papers. p 1–16.
- Evans AR, Wilson GP, Fortelius M, Jernvall J. 2007. High-level similarity of dentitions in carnivorans and rodents. *Nature* 445:78–81.
- Jernvall J, Jung H-S. 2000. Genotype, phenotype, and developmental biology of molar tooth characters. *Yearbook Phys Anthropol* 43:171–190.
- Jernvall J, Kettunen P, Karavanova I, Martin LB, Thesleff I. 1994. Evidence for the role of the enamel knot as a control center in mammalian tooth cusp formation: non-dividing cells express growth stimulating *Fgf-4* gene. *Int J Dev Biol* 38: 463–469.
- Jernvall J, Thesleff I. 2000. Reiterative signaling and patterning during mammalian tooth morphogenesis. *Mech Dev* 92: 19–29.
- Kimura O, Dykes E, Fearnhead RW. 1977. The relationship between the surface area of the enamel crowns of human teeth and that of the dentine-enamel junction. *Arch Oral Bio* 22:67–683.
- Kinsey W. 1992. Dietary and dental adaptations in the Pitheciinae. *Am J Phys Anthropol* 88:499–514.

- Kono RT. 2004. Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. *Anthropol Sci* 112:121–146.
- Korenhof CAW. 1960. Morphogenetical aspects of the human upper molar. Utrecht: Uitgeversmaatschappij Neerlandia.
- Korenhof CAW. 1961. The enamel-dentine border: a new morphological factor in the study of the (human) molar pattern. *Proc Koninkl Nederl Acad Wetensch B* 64:639–664.
- Korenhof CAW. 1982. Evolutionary trends of the inner enamel anatomy of deciduous molars from Sangiran (Java, Indonesia). In: Kurtén B, editor. *Teeth: form, function and evolution*. New York: Columbia University Press. p 350–365.
- Kraus BS, Jordan R. 1965. The human dentition before birth. Philadelphia: Lea and Febiger.
- Kraus BS, Oka SW. 1967. Wrinkling of molar crowns: new evidence. *Science* 157:328–329.
- Macchiarelli R, Bondioli L, Debénath A, Mazurier A, Tourne-piche J-F, Birch W, Dean C. 2006. How Neanderthal molar teeth grew. *Nature* 444:748–751.
- Nager G. 1960. Der vergleich zwischen dem räumlichen verhalten des dentin-kronenreliefs und dem schmelzrelief der zahnkrone. *Acta Anat* 42:226–250.
- Olejniczak AJ, Martin LB, Ulhaas L. 2004. Quantification of dentine shape in anthropoid primates. *Ann Anat* 186:479–485.
- Olejniczak AJ, Tafforeau P, Feeney RNM, Martin LB. 2008. Three-dimensional primate molar enamel thickness. *J Hum Evol* 54:187–195.
- Sakai T, Hanamura H. 1973. A morphology study of enamel-dentin border on the Japanese dentition. VII. General conclusion. *J Anthropol Soc Nippon* 81:87–102.
- Sasaki K, Kanazawa E. 1999. Morphological traits on the dentino-enamel junction of lower deciduous molar series. In: Mayhall JT, Heikkilä T, editors. *Proceedings of the 11th International Symposium on Dental Morphology*, Oulu, Finland, 1998. Oulu: Oulu University Press. p 167–178.
- Schulze MA, Pearce JA. 1994. A morphology-based filter structure for edge-enhancing smoothing. In: *Image Processing, 1994. Proceedings ICIP-94, IEEE International Conference*. Vol 2, p 530–534.
- Schwartz GT, Thackeray JF, Reid C, van Reenen JF. 1998. Enamel thickness and the topography of the enamel-dentine junction in South African Plio-Pleistocene hominids with special reference to the Carabelli trait. *J Hum Evol* 35:523–542.
- Schwarz R. 1927. *Anthropologie*. In: Misch J, editor. *Die Fortschritte der Zahnheilkunde nebst Literaturarchiv*. Leipzig: Thieme. p 718–748.
- Skinner M. 2008. Enamel-dentine junction morphology in extant hominoids and fossil hominins. Ph.D. dissertation, George Washington University.
- Skinner MM, Wood BA, Boesch C, Olejniczak AJ, Rosas A, Smith TM, Hublin J-J. 2008. Dental trait expression at the enamel-dentine junction of lower molars in extant and fossil hominoids. *J Hum Evol* 54:173–186.
- Skinner MM, Wood BA, Hublin J-J. 2009. Protostyliid expression at the enamel-dentine junction and enamel surface of mandibular molars of *Paranthropus robustus* and *Australopithecus africanus*. *J Hum Evol* 56:76–85.
- Tafforeau P. 2004. Aspects phylogénétiques et fonctionnels de la microstructure de l'email dentaire et de la structure tridimensionnelle des molaires chez les primates fossiles et actuels: apports de la microtomographie à rayonnement X synchrotron. Ph.D. dissertation, Université de Montpellier II.
- Tafforeau P, Bentaleb I, Jaeger J-J, Martin C. 2007. Nature of laminations and mineralization in rhinoceros enamel using histology and X-ray synchrotron microtomography: potential implications for palaeoenvironmental isotopic studies. *Palaeogeogr Palaeoclim Palaeoecol* 246:206–227.
- Weidenreich F. 1937. The dentition of *Sinanthropus pekinensis*: a comparative odontology of the hominids. *Palaeontol Sin Series D* 1:1–180.
- Weidenreich F. 1945. Giant Early Man from Java and South China. *Anthropol Pap Am Mus Nat Hist* 40:1–134.