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Dental trait expression at the enamel-dentine junction of lower molars in extant and fossil hominoids

Matthew M. Skinner^{a,b,*}, Bernard A. Wood^c, Christophe Boesch^d,
Anthony J. Olejniczak^b, Antonio Rosas^e, Tanya M. Smith^b, Jean-Jacques Hublin^b

^a *Hominid Paleobiology Doctoral Program, Department of Anthropology, 2110 G Street NW, The George Washington University, Washington, DC 20052, USA*

^b *Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany*

^c *Center for the Advanced Study of Human Paleobiology, Department of Anthropology, 2110 G Street NW, The George Washington University, Washington, DC 20052, USA*

^d *Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany*

^e *Department of Paleobiología, Museo Nacional de Ciencias Naturales, CSIC, C/José Gutiérrez Abascal 2, 28006 Madrid, Spain*

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Abstract

Discrete dental traits are used as proxies for biological relatedness among modern human populations and for alpha taxonomy and phylogeny reconstruction within the hominin clade. We present a comparison of the expression of lower molar dental traits (cusp 6, cusp 7, trigonid crest pattern, and protostylid) at the enamel-dentine junction (EDJ) in a variety of extant and fossil hominoid taxa, in order to assess the contribution of the EDJ to the morphology of these traits at the outer enamel surface (OES). Molars ($n = 44$) were imaged nondestructively using high-resolution microCT, and three-dimensional surface models of the EDJ and OES were created to compare trait expression at each surface. Our results indicate that these dental traits originate at the EDJ, and that the EDJ is primarily responsible for their degree of expression at the OES. Importantly, variable trait morphology at the EDJ (often not easily recognizable at the OES) indicates that different developmental processes can produce traits that appear similar at the enamel surface, suggesting caution in intra- and intertaxonomic comparisons. The results also highlight the importance of the EDJ for understanding the morphological development of discrete traits, and for establishing graded scales of variation to compare trait frequency among groups for the purpose of taxonomic and/or phylogenetic analysis. Finally, this study demonstrates that imaging the EDJ of both worn and unworn fossil hominin teeth provides a novel source of information about tooth development and variation in crown morphology.

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Introduction

Tooth crown morphology plays a critical role in hominin systematics in that it is relevant to hypotheses of alpha taxonomy, the assignment of fossil specimens to hominin taxa, and the reconstruction of the evolutionary history of the hominin clade. The presence and degree of expression of discrete traits at the outer enamel surface (OES) of teeth is an important

* Corresponding author. Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany. Tel.: +49 341 355 0767.

E-mail address: skinner@eva.mpg.de (M.M. Skinner).

component of these morphological analyses. Over the last three decades, a concerted effort has been made to standardize the classification of dental traits and to investigate how their expression varies within and among modern human populations (e.g., Turner et al., 1991). Discrete dental traits have come to play a central role in inferring biological relationships among modern humans (Scott and Turner, 1997, and references therein), living nonhuman primates (Johanson, 1974; Uchida, 1996; Pilbrow, 2003), fossil hominoids (Pilbrow, 2006), and fossil hominins (e.g., Weidenreich, 1937; Robinson, 1956; Wood and Abbott, 1983; Suwa et al., 1996; Bailey, 2002; Hlusko, 2004; Bailey and Lynch, 2005; Guatelli-Steinberg and Irish, 2005; Bailey and Wood, 2007; Martín-Torres et al., 2007).

Traditional analyses of discrete traits make two assumptions. First, trait morphology that appears similar at the OES in different teeth is the result of developmental processes that are similar enough to allow valid comparisons within and between groups. Second, the OES is adequate for the formulation of standardized classifications of trait variation (often taking the form of grades from minor to marked trait expression). However, given how teeth grow, it is possible that different developmental processes can result in similar morphology at the OES, confounding the definition, classification, and comparison of discrete-trait morphology. During molar tooth development, major aspects of crown morphology such as cusps form on a basement membrane (*membrana praeformativa*) that serves as the template upon which a layer of enamel is deposited (Butler, 1956, 1999). In mature teeth, the shape of this membrane is preserved as the enamel-dentine junction (EDJ), and trait expression at the OES is the culmination of EDJ shape and differential enamel distribution. This study tests these assumptions about trait morphology at the OES by examining the shape of the enamel-dentine junction (EDJ) as a proxy of trait development that is preserved in fully formed teeth.

To understand how different developmental processes can result in similar trait morphology at the OES, consider the following analogy. An artist is producing two sculptures (equivalent to the fully formed tooth crown) using a wireframe template (equivalent to the EDJ) and clay (equivalent to enamel). The artist can produce two sculptures that are identical at their outer surfaces in two ways. First he can begin with identically shaped wireframes and place an identical distribution of clay over each. Conversely, he can begin with wireframes that differ in shape but apply different distributions of clay over each to produce an identical shape at the surface. Furthermore, two sculptures that differ in the shape of their surfaces can each contain identical wireframes. Few studies of discrete dental traits have included information about the shape of the wireframe, or EDJ, template (but see Schwartz et al., 1998).

The utility of the EDJ for understanding the developmental basis of crown morphology has been demonstrated by a number of previous studies (Kraus, 1952; Korenhof, 1960, 1961, 1982; Nager, 1960; Kraus and Jordan, 1965; Sakai et al., 1965, 1967a,b, 1969; Sakai and Hanamura, 1971, 1973a,b; Corruccini, 1987a,b, 1998; Schwartz et al., 1998; Sasaki and

Kanazawa, 1999; Olejniczak et al., 2004; Macchiarelli et al., 2006). Most of these studies showed that the *gross* morphology of the OES is primarily determined by the shape of the EDJ, with the shape of the enamel cap having only a minor influence on the morphology of the OES. Butler (1956: 32–33) noted: “Allowing for such modifications due to the deposition of enamel it remains true that the main features of the crown pattern, and many of its minor details, are already present in the membrane *praeformativa* before the hard tissues have developed.” However, the relative contribution of the EDJ and the enamel cap to the expression of the smaller morphological features of the tooth crown, which constitute discrete traits of fossil and living hominins and hominoids, remains a topic of debate. Depending on the feature in question, both concordance and a lack of concordance between the EDJ surface and OES have been reported (e.g., Korenhof, 1960; Kraus, 1952; Corruccini and Holt, 1989; Schwartz et al., 1998; Olejniczak et al., 2004).

Nager (1960) decalcified 96 human teeth to compare the shapes of the OES and the EDJ of the same tooth. Based on his observations he defined three types of structures. (Nager [1960] used the term *crown relief* to refer to morphological structures, but for the purpose of this discussion, we will use the term *trait*.) A “primary-definitive” trait consists of structures that are present on both the EDJ and on the unworn OES. This category includes structures whose morphology is altered slightly when enamel is deposited over the surface of the growing tooth (e.g., the discrepancy between a pointed dentine horn and its overlying, more blunt enamel cusp does not preclude the “cusp” from being a primary-definitive trait). A “primary-temporary” trait consists of structures that are present on the EDJ, but cannot be observed on the unworn OES. An example of the latter is the hypocone-protocone ridge present at the EDJ of human upper molars, which is not visible at the enamel surface (Korenhof, 1960: Plate XIII, specimen MMSD 381). A “secondary” trait consists of structures not seen on the EDJ, but which are evident on the OES (e.g., primary occlusal fissures present at the OES that have no corresponding fissure-like morphology at the dentine surface).

This study examines four dental traits of the lower molars—cusp 6, cusp 7, trigonid crest pattern, and the protostylid—with the aim of determining the relative contributions of the EDJ and the enamel cap to their expression at the OES in a variety of extant and extinct hominoids (Fig. 1). These traits are found in all hominin and extant great ape species, and they are thought to provide information about taxonomy and/or phylogeny (e.g., Johanson, 1974; Wood and Abbott, 1983; Suwa et al., 1996; Uchida, 1996; Pilbrow, 2003; Bailey, 2002, 2006; Bailey and Hublin, 2006; Bailey and Wood, 2007; Martín-Torres et al., 2007). A cusp 6 (also called a tuberculum sextum or entoconulid, and referred to hereafter as C6) is a cusp or cuspule on a lower molar within the distal fovea, lingual to the hypoconulid, or cusp 5 (Turner et al., 1991). A cusp 7 (also called a tuberculum intermedium, interconulid, or metaconulid, and referred to hereafter as C7) is a cusp or cuspule occurring in the lingual groove between the metaconid and entoconid (Turner et al., 1991; Hlusko, 2002). Trigonid crest

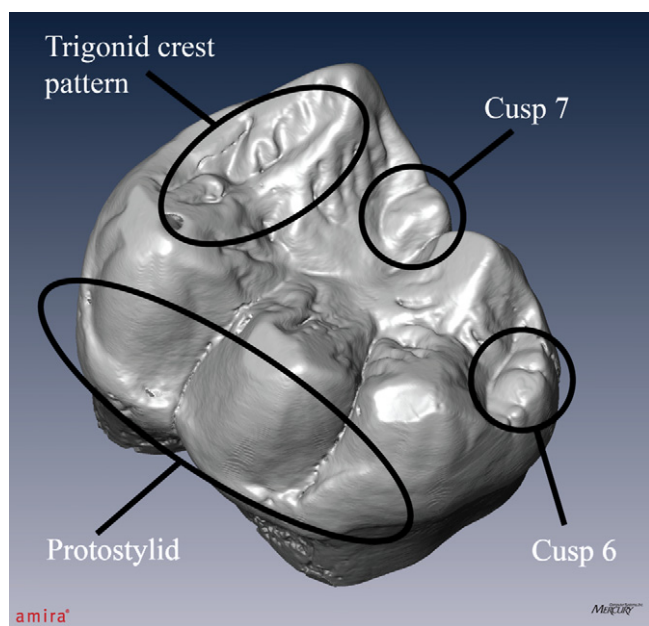


Fig. 1. Virtual reconstruction of a *Gorilla gorilla beringei* lower left second molar highlighting the four discrete traits examined in this study: cusp 6, cusp 7, protostylid, and trigonid crest pattern (identified by black circles). The cusp 6 in this molar could be considered a double cusp 6 (discussed in text).

pattern refers to the midtrigonid crest (defined as a transverse ridge or loph that connects the middle part of the two mesial cusps) and the distal trigonid crest (defined as a transverse ridge or loph that connects the distal aspect of the two mesial cusps) (Korenhof, 1982; Wu and Turner, 1993). A protostylid was described by Dahlberg (1950: 16) as “an elevation or ridge of enamel on the anterior part of the buccal surface of the lower molars, which ascends from the gingival end of the buccal groove and extends mesio-occlusally.”

We ask three questions about each trait. Does it originate at the EDJ? What is the relative contribution of the EDJ to trait expression at the OES? Is the process of trait development, as inferred from the shape of the EDJ and overlying enamel cap, consistent among the study taxa? If a trait can be considered primary-definitive under Nager's classification, then the EDJ expression of a trait can be incorporated into its formal definition and may inform the establishment of taxon-specific trait-scoring standards; the importance of the latter has been noted by a number of authors (e.g., Reid and Van Reenen, 1995; Van Reenen and Reid, 1995; Irish and Guatelli-Steinberg, 2003; Hlusko, 2004; Bailey and Wood, 2007). Furthermore, if it is shown that the EDJ is either a proxy for OES morphology or is more informative than the OES, then worn fossil teeth may be used in the analysis of discrete traits.

Materials and methods

Study sample

Table 1 lists the molars included in this study. A range of living and extinct hominid and hominin taxa (following the

Table 1

Composition of the lower molar sample

Taxon	n	M ₁	M ₂	M ₃	Source
<i>P. t. verus</i>	19	6	13		MPI-EVA
<i>G. g. beringei</i>	2		1	1	NMNH
<i>P. pygmaeus</i> ssp.	3	3			ZMB
<i>G. blacki</i>	1		1		SFN
<i>H. sapiens</i>	7	3	4		NMNH, MPI-EVA
<i>H. neanderthalensis</i>	4	4			MNCN
<i>P. robustus</i>	4	3	1		TM, UW
<i>A. africanus</i>	4	1	2	1	TM, UW

Source codes: MPI-EVA, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; NMNH, National Museum of Natural History, Washington, DC, USA; ZMB, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; SFN, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; TM, Transvaal Museum, Pretoria, South Africa; UW, University of Witwatersrand, Johannesburg, South Africa.

taxonomy of Wood and Richmond, 2000) were included to capture variation for each trait within taxa, as well as variation in trait morphology among taxa. While sex is known for some specimens, it is not incorporated as a variable in our analysis due to the limited sample sizes for all taxa. First, second, and third molars were included, and in a few cases, metameric teeth from the same individual were examined. Modern human specimens include North American aboriginals and Early Bronze Age specimens from Great Britain. Extant hominoids include *Pan troglodytes verus*, *Gorilla gorilla beringei*, and *Pongo pygmaeus* ssp. The fossil taxa include *Gigantopithecus blacki*, *Australopithecus africanus*, *Paranthropus robustus*, and *Homo neanderthalensis*.

Micro-computed tomography and surface reconstruction

In order to produce three-dimensional reconstructions of the EDJ and the OES, each tooth was scanned using either the SKYSCAN 1172 Desktop MicroCT (scan parameters: 100 Kv, 94 μ A, 2.0 mm aluminum and copper filter, 2048 \times 2048 matrix, 0.12 rotation step, 360° of rotation, 2 frame averaging) or SCANCO μ CT40 (scan parameters: 70 Kv, 114 μ A, 1024 \times 1024 matrix, 0.36 rotation step, 180° of rotation) computed tomographic scanner. Pixel dimensions and slice thickness between reconstructed serial images were isometric with resolutions ranging between 13 and 50 microns (μ m) (e.g., isometric voxels of 13 μ m \times 13 μ m \times 13 μ m to 50 μ m \times 50 μ m \times 50 μ m).

To facilitate tissue segmentation, the complete image stack for each tooth was filtered using a three-dimensional median filter (kernel size of 3), followed by a mean of least variance filter (kernel size of 3), implemented as a computer-programmed macro. This filtering process results in more homogenous tissue classes (e.g., enamel vs. dentine) and allocates pixels with intermediate gray-scale values at tissue interfaces (i.e., air-enamel, enamel-dentine, air-dentine) to the appropriate tissue (Schulze and Pearce, 1994). The effect of the filtering process on the morphology of the reconstructed surfaces was assessed by overlaying surfaces derived from

unfiltered images over surfaces derived from filtered images and examining differences in shape. The effect of filtering on surface morphology is minimal compared to the size of the structures (e.g., cusps and crests) that constitute the discrete traits being analyzed. An exception is that the size and shape of very small tubercles (e.g., <0.5 mm in length) cannot be discerned using this methodology (discussed below).

Filtered image stacks were imported into the Amira software package (v4.1, www.amiravis.com), and enamel and dentine tissues were segmented by evaluating the 3D-voxel-value histogram and its distribution of gray-scale values, which typically presents a trimodal distribution with one peak representing dentine, another peak representing enamel, and a third peak representing air and background noise in the images. For unfossilized teeth of extant taxa, in which enamel and dentine tissues differ substantially in their degree of mineralization (and therefore their densities and the ability of X-rays to pass through them), the filtering process results in gray-scale pixel-value distributions for each tissue that do not overlap. In fossil teeth, diagenetic alteration (e.g., dentine remineralization) sometimes results in similar tissue densities for enamel and dentine, and thus overlapping gray-scale pixel-value ranges for each tissue (Olejniczak and Grine, 2006). Even after filtering, there is often an incomplete separation between the two, and a decision must be made about the range of gray-scale values allocated to each tissue. All of the teeth in this study evinced a clear separation of enamel and dentine, resulting in well-distinguished gray-scale values and accurate representations of the EDJ. Specimens that could not be

segmented to produce accurate surface reconstructions were excluded from the study.

After segmentation, the OES and the EDJ were reconstructed as triangle-based surface models in Amira 4.0 (surface generation module using unconstrained smoothing parameter), which can be rotated and enlarged interactively to view and compare trait expression. In specimens that preserved only the enamel cap, a surface model of the EDJ was created by digitally removing the occlusal surface of the model of the reconstructed enamel cap surface.

Results

The manifestation of each trait at the EDJ and the influence of enamel deposition on trait manifestation at the OES are described below. Trait distribution within and among taxa is addressed, although sample sizes are too small to warrant strong inferences to be drawn regarding intertaxonomic differences in trait presence/expression.

Cusp 6

Variation in C6 manifestation at the EDJ of molars in the study sample is summarized schematically in Fig. 2 and can be separated into two types. The first type, referred to here as the “hypoconulid-type” C6, is characterized by a dentine horn (DH) on the lingual slope of the hypoconulid DH (Figs. 2b and 3a). The shape of this feature resembles a smaller version of the adjacent hypoconulid DH. In a number of

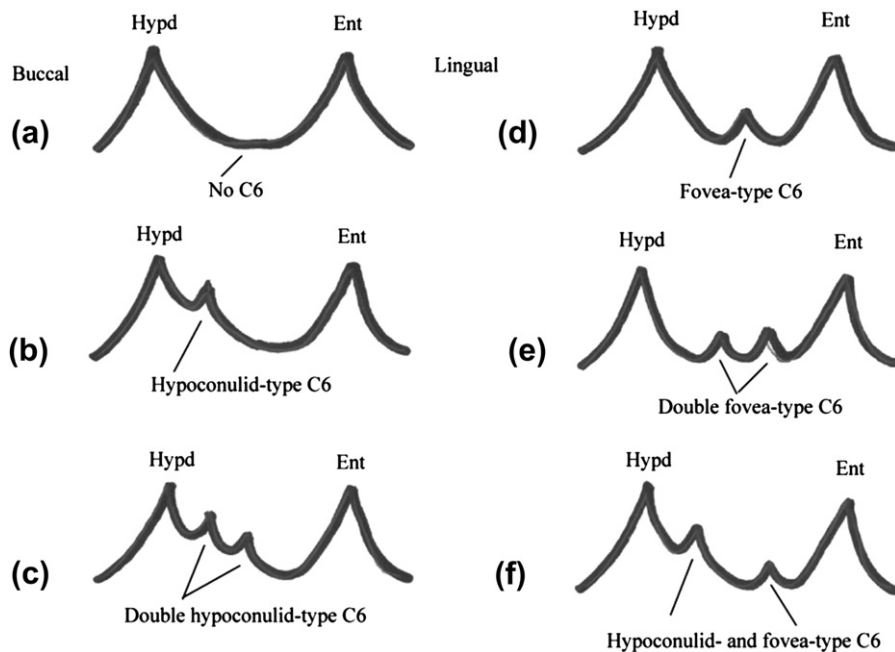


Fig. 2. Schematic representation of C6 morphology present at the EDJ in the study sample. View is towards the distal face of the EDJ surface between the DHs of the hypoconulid (Hypd) and entoconid (Ent). (a) No C6 manifestation at the EDJ; (b) single hypoconulid-type C6 manifested as a DH-like feature on the lingual ridge of the hypoconulid; (c) double hypoconulid-type C6 manifested as two DH-like features on the lingual ridge of the hypoconulid DH; (d) single fovea-type C6 manifested as a DH-like feature between the hypoconulid DH and entoconid DH with no tendency for spatial association to either; (e) double fovea-type C6 manifested as two DH-like features between the hypoconulid DH and entoconid DH; (f) C6 complex exhibiting a single hypoconulid-type and single fovea-type DH between the hypoconulid DH and the entoconid DH.

specimens, this DH was duplicated, with both horns occurring in proximity to the hypoconulid DH and resembling serially developed structures. These specimens are characterized as having a double hypoconulid-type C6 (Figs. 2c and 3b). These types of C6 are most common in the *P. t. verus* sample but were also present in the *H. sapiens* sample (Table 2). The close association of this type of C6 with the hypoconulid is not always apparent from the OES, particularly in partially worn teeth. Furthermore, in some chimpanzee teeth, a double hypoconulid-type C6 can only be identified at the EDJ (Fig. 3b) due to tooth wear on the distal margin of the tooth crown.

The second type of C6, referred to here as the “fovea-type” C6, takes the form of a DH on the marginal ridge of the distal fovea between the hypoconulid and entoconid (Figs. 2d and 3c). This type can be differentiated from the hypoconulid-type because its DH is separate from the hypoconulid DH and entoconid DH. In high-cusped teeth, such as those of *G. g. beringei*, this type of C6 can be a tubercle on a cingulumlike shelf on the distal marginal ridge of the EDJ (seen on the OES of Fig. 1). Taxa exhibiting the fovea-type C6 include *G. blacki*, *A. africanus*, *P. robustus*, *H. neanderthalensis*, *P. pygmaeus* ssp., and *G. g. beringei*. Similar to the hypoconulid-type discussed above, the fovea-type C6 can also appear in a duplex form, with two DH-like features on the margin of the distal fovea (schematically represented in Fig. 2e). One specimen of *H. sapiens* had both types of C6 at the EDJ (schematically represented in Fig. 2f).

In both *A. africanus* and *P. robustus*, which have the fovea-type C6 when present, enamel distribution has a marked influence on the shape of the C6 at the OES. The small DH(s) at the EDJ corresponds with a relatively large cusp at the OES. This contrasts with all of the other taxa, in which the relative size of the C6 DH(s) is similar to the relative size of the C6 cusps at the OES. Thus, in these thickly enameled taxa (Grine and Martin, 1988), enamel distribution has a greater influence on C6 shape at the OES than in thinly enameled taxa.

Another variant (possibly similar developmentally to a C6) was observed in one *P. t. verus* molar and in one *G. g. beringei* molar (Fig. 3d). In these specimens, a small cusp is present on the OES on a crest that joins the entoconid to the hypoconulid (the presence of this crest is variable within and among most of the study taxa). In both teeth, this cusp corresponds to

a DH at the EDJ located on a crest between the entoconid DH and hypoconulid DH.

Cusp 7

Variation in C7 manifestation at the EDJ of molars in the study sample is summarized schematically in Fig. 4. Like the C6 trait, there are two main types of C7. The first type of C7, referred to as the “metaconulid-type,” is manifested at the EDJ as a protuberance or DH-like feature on the end of a shoulder on the distal ridge of the metaconid DH (Figs. 4c and 5a). This shoulder can be faint or pronounced, and it can occur at varying distances from the metaconid DH (Figs. 4d and 5b). This type seems consistent with grade 1A of the ASUDAS classification of cusp 7 (Turner et al., 1991).

The second type of C7, referred to as the “interconulid-type,” is manifest at the EDJ by a DH of variable size on the low point of the marginal ridge between the DHs of the metaconid and entoconid (Figs. 4f and 5c,d). In some cases, this type of C7 appears more spatially associated with the metaconid, as evidenced by a less-developed trough between the C7 DH and the metaconid compared to the trough between it and the entoconid DH (Fig. 4e). This type corresponds with grades 1–4 of the ASUDAS classification of cusp 7. The metaconulid-type C7 is present in *P. t. verus*, *G. g. beringei*, and *A. africanus*, while the interconulid-type is present in *H. sapiens*, *H. neanderthalensis*, *P. robustus*, *A. africanus*, and *G. blacki*; no C7 was observed in *P. pygmaeus*.

Differential enamel distribution does not greatly influence the manifestation of C7 at the OES, but distinguishing between a cusplike at the OES over a pronounced shoulder of the metaconid, and a cusplike at the OES over a small DH on the shoulder of the metaconid, is difficult based on OES morphology alone. Dental attrition does not obscure C7 morphology at the OES in this sample. In one *A. africanus* (STW 560A) specimen, the OES exhibits both of the types of C7 discussed here (the EDJ presenting a DH under the interconulid-type but only a slight ridge elevation below the metaconulid-type C7).

Trigonid crest pattern (TCP)

Variation in trigonid crest patterning at the EDJ is summarized schematically in Fig. 6. The first type consists of either weakly pronounced or well-pronounced crests on the slopes of the protoconid and metaconid DHs, which extend from the tips of the DHs towards the occlusal basin (Figs. 6a,b and 7a). The second type consists of pronounced but separate crests that extend across the occlusal basin (Figs. 6c and 7c). The third type is a single crest between the tips of the metaconid and protoconid DHs, with or without accompanying minor crests (Figs. 6e and 7b). In the fourth type, mesial and middle crests (either both complete or one interrupted) link the protoconid and metaconid DHs (Figs. 6f,g and 7d). Other minor variations in the study sample are not discussed here (e.g., Fig. 6d,h).

Table 2
C6 frequency (as a ratio) by taxon and type¹

C6	Absent	Fovea	Hypoconulid	Double-F ²	Double-H ²
<i>P. t. verus</i>	4/19		12/19		3/19
<i>G. g. beringei</i>	1/2			1/2	
<i>P. pygmaeus</i> ssp.	2/3	1/3			
<i>G. blacki</i>		1/1			
<i>H. sapiens</i> ³	4/7		1/7		1/7
<i>H. neanderthalensis</i>	3/4	1/4			
<i>P. robustus</i>	1/4	1/4		2/4	
<i>A. africanus</i>		3/4		1/4	

¹ Pooled analysis of all molar types (M_{1–3}).

² Double-F: double fovea-type; Double-H: double hypoconulid-type.

³ One *H. sapiens* molar presented both a fovea-type and a hypoconulid-type C6.

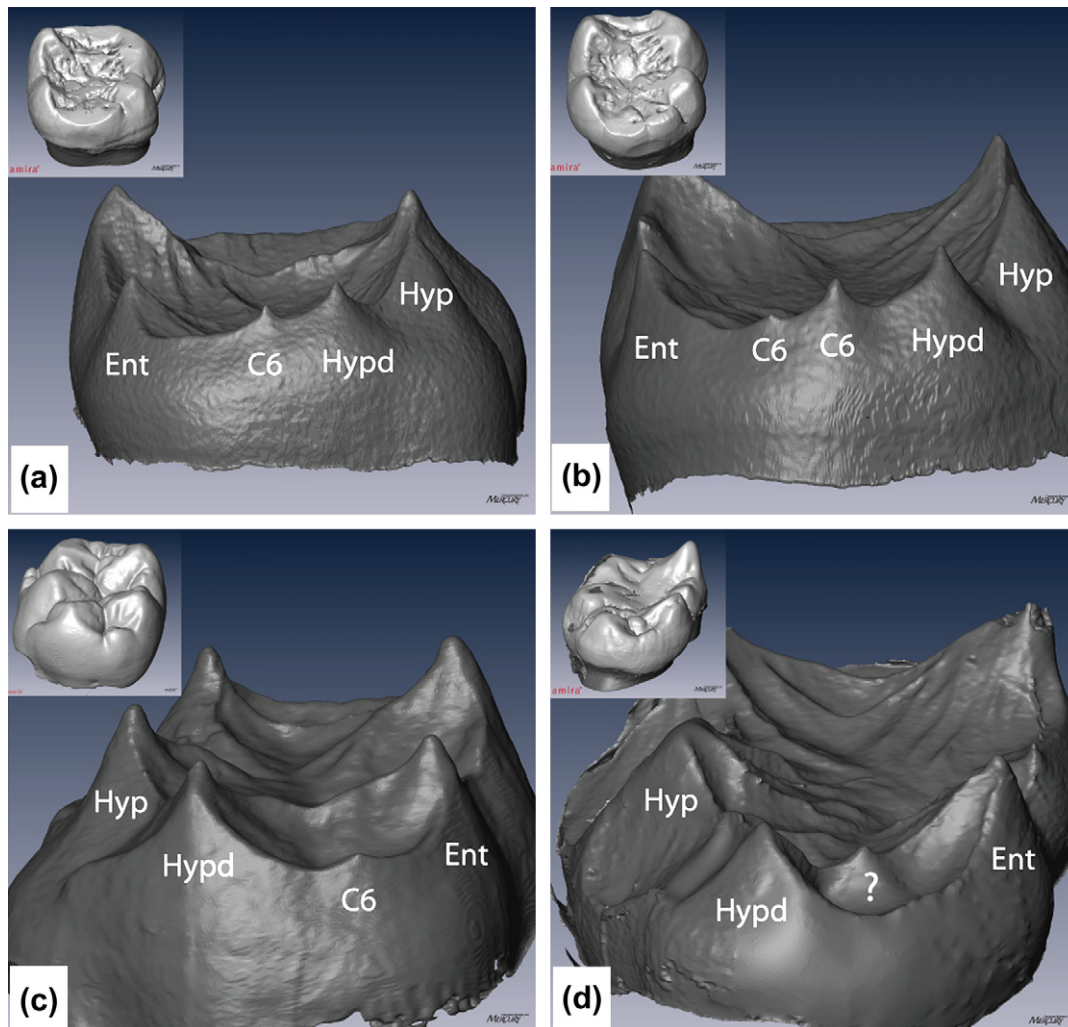


Fig. 3. Selected examples of C6 expression at the EDJ in the study sample (OES of each specimen is inset in top left corner). Abbreviations are: Ent = entoconid, Hyp = hypoconid, Hypd = hypoconulid. (a) Single hypoconulid-type C6 on a lower second molar of *P. t. verus* (TAI 15012); (b) double hypoconulid-type C6 on a lower second molar of *P. t. verus* (TAI 11800); (c) single fovea-type C6 on a lower first molar of *A. africanus* (STW 421B); (d) DH-like feature located on a crest joining the entoconid and hypoconulid DHs of a lower second molar of *G. g. beringei* (NMNH 543034). The status of this feature as a manifestation of C6 is unclear. Images are not to scale.

Homo neanderthalensis exhibits the most prominent trigonid crest expression at the EDJ, characterized in some specimens by a single sharp crest between the metaconid and protoconid DHs with no other associated crest features. *Pan. t. verus* is most variable in TCP, while *P. robustus*, *A. africanus*, and *G. blacki* present little in the way of trigonid crest morphology. The relationship between the informal types of TCP above and two other discrete dental traits, mesial and distal trigonid crests (Korenhof, 1982; Sasaki and Kanazawa, 1999), is addressed below.

In unworn teeth, the TCP can, in most cases, be inferred accurately from the OES; however, moderate wear can make the interpretation of TCP difficult. In worn molars, the EDJ preserves trigonid crest features that form during the development of the tooth. Generally, our analysis supports the conclusion that trigonid crest pattern is primary-definitive in nature, with crest features present at the OES associated with matching crest features at the EDJ. Even small accessory crests observable at the OES have dentine analogues.

Protostylid

Variation in protostylid expression at the EDJ is summarized schematically in Fig. 8. In this schematic representation, we have included morphological features on the mesial border of the protoconid DH and on the distal border of the hypoconulid DH. In minor forms of protostylid expression (Figs. 8b,c and 9a), small wrinkles/depressions are present at the EDJ. Such features may be located mesially on the slope of the protoconid DH, centrally between the protoconid and hypoconid DHs, and/or distally between the hypoconid and hypoconulid DHs. When the protostylid is strongly expressed, the circular shelf is large, and it is the shape of the buccal slopes of the protoconid and hypoconid DHs that dictate the morphology of the buccal crown surface (Figs. 8d–f and 9b–d). We see no reason to exclude mesial and distal circular features from the “protostylid” complex, and thus our analysis differs from some previous studies of this trait (e.g., Hlusko, 2004). Examination of the EDJ of

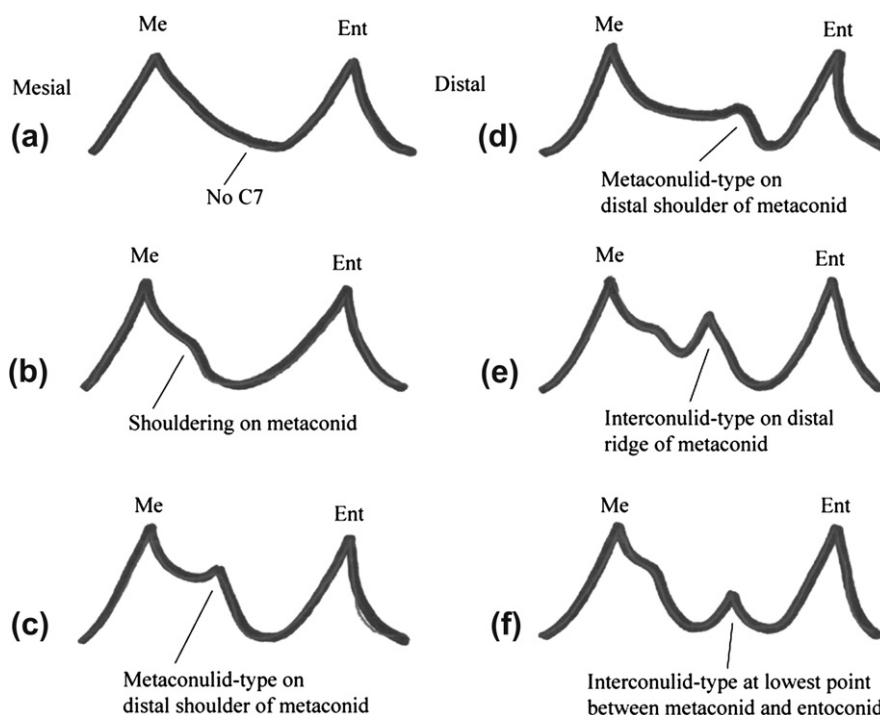


Fig. 4. Schematic representation of C7 morphology present at the EDJ in the study sample. View is towards the lingual face of the EDJ surface between the DHs of the metaconid (Me) and entoconid (Ent). (a) No C7 manifestation at the EDJ; (b) moderately pronounced shoulder on the distal ridge of the metaconid DH; (c) metaconulid-type C7 on the distal shoulder of the metaconid DH, which in some cases can resemble a small DH-like feature; (d) a second example of a metaconulid-type C7 in which a DH-like feature is not closely associated with the metaconid DH; (e) interconulid-type C7 with a DH-like feature on the distal ridge (but separated from the shoulder by a trough) of the metaconid DH; (f) interconulid-type C7 with a DH-like feature at the low point on the ridge between the metaconid DH and entoconid DH.

molars in this sample suggests that these morphological features the result of the same developmental processes. Taxa with marked protostylid expression include *A. africanus*, *P. robustus*, and *G. g. beringei*. All of the other taxa present minor expression of the protostylid (with the exception of the single *G. blacki* molar, which presents no protostylid morphology).

All of the OES structures included as a protostylid originate at the EDJ, with only a minor influence due to the differential deposition of enamel. In almost all cases, there is a consistent relationship between protostylid manifestations at the EDJ and at the OES, and therefore the protostylid is a primary-definitive trait. Even when the OES expression of the protostylid is complex, it is matched by an equivalent morphology at the EDJ (Fig. 9d). In a small number of cases, minor surface features on the buccal side of the buccal DHs could not be detected at the OES, but the influence of dental attrition on the manifestation of this trait at the OES could not be ruled out in these cases.

Discussion

The aim of this study was to address three questions related to the development of discrete dental traits: Do the four dental traits originate at the EDJ? What is the contribution of the EDJ to trait expression at the OES? Is the process of trait development, as inferred from the shape of the EDJ and overlying enamel cap, consistent among the study taxa? With respect to the first two questions, our results are consistent:

the presence and degree of morphological expression of C6, C7, trigonid crest pattern, and protostylid are dictated primarily by the EDJ. Enamel deposition rarely masks trait presence at the EDJ, nor are there any OES traits in the absence of EDJ expression. These results mean that the EDJ of moderately worn teeth may be used to assess the presence or absence of traits (e.g., the second C6 in Fig. 3b), and in unworn teeth, information about the EDJ may clarify the developmental basis of traits present at the OES. Our results demonstrate a strong correlation between the EDJ and OES morphology for the traits studied here, and they suggest a consistent predictive relationship between EDJ and OES morphology for the majority of dental traits incorporated into anthropological analyses (contra Kraus, 1952; Schwartz et al., 1998; Olejniczak et al., 2004).

The traits C6 and C7 are discussed together because they are both accessory cusps, albeit present in different parts of the tooth crown. In all molars, a feature scored as a C6 at the OES was located directly above a DH-like feature at the EDJ. In some cases, this DH was similar in shape to the DHs of the adjacent primary cusps (i.e., hypoconulid and entoconid) in its degree of pointedness and slope shape, while in other cases, the DH was more like a tubercle with a low, blunt tip. The resolution of the microCT scan may influence the morphology of small EDJ features, and this must be considered in assessments of the original shape of diminutive DHs at the EDJ. Nonetheless, all C6s in the study sample can be classified as primary-definitive traits (sensu Nager, 1960),

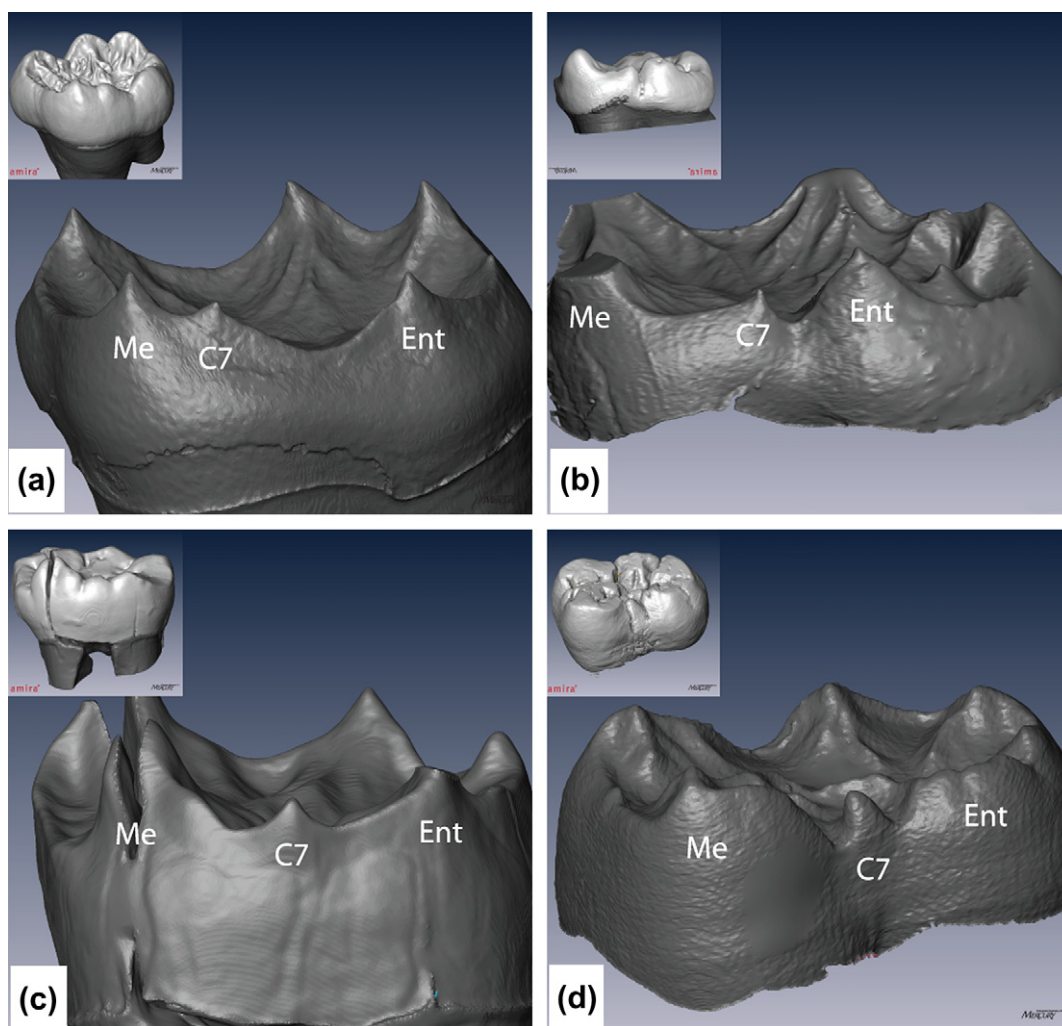


Fig. 5. Selected examples of C7 expression at the EDJ in the study sample (OES of each specimen is inset in top left corner). Abbreviations are: Me = metaconid and Ent = entoconid. (a) Metaconulid-type C7 on the distal shoulder of the metaconid DH of a lower third molar of *P. t. verus* (TAI 11790); (b) metaconulid-type C7 farther removed from the metaconid DH of a lower second molar of *G. g. beringei* (NMNH 543034); (c) interconulid-type C7 on a lower second molar of *H. neanderthalensis* (SD 756); (d) interconulid-type C7 on a lower second molar of *G. blacki* (CA 736). Images are not to scale.

with clear evidence that the trait originates at the EDJ. As with most cusps, enamel deposition alters the shape of the DH through the creation of more convex cusp slopes and a blunter, rounded cusp tip.

In all teeth in which the C7 is large in relation to adjacent cusps, there is an equivalent DH-like feature at the EDJ. Even in teeth in which a small cusplike feature is located in the valley between the metaconid and entoconid, there is a corresponding elevation at the EDJ. Some manifestations of C7 at the OES (those corresponding to a type 1A under the ASUDAS) are more ambiguous at the EDJ. For example, while a cusplike morphology could be argued for the OES, the corresponding EDJ is marked by a protuberance rather than a distinct, isolated elevation of tissue that would be expected to underlie an enamel cusplike feature. Nonetheless, although concordance between the OES and EDJ in the metaconulid-type C7 is not as pronounced as the interconulid-type, it is still a primary-definitive trait under Nager's classification.

The nature of the developmental processes underlying accessory-cusp formation relates directly to our third question

regarding developmental similarity of traits both within and between different taxa. Should a hypoconulid-type C6 in a *P. t. verus* specimen and a fovea-type C6 in a *G. g. beringei* specimen be coded as the same discrete trait for the purpose of phylogenetic analysis? From our observations, these two types appear to be the result of subtly different developmental processes (as an aside, we suggest that the term "entoconulid" as a synonym for C6 is inappropriate unless one is specifically highlighting the spatial association of this accessory cusp with the entoconid). Similarly, the two types of C7, observed between the metaconid and entoconid, appear to represent different underlying developmental processes. This conclusion is supported by one *A. africanus* specimen (STW 560A) that exhibits both a metaconulid-type and interconulid-type C7 (complicating attempts to classify these two features under one trait).

Can developmental genetic research throw any light on these results? Recent research into cusp patterning on murine teeth (Jernvall and Jung, 2000; Jernvall and Thesleff, 2000) suggests that an accessory cusp at the OES, associated with

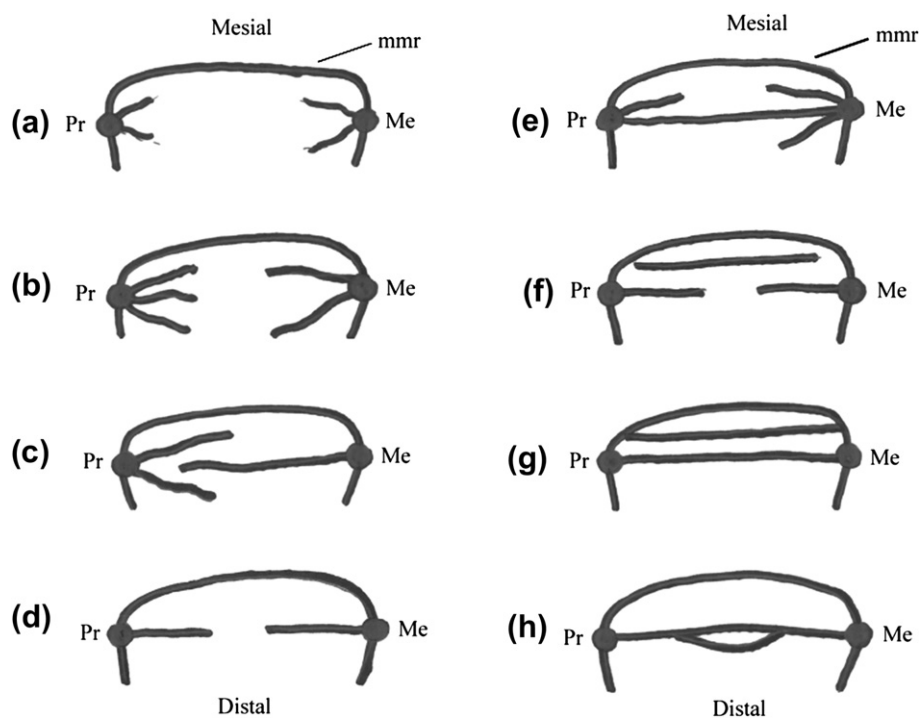


Fig. 6. Schematic representation of TCP present at the EDJ in the study sample. View is towards the occlusal surface of the EDJ including the mesial marginal ridge (mmr) and the tips of the DHs (represented as solid black circles) of the protoconid (Pr) and metaconid (Me). (a) Small, minor crests associated with the Pr and Me DHs; (b) multiple large crests running towards the occlusal basin; (c) pronounced but separate crests that extend across the occlusal basin; (d) single pronounced crests running medially towards each other but not joined in the occlusal basin; (e) a single pronounced crest between the Pr and Me DHs with additional less pronounced crests also present; (f) a mesial crest and a middle crest, one of which is not complete; (g) a mesial (originating at or mesial to the DHs) and middle crest that are complete; (h) a middle crest with a small secondary crest in the occlusal basin. This schematic does not exhaust the manifestations of trigonid crest pattern seen in the study sample.

a DH at the EDJ, corresponds to a secondary enamel knot, the presence and location of which is determined by the genetic pathways that control the expression domains of the gene products (Kassai et al., 2005). It has been suggested that the pattern of primary and secondary cusps on a mammalian tooth crown is the outcome of an iterative cusp-patterning program (Polly, 1998; Jernvall and Jung, 2000; Jernvall and Thesleff, 2000; Salazar-Ciudad et al., 2003), which is influenced both by the genes that control the spacing and size of DHs and/or the overall size of the crown. Cai et al. (2007) showed that, in mice and rats, epithelial tissue dictates cusp size and the underlying mesenchymal tissue dictates crown size. Under this paradigm, it is unlikely that a tooth would exhibit morphology resulting from a gene for a C6 or double-C6; rather, the pattern of spacing of secondary enamel knots probably results in the formation of (1) an accessory cusp adjacent to the hypoconulid and (2) another accessory cusp adjacent to that (Fig. 3b). Similarly, the difference between a metaconulid-type and an interconulid-type C7 may reflect patterns of growth (or differentiation) rates within the developing tooth germ rather than a one-to-one relationship between a gene and a feature. Our observations indicate that DH-like features can appear in many locations on the EDJ (e.g., on a trigonid crest, between the hypoconid and hypoconulid DHs, or on a crest between the hypoconulid and entoconid DHs). Within a developmental paradigm that incorporates a patterning-cascade mode of cusp development (sensu Jernvall and Jung,

2000), it may be difficult to devise a simple coding scheme for accessory cusps that is consistent with their developmental origin. Examination of EDJ expression of accessory cusps reveals morphological variation that is less obvious at the OES, and that will need to be addressed as discrete-trait analysis extends beyond modern humans to other primate taxa.

While the majority of accessory cusps have corresponding DHs underlying them at the EDJ, in some specimens, there is only a faint corresponding elevation at the EDJ. In a number of specimens, C6s at the OES (in the range of 0.5–1.0 mm in diameter) presented morphology that, in terms of cusplike shape, must be attributed to the growth of the enamel rather than the EDJ template. Histological analyses of hominoid enamel formation have determined that the ameloblasts deposit more enamel per day over cusp tips (on average) compared to lateral or cervical regions of the tooth crown (Beynon et al., 1991). Assuming that DHs of C6s form in a similar manner to the DHs of the primary cusps (i.e., with the initiation of a secondary enamel knot), then ameloblasts in these locations may be depositing proportionately thicker enamel than adjacent regions. This could result in cusplike morphology at the OES and explain the apparent discrepancies between EDJ shape and the OES expression of accessory cusps seen in some teeth. Histological analysis of accessory cusps may throw light on the ontogeny of these features.

Examination of the EDJ proved especially valuable for the assessment and interpretation of trigonid crest expression in

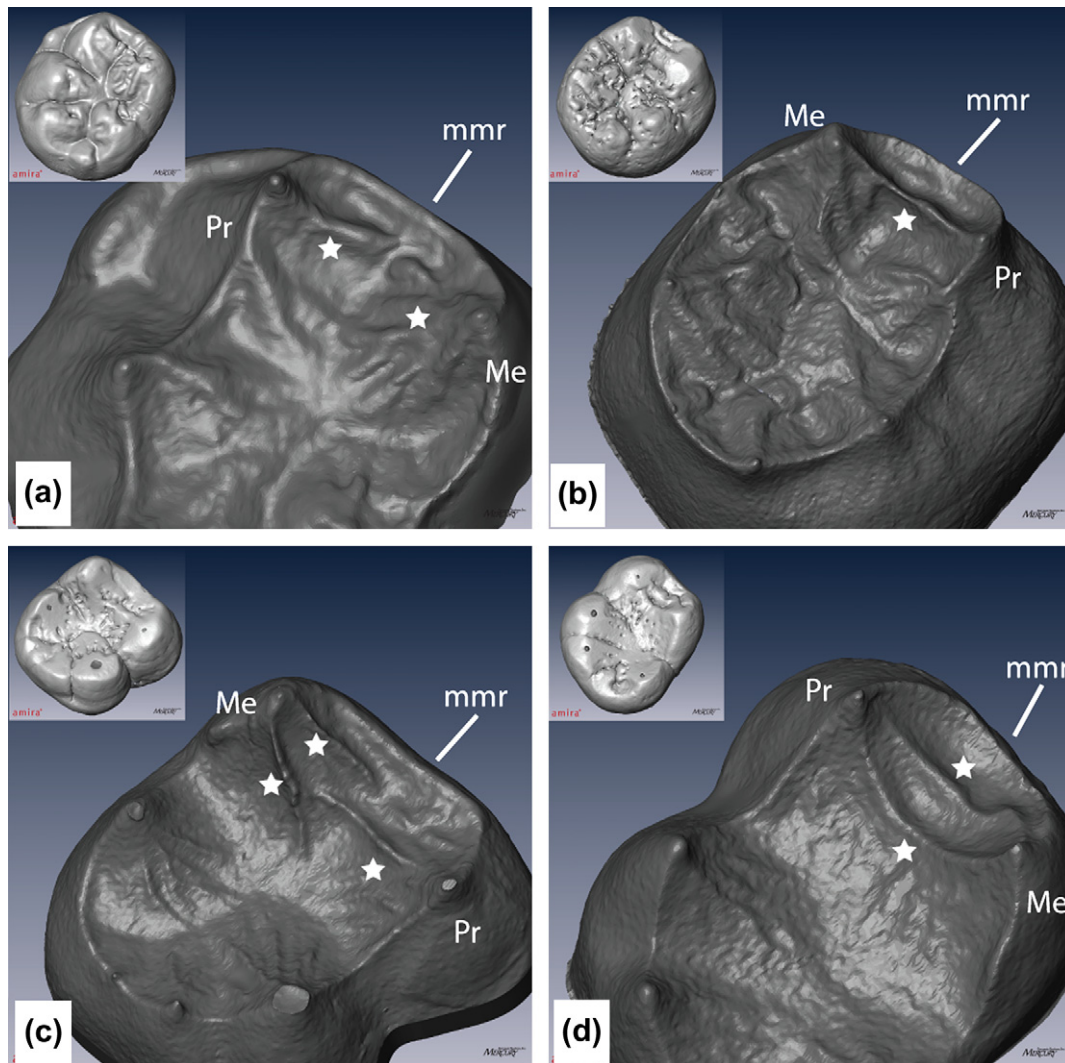


Fig. 7. Selected examples of TCP expression at the EDJ in the study sample (OES of each specimen is inset in top left corner). Abbreviations: Pr = protoconid, Me = metaconid, mmr = mesial marginal ridge. Crest features are adjacent to white stars. (a) A large crest from the protoconid DH with multiple small crests on the metaconid DH (lower second molar of *A. africanus*, STW 424); (b) single, pronounced middle crest (lower first molar of *H. neanderthalensis*, SD 540); (c) two crests from the metaconid DH and one crest from the protoconid DH that do not join (lower second molar of *P. t. verus*, TAI 11779); (d) mesial and middle crests (lower first molar of *P. t. verus*, TAI 13433). Images are not to scale.

the study sample. Like accessory cusps, trigonid crest patterns present at the OES derive from the EDJ. The high prevalence of a middle crest on the EDJ of the *H. neanderthalensis* sample supports conclusions by Bailey (2002) that the midtrigonid crest is a characteristic feature of this taxon compared to modern humans. However, more comparative studies are needed before it will be possible to say whether the manifestation of this trait in *H. neanderthalensis* is derived or primitive. Investigation of the EDJ has shown that trigonid crest patterning can be highly variable, and that sorting this variation into mid-trigonid (Wu and Turner II, 1993; Bailey, 2002) and a distal trigonid crest traits (Korenhof, 1982; Sasaki and Kanazawa, 1999) may be unwarranted for some taxa (e.g., *P. troglodytes* ssp.). Crest features between DHs, including mesial, middle, and distal trigonid crests, as well as the crest that periodically forms between the entoconid and hypoconulid DHs (Fig. 3d), may be related to structural properties (e.g., elasticity or

turgidity) of the tissues involved in tooth growth and to their interactions during development. Butler (1956: 60–61) noted that ridges/crests “are probably produced by tensions set up in the epithelium by the relative movement of cusps, owing to unequal growth or to changes in the shape of the follicle.” Crests may reflect the timing and rate of DH growth and their placement with respect to other DHs on the developing tooth germ.

Our analysis of the EDJ suggests that protostylid expression is influenced by three primary factors. First is the relative location of the DHs of the main buccal cusps (i.e., the DHs of the protoconid, hypoconid, and hypoconulid) with respect to the buccal margin of the tooth crown (e.g., centrally placed versus located near the lingual margin of the crown base). The relative placement of the buccal DHs can also be influenced by buccal expansion of the tooth crown base during growth. The second factor is the shape of the buccal aspect of the

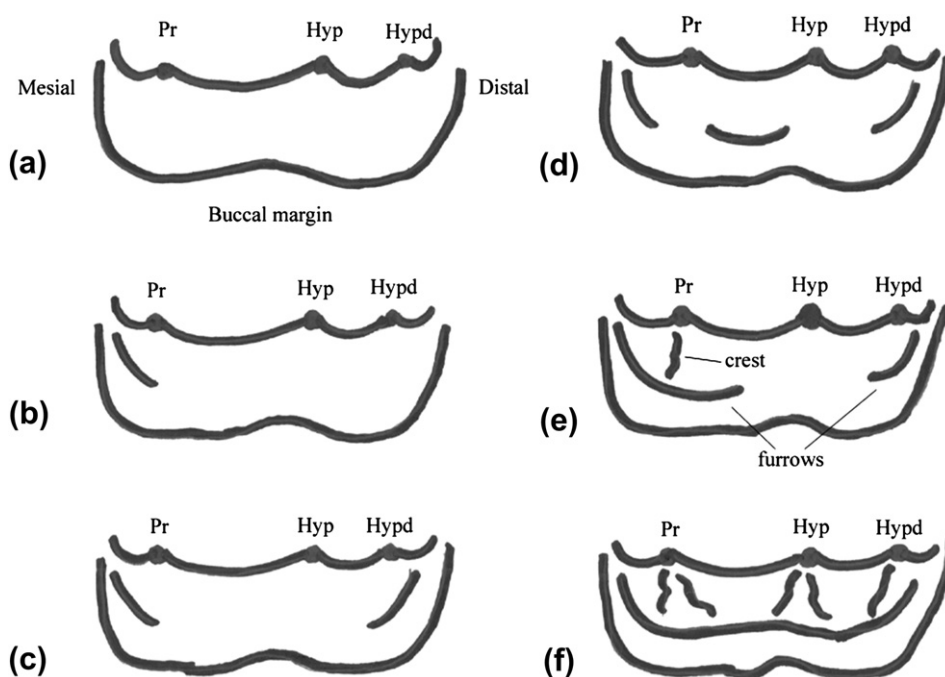


Fig. 8. Schematic representation of protostylid variation present at the EDJ in the study sample. View is towards the buccal face of the EDJ including the buccal margin, the tips of the DHs (represented as solid black circles) of the protoconid (Pr), hypoconid (Hyp), and hypoconulid (Hypd), and the marginal ridge that runs between them. (a) No protostylid morphology along the buccal margin of the EDJ crown surface; (b) minor furrow on the mesial surface of the protoconid DH; (c) similar to (b) and a second furrow on the distal surface of the hypoconulid DH; (d) similar to (c) with a cingulumlike furrow between the protoconid DH and hypoconid DH; (e) pronounced furrow running from the mesial border of the protoconid DH to the mesial surface of the hypoconid DH with a furrow on the distal surface of the hypoconulid DH (small crests are variably manifest on the surface of the protoconid DH); (f) a continuous, cingulumlike furrow across the whole buccal margin of the EDJ in association with crests on the surfaces of the buccal DHs. This schematic is not exhaustive of the manifestations of protostylid morphology present in the study sample.

protoconid and hypoconid DHs (e.g., the presence of crests running towards the cervical margin of the tooth; Figs. 8e,f and 9d), and the third factor (though of a lesser influence) is the thickness and distribution of enamel on the buccal side of the dentine crown. Thus, protostylid morphology, including crests, depressions, cusps, cuspsules, wrinkles, and fissures, derives from the EDJ with only minor modification caused by the differential deposition of enamel. A possible exception to the minor influence of enamel deposition on OES expression of the protostylid is *P. robustus*; an ongoing analysis of a larger sample of molars from this taxon (Skinner et al., unpub. data) indicates that the relatively thick enamel of this taxon can mask EDJ expression in some cases. In answer to our third question, protostylid development appears similar among the study taxa.

If cingular remnants and furrowlike features on the mesial and distal portions of the buccal side of the crown are developmentally related, then they should not be considered as separate traits for the purpose of dental trait analysis (contra Hlusko, 2004). Robinson (1956: 199–120) considered the protostylid a complex character in South African fossil hominins due to “remnants of a cingulum farther back on the buccal surface as well as on the whole of the mesial face of the crown.” The complexity of this trait within the hominoid clade has also been noted by Bailey and Wood (2007). If further evidence supports developmental nonindependence among mesial, central, and distal components of protostylid morphology, this

trait could prove to be difficult to objectively and meaningfully subdivide into an ordinal scale. Examination of crown size and DH size/spacing, which are thought to be under separate genetic control (Harris and Dinh, 2006; Cai et al., 2007), may lead to a better understanding of protostylid variation within and among taxa.

Further research will explore the interaction between DH height and placement, the overall size of the molar crown, and the collective influence of all of these factors on the expression of C6s, C7s, trigonid crest pattern, and protostylids. We agree with Bailey and Wood (2007) that new scoring criteria need to be developed for several of the traits relevant to the study of early hominins, and we suggest that simultaneous examination of the EDJ in addition to the OES may help in the identification of independent discrete traits with a demonstrably similar pattern of development.

Conclusion

The results of this analysis indicate that the presence and degree of morphological expression of four dental traits (C6, C7, trigonid crest pattern, and protostylid) is largely determined by the factors controlling the shape of the EDJ, and that differential enamel deposition does not significantly alter the morphology of these traits or create traits at the outer enamel surface that are not present at the EDJ. For some traits, such as the protostylid and trigonid crest pattern, EDJ

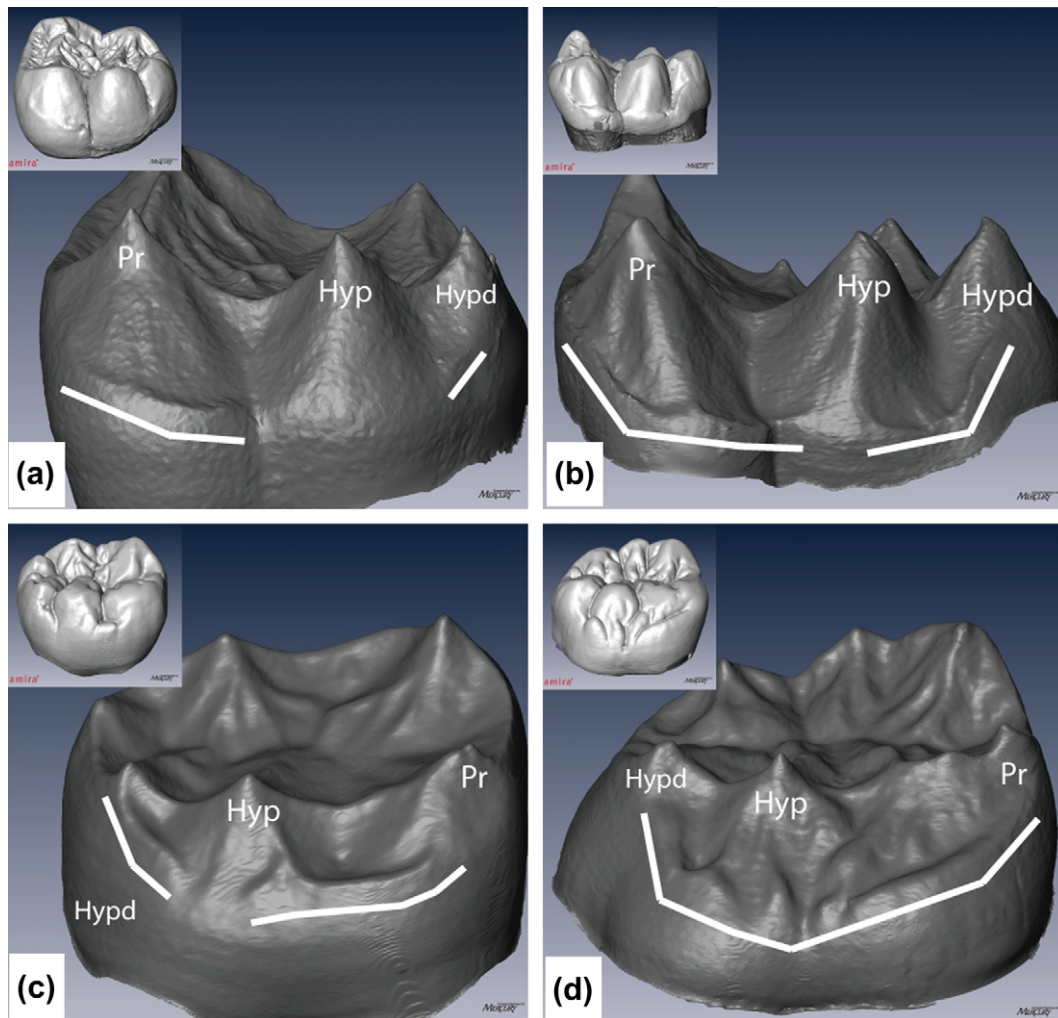


Fig. 9. Selected examples of protostylid expression at the EDJ in the study sample (OES of each specimen is inset in top left corner). Abbreviations are: Pr = protoconid, Hyp = hypoconid, Hypd = hypoconulid. Features associated with the protostylid are highlighted by white solid lines. (a) Minor furrows extending across the buccal face of the protoconid DH and below the hypoconulid DH (lower second molar of *P. t. verus* (TAI 13437)); (b) cingulumlike furrows extending across most of the buccal face (lower second molar of *G. g. beringei*, NMNH 543037); (c) prominent furrows below the hypoconulid DH and between the hypoconid and protoconid DHs (lower second molar of *P. robustus*, SK 3974); (d) prominent furrows along the mesiobuccal face of the EDJ with small tubercle features below the hypoconid DH that are also expressed on the enamel surface (lower second molar of *A. africanus*, STW 560E). Images are not to scale.

expression reveals considerable variation within nonhuman primate taxa that will require new trait descriptions and standardized classifications for comparison within and between taxa. In some cases, EDJ morphology suggests that traits that appear similar at the enamel surface in different taxa may not be the result of similar patterns of development, thus limiting their utility for phylogenetic analysis. Furthermore, because of the significant morphological contribution of the EDJ to trait expression at the OES, the EDJ of worn teeth may be used as a proxy for the OES expression of these traits, and this may well result in increases in the size of study samples of early hominin taxa.

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