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Homology and Variability of Accessory Cusps in Hominoid Molars Uncovered at the Enamel-Dentine Junction

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Short Running Title: Accessory cusps in hominoid molars

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Abstract

Evolutionary studies of mammalian teeth have generally concentrated on the adaptive and functional significance of dental features, whereas the role of development on phenotypic generation and as a source of variation has received comparatively little attention. The present study combines an evolutionary biological framework with state-of-the-art imaging techniques to examine the developmental basis of variation and homology of accessory cusps. Scholars have long used the position and relatedness of cusps to other crown structures as a criterion for developmental homology, which can be evaluated with greater accuracy at the enamel-dentine junction (EDJ). Following this approach, we collected digital models of the EDJ and outer enamel surface of more than 1,000 hominoid teeth to examine whether cusp 5 of the upper molars (UM C5) and cusps 6 and 7 of the lower molars (LM C6 and LM C7) were associated each with a common developmental origin across species. Results revealed that each of these cusps can develop in a variety of ways, in association with different dental tissues (i.e. oral epithelium, enamel matrix) and dental structures (i.e. from different cusps, crests and cingula). Both within and between species variability in cusp origin was highest in UM C5, followed by LM C7, and finally LM C6. The lack of any species-specific patterns suggests that developmental homology may not be useful for identifying phylogenetic homology, at least with respect to accessory cusps in hominoids. An important and unanticipated finding of this study was the identification of a new taxonomically informative feature at the EDJ of the upper molars, namely the post-paracone tubercle (PPT). We found that the PPT was nearly ubiquitous in *H. neanderthalensis* and the small sample of Middle Pleistocene African and European humans (MPAE) examined, differing significantly from the low frequencies observed in all other hominoids, including Pleistocene and recent *H. sapiens*. We emphasize the utility of the EDJ for human evolutionary studies and demonstrate how features that look similar at the external surface may be the product of different developmental patterns. This study also highlights the importance of incorporating both developmental and morphological data into evolutionary studies in order to gain a better understanding of the evolutionary significance of dental and skeletal features.

Key words: dental development, accessory cusps, hominoid molars, developmental homology

Introduction

The concept of homology has been the subject of intense debate since it was delineated in the mid-nineteenth century by Sir Richard Owen as “the same organ in different animals under every variety of form and function”. The history of modern debates on homology has been extensively documented elsewhere (see Patterson, 1982; Hall, 1994 and references therein). Within an explicitly phylogenetic framework, homology is defined as similarity between taxa that is inherited from their last common ancestor, and is distinguished from homoplasy, which is regarded as any morphological resemblance that results from processes other than common ancestry (Simpson, 1961; Hennig, 1966; Patterson, 1982; Lieberman, 1999; Lockwood & Fleagle, 1999). Unless otherwise noted, we use these definitions here.

Because the fossil record of many mammals is represented predominantly by teeth, studies on cusp homologies have been central for understanding the evolution of tribosphenic molars from single-cusped reptilian teeth, and concomitantly early mammalian evolutionary history (Butler, 1939, 1978, 1990; Patterson, 1956; Hershkovitz, 1971). These studies also document the limited number of ways in which teeth can vary and evolve. All therian mammals form a monophyletic group, which descended from a common ancestor with tribosphenic molars in which the paracone, protocone and metacone of the upper molars form the trigon, and the protoconid, paraconid and metaconid of the lower molars form the trigonid (Hershkovitz, 1971; Luo et al. 2001). However, accessory cusps and cuspules forming in addition to these structures are particularly prone to parallel evolution. In fact, considering the great diversity of mammalian tooth shapes, homoplasy of dental features appears to be pervasive (Jernvall, 1995). Butler (1978), for example, reported that the mesostyle and metastylid have developed independently in several groups, and noted that the exact developmental origin of these and other structures is generally unknown. In a classic example, Hunter and Jernvall (1995) noted that the hypocone has independently evolved more than 20 times in mammals (see also Butler, 1956; van Valen, 1982). They found that this cusp most commonly derived from either the lingual cingulum or the metaconule. The hypocone may also develop from the metacone or protocone, and in some taxa its mode of origin remains unknown. Even within the primate order the hypocone may have evolved more than once (Gregory, 1922; Butler, 2000; but see Butler, 1963; Hershkovitz, 1977). This appears to be the case for Eocene primates whose hypocone evolved from the lingual cingulum in European adapines and from the *Nannopithex* fold in North American notharctines (Gregory, 1922; Butler, 2000; Anemone et al., 2012).

Given the high likelihood for homoplasy, Butler (1978, 1985) and van Valen (1994) proposed that cusp names should only be used as topographical terms, without implying phylogeny. However, even the “identity” of cusps has sometimes proven difficult to determine. For example, Sánchez-Villagra and Kay (1996) disproved the long-held view that the upper molars of diprotodont marsupials possessed a metaconule rather than a hypocone. More recently, Jernvall et al. (2008) found that the paracone of *Hapalemur simus* upper premolars has shifted distally to become the metacone. Jernvall et al. (2008) also stress the need to incorporate developmental data in identifying homologous cusps in the phylogenetic sense. Direct experimental testing in fossils is impossible; and, in most extant mammals it is unfeasible. However, addressing cusp homology within a developmental framework can be at least partially achieved through the analysis of the internal surface of teeth at the enamel-dentine junction (EDJ), as shown by the pioneering studies of Kraus (1952), Korenhof (1960), and Corruccini (1987, 1998).

The EDJ is the interface between the enamel cap and dentine crown and preserves the end point of growth of the inner enamel epithelium, whose size and shape determine the main crown configuration (Schour and Massler, 1940; Butler, 1956; see also Skinner, 2008; Ortiz et al. 2012; Morita et al. 2016). Recently, Anemone et al.'s (2012) study of adapid upper molars at the EDJ supported early assessments by Gregory (1922) and Butler (2000) that the hypocone evolved convergently among closely related primate groups from the Eocene. A preliminary study of the EDJ by Skinner et al. (2008) also suggested that cusp 6 of hominoid lower molars can form in association with the hypoconulid or within the distal fovea. Similarly, they found that cusp 7 can originate in two developmentally different ways, such that it can derive from either the metaconid or interconulid.

The presence and degree of expression of accessory cusps have been used widely in species diagnoses and phylogenetic reconstructions of the hominin fossil record (Wood et al. 1983; Wood & Engleman, 1988; Suwa et al. 1996; Bailey, 2002; Bailey & Wood 2007; Bailey et al. 2009; Martinón-Torres et al. 2007, 2008, 2012; Irish et al. 2013). However, it is unknown whether or not each of these cusps is associated with a single developmental origin, and therefore, the evolutionary implications for homology remain uncertain. Building upon previous studies by Skinner et al. (2008, 2014) and Anemone et al. (2012), we use micro-computed tomography (microCT) to assess accessory cusp variation at the EDJ in a taxonomically broad sample of 1,168 extant and fossil hominoid molars. Specifically, we focus our analyses on cusp 5 (also known as the metaconule by Turner et al. 1991; but see below) of the upper molars and cusps 6 and 7 (Turner et al.'s [1991] entoconulid/*tuberculum sextum* and metaconulid/*tuberculum intermedium*, respectively) of the lower molars. We examine the different developmental ways in which these accessory cusps and cuspules can form in the hominoid lineage and whether or not there are any species-specific patterns that can inform us about homology. Our main hypothesis is that accessory cusps and cuspules that look superficially similar at the external surface may have different origins and that the likelihood of homoplasy of these dental features in hominoids is high. We also examine variation in the post-paracone tubercle (PPT) of the upper molars and its usefulness for hominoid systematics.

Materials and methods

Study sample

Our sample includes three-dimensional (3D) models of the EDJ and outer enamel surface (OES) of 466 upper and 702 lower molars of extant and extinct hominoids (Table 1). All data derive from original specimens subjected to microCT. The fossil sample comprises the following species (with number of teeth in brackets): *Australopithecus anamensis* (n=17), *A. afarensis* (n=20), *A. africanus* (n=112), *Paranthropus aethiopicus* (n=2), *P. boisei* (n=14), *P. robustus* (n=113), *Homo* sp. (n=21; mainly specimens attributed to *H. habilis sensu lato*), *H. erectus s. l.* (n=14), the Middle Pleistocene African and European group (MPAE) (n=8), *H. neanderthalensis* (n=147), and Pleistocene *H. sapiens* (n=66). This reflects the taxonomic nomenclature most commonly used by researchers to date. The inclusive categories *H. habilis s.l. H. erectus s.l.* and MPAE were used here given the small number of available specimens assigned to these groups. The detailed list of the fossil specimens used can be found in Tables S1 and S2.

Extant samples include contemporary *H. sapiens* (n= 267), *Pan paniscus* (n=34), *P. troglodytes* ssp. (n=179), *Gorilla* sp. (n=72), and *Pongo* sp. (n=82). The contemporary *H. sapiens* sample comprises individuals of European or African ancestry, or of unknown geographic provenience. The *P. troglodytes* sample includes *P. t. verus* (UM=39 and LM=54), *P. t. troglodytes* (UM=11 and LM=23), *P. t. schweinfurthii* (UM=8 and LM=7), and *P. troglodytes* of unknown subspecific affiliation (UM=12 and LM=25). The *Gorilla* sample includes *G. gorilla* (UM=34 and LM=31), and *G. beringei* (UM=2 and LM=5), and that of *Pongo* consists of *P. pygmaeus* (UM=8 and LM=15), *P. abelii* (UM=14 and LM=12), and *Pongo* sp. (UM=12 and LM=21). Sample size per trait varies due to differential preservation and wear. Although we did not include known antimeres, some individuals are represented by more than one molar (see Tables S1 and S2). Given that sex is unknown for most fossil specimens, we made no attempt to control for sex. However, it has been demonstrated that, with few exceptions, dental morphological traits show no consistent sexual dimorphism in living humans (Scott and Turner, 1997). This is also true of extant great apes, despite marked differences in tooth size between males and females (Uchida, 1996; Pilbrow, 2003).

Data collection procedures and analyses

Each specimen was scanned using microCT, with either a BIR ACTIS 225/300 (130 kV, 100 µA, 0.25 brass filter) or a Skyscan 1172 (100 kV, 94 µA, 2.0 mm aluminum and copper) scanner. Pixel dimensions and slice spacing of the resultant images ranged between 10 and 30 microns. The complete image stack of each tooth was filtered using a computer-programmed macro that employs a three-dimensional median and mean-of-least-variance filter (each with a kernel size of one or three) to improve tissue gray-scale homogeneity and facilitate tissue segmentation (Wollny et al., 2013). Filtered image stacks were imported into the Avizo (FEI Visualization Sciences Group), and enamel and dentine tissues were segmented manually. Only teeth with well-distinguished gray-scale pixel values and thus with a clear separation of the enamel and dentine tissues were segmented. Digital surface models (.ply format) of the EDJ and OES were produced in Avizo using the surface generation module with the unconstrained smoothing parameter.

The definition of cusp 5 of the upper molars (UM C5) and cusps 6 and 7 of the lower molars (LM C6 and LM C7, respectively) followed standards outlined by the Arizona State University Dental Anthropology System (ASUDAS) (Turner et al. 1991). In order to assess the degree of trait correspondence between the EDJ and OES, cusps were classified as present at a given surface if any expression other than ASUDAS grade 0 was detected. When more than one cusps/cuspules were present at the "regular" position of a given accessory cusp, these were considered (at least preliminarily) part of the same accessory cusp complex (e.g. LM "double" C6 reported by Bailey and Wood [2007] and Skinner et al. [2008]). For each trait, the correspondence between the EDJ and OES was examined using the following scoring system: a) grade 0: accessory cusp absent; b) grade 1: one cusp present; c) grade 2: two cusps present; and d) grade 3: three or more cusps present. This system allowed us to assess whether these cusps can develop entirely from enamel deposition. Following Skinner and Gunz (2010), a "suspected" category was also included to incorporate those cases where it was unclear whether or not an accessory cusp was present (see also Turner et al. [1991] for additional examples of indecisive categories). Each "suspected" accessory cusp was given a score of 0.5. Data were collected both at the EDJ and OES and to avoid errors associated with worn or poorly preserved teeth, only complete molars with little-to-no dental wear (equivalent to Molnar's [1971] first three wear stages) were included for analysis. Concordance in trait expression between the two surfaces was tested using the non-parametric Spearman's rank correlation coefficient, calculated in PAST (Hammer et al. 2001).

If the accessory cusp was not entirely the result of enamel deposition, the developmental origin of each feature was examined at the EDJ. Following van Valen (1994), assessments of trait origin were based on topological relationships between two given dental structures such as crests, cusps/cuspules or cingula. For this purpose, tooth nomenclature followed Szalay (1969), Rosenberger and Kinzey (1976) and Swindler (2002). As they represent the majority of cases, analyses of trait origin focused on single-cusped features, although data on their multi-cusped variants are also briefly discussed. All teeth were scored twice, with scoring sessions separated by at least one month. When discrepancies between the two scoring sessions occurred, trait presence and origin were scored a third time and scores that matched between two given assessments were used as final data points. This third scoring session was also separated by a month from the second one. All molar types were pooled into two categories (upper and lower molars) to maximize sample sizes per taxon.

We also evaluated the post-paracone tubercle (PPT) of the upper molars, which occurs on the distal slope of the paracone. This feature was identified in Neandertals by Martin et al. (in press), but until now its presence and variation in other extant and fossil hominoids has not been assessed. This trait should not be confused with the lingual paracone tubercle, which occurs on the occlusal surface, distal to the mesial marginal tubercles (Kanazawa et al. 1990). Expressions of the PPT were classified into four categories: a) grade 0: PPT absent (distal slope of paracone is smooth); b) grade 1: shouldering present only; c) grade 2: faint-to-moderate tubercle present; and d) grade 3: marked tubercle present (Fig. 1). For PPT, the significance of the observed patterns was tested via bootstrapping (1,000 iterations) performed in R (R Core Team, 2012).

Results

Cusp 5 of the upper molars

Results of the Spearman's correlation coefficient provided in Table 2 reveal a high and significant concordance between UM C5 expressions at the EDJ and OES in extant great apes, *H. sapiens* (Pleistocene and recent), and *H. neanderthalensis*. For these taxa, only subtle differences in trait expression at the EDJ and OES were observed, with correlation coefficients ranging between 0.829 and 1. With the exception of two *H. neanderthalensis* specimens (see below), discrepancies always involved the "suspected" category. These discrepancies in most cases occur when subtle or blunt dentine horns were classified as "suspected" at the EDJ, but UM C5 was either present or absent at the OES. Interestingly, two molars from a sample of 41 Neandertal specimens exhibited a UM C5 cuspule at the OES with no equivalent structure at the EDJ. Although sample sizes for *P. paniscus* and MPAE were too small to run any statistical analyses, no trait expression differences were observed in the specimens examined.

The concordance between UM C5 expression at the EDJ and OES for *Australopithecus*, *Paranthropus* and early *Homo* species was moderate, with correlation coefficients ranging from 0.56 to 0.697 (Table 2). All correlations were statistically significant with *P. robustus* showing the lowest correlation between the two surfaces. The main source of discrepancy in these three groups was the result of one or more UM C5 cuspules present at the OES with no associated dentine horn(s) on its underlying surface. Although such cases were primarily represented by specimens with no UM C5 at the EDJ and one cuspule at the OES, there were instances in which UM C5 was present at both surfaces but the number of dentine horns at the EDJ did not correspond to the number of cuspules at the OES (Fig. 2). This was particularly evident in *Paranthropus*. It should be noted, however, that in no case was a moderate-sized or large UM C5 observed as present at the external surface when a dentine horn was absent at the EDJ.

Table 3 summarizes UM C5 frequency by taxon and developmental origin. Although the frequency of occurrence of this cusp was low in most taxa, when present, UM C5 may have its origin on the hypocone, metacone, or distal fovea/middle portion of the distal marginal ridge (Fig. 3). It may also arise directly from the buccal cingulum or from the occlusal surface in association with a distal crest (e.g. crest connecting the distal ridge with either the metacone or hypocone, or an independent crest on the distal fovea). Weak expressions of UM C5 can also appear later during tooth morphogenesis as a result of enamel deposition only. Although UM C5 most frequently arises as an outgrowth of the distal fovea/middle portion of the distal marginal ridge, there is a high degree of variability in its origin, both within and between species (Table 3). *A. africanus* exhibits a unique pattern in which UM C5 originates from the buccal cingulum in the majority of cases (42.9%). This is followed by cases of UM C5 derived from enamel deposition only (28.6%) and from the distal fovea (19%). The origin of UM C5 at the buccal cingulum was not observed in other taxa. Thick-enameled and megadont *P. robustus* and *P. boisei* also exhibited a relatively high frequency of UM C5 derived entirely from enamel deposition (39.1% and 33.3%, respectively), although in the majority of cases this cusp appears earlier during tooth development at the EDJ and arises from the distal fovea. In all cases of enamel-derived UM C5s, the cuspule does not exceed ASUDAS grade 2. Chimpanzees also show a distinct pattern in which UM C5 originates from the hypocone in highest frequency (57.1%). The high frequency of UM C5 deriving from the hypocone in *P. troglodytes* contrasts with the low incidence (0%-15.4%) of this variant in other taxa.

When present, UM C5 most commonly occurs as a single-cusped feature. However, cases of two or more "UM C5" dentine horns observed at the EDJ were also found in most groups (Table S3). In these cases, the dentine horns may have their origins from the same (e.g.

hypocone) or different (e.g. hypocone and buccal cingulum) structures. Most cases of multiple "UM C5" dentine horns involved the distal fovea/distal marginal ridge. Among samples with more than ten observations, the presence of two "UM C5" cusps deriving from two different structures was highest in *A. africanus* and *H. neanderthalensis* (8.3% and 7.0%, respectively).

Post-paracone tubercle of the upper molars

Frequencies and degrees of expression of the post-paracone tubercle (PPT) at the EDJ are provided in Table 4. Results reveal that this feature is nearly ubiquitous in Neandertals, with only 1.6% of the 64 specimens examined showing a smooth surface on the distal paracone. When present, 70.3% of Neandertal upper molars exhibit either a pronounced or blunt additional dentine horn, distal to that associated with the tip of the paracone. The remaining Neandertal specimens examined (28.1%) exhibit at least some shouldering on the distal slope of this cusp. Steinheim (UM1, UM2 and UM3) and Thomas Quarry I (UM1 and UM3) were the only MPAE upper molars available for study. Both show some expression of PPT on all molars. The nearly ubiquitous presence of the PPT in *H. neanderthalensis* (and MPAE if the above sample is representative) contrasts with the low frequency of this trait in all other hominoids, where more than 67% of individuals in each taxon (except for Pleistocene *H. sapiens*) lack it completely, and when present, the PPT is mainly represented by the shouldering type (Fig. 4). The majority of the Pleistocene *H. sapiens* teeth lack a PPT (52.4%), but a marked or blunt dentine horn on the distal paracone was found in 28.5% of the sample (9.5% for marked and 19% for blunt PPT). Although most similar to *H. neanderthalensis* (and MPAE) frequencies compared to other taxa, a value of 28.5% is far below the 70.3% seen among Neandertals. Cases of marked expression of PPT were also found in recent *H. sapiens* (2.5%), as well as in *Pongo* (3.6%). The only case seen in *Pongo*, however, was located more distally on the paracone relative those observed in *Homo* species. Table S4 presents the results of the bootstrapping analysis (95% confidence), which reveals that both moderate (blunt) and marked expressions of the PPT in *H. neanderthalensis* (39.9%-59.2% and 17.1%-29.6%, respectively) differ significantly from all other hominoid groups examined (0%-28.6% for moderate expressions and 0%-16.9% for marked expressions), including Pleistocene *H. sapiens.*

Cusp 6 of the lower molars

Table 5 provides the correlation coefficients for LM C6 expressions at the EDJ and OES. Except for *P. robustus* (r=0.63), all taxa show a high correlation in trait expression between the two surfaces, with values ranging between 0.79 and 1. All values are statistically significant (*p*<0.001). As in cusp 5 of the upper molars, the few cases of disagreement observed for LM C6 involved the "suspected" category either at the EDJ or OES. These discrepancies resulted primarily from small dentine horns that were not clearly represented by a cusp at the OES. Less frequent were cases in which a LMC6 was "suspected" at the EDJ but either absent or present at the OES. Out of the more than 500 extant and fossil hominoid molars examined, only two specimens (one recent *H. sapiens* and one *P. troglodytes*) showed a small but clear dentine horn at the EDJ with no equivalent structure at the OES. In contrast, cases of small LM C6 cuspules produced entirely by enamel deposition were found in *P. robustus* and *P. boisei*, and to a lesser extent in *A. africanus*. In all cases LM C6 structures resulting entirely from enamel deposition were small (> ASUDAS grade 2).

Table 6 summarizes LM C6 trait frequency in developmental origins by taxon as revealed by the examination of 612 lower molars. This study supports Skinner et al.'s (2008, 2014) conclusions suggesting that LM C6 may form in proximity to the dentine horn of either the hypoconulid or entoconid. LM C6 may also arise independently from the distal fovea, and in rare occasions, this cusp may originate from a dentine horn on the entoconid-hypoconulid crest (or an independent crest on the distal fovea) at the distal portion of the occlusal surface (Fig. 5). Cases of enamel-derived LM C6 with no underlying dentine horn associated with the cusp are rare (2.5%-5.9%). Despite the different developmental ways in which LM C6 may form, this cusp appears to be less variable than the UM C5, both within and between species. With some exceptions (see below), all observations from *Australopithecus, Paranthropus, H. habilis s.l.,* MPAE*, H. sapiens*, *P. paniscus,* and *Gorilla* suggest that the distal fovea is the primary, and in some species only, source of LM C6 origin. Exceptions include the enamel- or occlusal-derived LM C6s present in *A. africanus* and *P. robustus*. The frequency of LM C6 formed on the occlusal surface without involvement of the marginal ridge was also particularly high in *Gorilla* (25%). Furthermore, *H. neanderthalensis* is the only hominin sample in which a moderate frequency (24.1%) of LM C6s originated from the hypoconulid. A similar pattern was observed in chimpanzees (31.1%). Finally, cases of LM C6 arising from the entoconid were only observed in *Pongo* (10%).

Examination at the EDJ shows that cases of two or more “LM C6” dentine horns are not rare in hominoids, with frequencies ranging from 2.2% to 27.3% (Table S5). For samples with more than ten observations, absence of this feature was only found in *A. afarensis*, *H. habilis s.l.* and *H. sapiens* (both Pleistocene and recent). Multiple LM C6s usually arise from the same structure and rarely from different structures. Except for one *H. neanderthalensis* and one *P. troglodytes* showing a LM “double” C6 entirely arising from the hypoconulid, all cases of multiple "LM C6" dentine horns originating from the same structure were associated with the distal fovea.

Cusp 7 of the lower molars

All taxa show a high and significant correlation in LM C7 expressions at the EDJ and OES (Table 7). Correlation coefficients range from 0.73 to 1, with the lowest values found in recent *H. sapiens* (r=0.73), *A. africanus* (r=0.75), and *P. robustus* (r=0.77). However, discrepancies are not substantial and in the majority of cases involve the "suspected" category. Major sources of discrepancy include the presence of a marked (and sometimes pointed) shouldering on the distal slope of the metaconid as revealed at the EDJ, which may or may not be associated with a clear LM C7 at the OES. This is particularly the case in *H. sapiens* (Pleistocene and recent), *P. paniscus*, and *P. troglodytes*. Except for one *A. africanus* and one recent *H. sapiens* specimen, there is no evidence of LM C7 formed entirely by enamel deposition. In these two cases, each molar shows one LM C7 dentine horn but two small cuspules associated with this cusp at the OES.

From the 665 hominoid molars examined, LM C7 is only present in 130 (19.5%) teeth. Frequencies of LM C7 morphological types per taxon following Skinner et al's (2008) criteria are given in Table S6. Variation in LM C7 origin is summarized in Table 8 and Fig. 6. This study supports Skinner et al. (2008), who suggested that LM C7 can form from either the distal shoulder of the metaconid (Skinner's metaconulid type) or the lingual groove (Skinner's interconulid type). Three additional variants were identified here such that LM C7 can derive from the mesial slope of the entoconid, the occlusal surface or from enamel deposition alone. However, these variants rarely occur and can be considered exceptions to the most common manifestations proposed by Skinner et al. (2008). The LM C7 most frequently arises from the metaconid in *Australopithecus*, *Paranthropus*, *Pan* and recent *H. sapiens*, whereas it is most commonly associated with the lingual groove in *Homo* (except for recent *H. sapiens*), *Gorilla* and *Pongo*. Some additional subtle patterns include the high occurrence of LM C7 in *H. habilis s.l.* (62.5%) compared to other groups, as well as the large number of molars with shouldering on the metaconid in *Pan* (*P. troglodytes* and *P. paniscus*) and to a lesser extent in *H. sapiens* (Pleistocene and recent). This contrasts with most other taxa examined, which generally exhibit a smooth surface on the metaconid when LM C7 is absent (see Table 8). Noteworthy is that the metaconid shouldering does not necessarily represent an earlier or interrupted stage of LM C7 formation, as shouldering can also occur in conjunction with the clear presence of this cusp. Turner et al.'s (1991) ASUDAS also included an indecisive category ("grade 1A: a faint tip-less cusp 7 occurs displaced as a bulge on the lingual surface of cusp 2" p.24) for LM C7 at the OES, which appears to correspond to the shouldering type observed at the EDJ. Analyses of the EDJ also show that molars with LM "double" C7s are extremely rare (Table S7). Only one chimpanzee presents this feature among the more than 650 hominoid teeth studied.

Discussion

The use of marginal tubercles on the paracone as taxonomic markers has been overlooked, likely because they are difficult to detect at the OES. This study has demonstrated that the post-paracone tubercle is highly distinctive of some hominoid groups. From the 64 Neandertal upper molars examined, only one specimen shows no traces of PPT. More than 70% of the Neandertal sample exhibits a PPT with either a clear or blunt tubercle next to the tip of the cusp. This appears to be derived in *H. neanderthalensis* (and possibly MPAE based on the five individuals examined) relative to ancestral condition seen in earlier hominins, which show a smooth surface on the distal slope of the paracone. The occasional presence of this trait in Pleistocene and, to a lesser extent, recent *H. sapiens,* also suggests that this taxon likely inherited the developmental predisposition for PPT from its last common ancestor with Neandertals. This is supported by a recent 3D cranial reconstruction of the hypothetical last common ancestor (LCA) of *H. neanderthalensis* and *H. sapiens* by Mounier and Lahr (2016), who suggested that this LCA was more similar to Neandertals. Under this scenario, the presence of PPT in *H. sapiens* may have been gradually lost through genetic drift and periods of drastic demographic change. The nearly ubiquitous presence of PPT in *H. neanderthalensis* compared to contemporaneous *H. sapiens* adds to the taxonomically informative morphological features identified by Bailey (2002, 2006) for differentiating the upper molars of these two taxa.

As expected given the diverse origins for the hypocone and other accessory cusps (Gregory, 1922; Butler, 1952, 1956, 1978; Jernvall, 1995; Hunter and Jernvall, 1995) and expanded on the findings of Skinner et al. (2008, 2014), this study shows that cusp 5 of the upper molars and cusps 6 and 7 of the lower molars can form in a variety of ways, in association with different dental tissues (i.e. oral epithelium, enamel matrix) and dental structures. Within and between group variability in trait origin is highest in UM C5, followed by LM C7 and finally LM C6, which shows a clear tendency across all hominoids to arise as an outgrowth of the distal fovea. This high degree of variability poses problems to a landmark-based approach to study evolutionary novelties. The inconsistency of cusp origin both within and between species unfortunately makes Klingerberg's (2008) proposed method of landmark duplication unsuitable for morphological innovations associated with hominoid molar shape.

Although most evolutionary biologists today have adopted a phylogenetic definition of homology, as a post hoc definition, this requires a good understanding of the evolutionary relationships among members of a clade and their patterns of character distribution (Simpson, 1961; Hennig, 1966; Hall, 1994; Rieppel, 1994; Lockwood and Fleagle, 1999). This is especially challenging when applied to the fossil record, and in particular, to hominin evolution. Furthermore, it has been argued that it is impossible to attribute morphological similarities to common ancestry without a clear understanding of other causes that may lead to these similarities (Lieberman, 1999). In order to overcome these limitations, alternative definitions of homology beyond the phylogenetic framework have been proposed over the past decades. Among them, the concept of developmental homology has been of main interest, which can broadly be defined as the sharing of common developmental processes (Roth, 1984; Lieberman, 1999). The lack of any species-specific patterns of UM C5, LM C6 and LM C7 origin suggests that developmental homology, in this case, may not be useful for identifying phylogenetic homology. These two concepts, however, are not always mutually exclusive, nor must they agree with each other (Lieberman, 1999).

Whether the approach followed here can be used as a valid criterion for determining cusp homologies at different taxonomic levels has been the subject of debate (Simpson, 1955; Butler, 1956, 1963, 2000; van Valen, 1994), but we suggest caution when using accessory cusps for assessing hominoid evolutionary relationships as cusps that look similar at the external surface may have originated from different dental structures or tissues. This issue is particularly clear for cases of “enamel cusps/cuspules”, which are entirely the product of enamel formation and appear later in tooth development compared to those associated with the growth and folding of the inner enamel epithelium. Cases of enamel-derived accessory cusps/cuspules are rare in hominoids (and other mammals), although they appear in moderate frequencies in *Paranthropus* and, to a lesser extent, *Australopithecus* upper molars. From the developmental standpoint, it is likely that the presence of enamel-derived cusps in these taxa (particularly in *Paranthropus*) is the product of a combination of factors, including the expansion of the distal segment of teeth (talon/talonid) and "hyper–thick" enamel (see Grine, 1988 and references therein), along with low and blunt molar cuspal configuration, which reduces the number of dentine horns (or more specifically, enamel knots) that can arise before reaching the developmental threshold for cusp formation and termination of crown morphogenesis (see Jernvall, 2000).

Identifying developmental homoplasy among accessory cusps formed prior to ameloblast-odontoblast differentiation may be more difficult. Current research on dental developmental genetics led by Jernvall and colleagues indicates that the number, size, and location of cusps (both primary and accessory cusps) within the tooth germ are dictated by the spatiotemporal pattern of enamel knot formation. Enamel knots are non-proliferative epithelial cells that appear sequentially at the tip of the future cusps. They produce both activator and inhibitor signaling molecules in a way that the presence and relationship of accessory cusps to other dental structures are largely determined by the size of the inhibition field. Only when escaping this inhibition field, a new enamel knot (and thus new cusp) can form. The effects of enamel knot formation within the developing tooth are cumulative. For this reason, later-forming cusps (as the accessory cusps studied here) are not only expected to be more variable, but also more subject to homoplasy (Jernvall, 1995, 2000; Jernvall & Jung, 2000; Jernvall et al. 2000; Thesleff et al. 2001; Salazar-Ciudad & Jernvall, 2002; see also Butler, 1967a,b). Within this framework, even small changes in the activator-inhibitor parameters may lead to structural changes in accessory cusp position, including its relationship to other cusps, crests and cingula.

Accessory cusps can develop not only in a variety of ways, but also their occurrence within the hominoid lineage appears to be highly variable. Although this variability makes the accessory cusps an important source of information for population-level studies of recent humans as demonstrated by Scott and Turner (1997), it brings into question their utility for assessing evolutionary relationships and discriminating between groups at higher taxonomic levels (Jernvall, 2000; Jernvall & Jung, 2000). Yet, some taxonomically informative patterns are evident: 1) UM C5 in *P. troglodytes* most frequently arises from the hypocone, which contrasts with the bucco-central position of the cusp in most hominins; 2) *A. africanus* presents a unique pattern where UM C5 most often derives from the buccal cingulum; and 3) *H. habilis s.l.* exhibits a notably high frequency of LM C7 at the EDJ (see also Wood and Abbott, 1983 for corresponding frequencies at the OES).

Given their variability and the strong likelihood of homoplasy, this study supports Butler (1978, 1985) and van Valen (1994) that accessory cusp terminology should only denote topography, without necessarily implying phylogenetic and/or developmental homology. However, the term metaconule, which has frequently been used to refer to UM C5 of the upper molars of recent humans, (Harris & Bailit, 1980; Townsend et al. 1986; Turner et al. 1991) may be inappropriate. This term was originally coined to denote a cusp occurring on the crista obliqua (postprotocrista) (Szalay, 1969, Rosenberger & Kinzey, 1976), and in fact, has been argued to be the source of hypocone development in several mammalian taxa (Hunter & Jernvall, 1995). Although the metaconule has been occasionally observed in humans and other hominoids (Hanihara, 1956; Kanazawa et al. 1990), this cusp more frequently occurs in platyrrhines and has also been observed in Oligocene *Parapithecus* (Rosenberger & Kinzey, 1976). Among the more than 450 upper molars examined, we only found four cases of a true metaconule (one recent *H.*

sapiens, one *H. neanderthalensis*, one *A. africanus*, and one *P. troglodytes*). Importantly, the *P. troglodytes* individual possesses both a metaconule *and* a small UM C5. The nature of the developmental processes underlying the formation of the metaconule and other occlusal-derived cusps, as well as whether or not they are similar to those arising from the marginal ridge remains unknown. Furthermore, the presence of UM "double" C5s (which can derive from similar or different structures) renders an additional complicating factor such that it is unclear if one of these cusps should be classified instead as UM C6. And if so, should it be so named regardless of its developmental origin? Cusp origin at the EDJ also suggests that the use of entoconulid and metaconilud for LM C6 and LM C7, respectively, may not be appropriate either as these terms imply an association of LM C6 with the entoconid and of LM C7 with the metaconid. While LM C7 in most cases does originate from the metaconid, cases of entoconid-derived LM C6 are infrequent. Although many questions remain to be answered, the results of this study not only have implications for cusp terminology, but also uncover previously unknown variation in tubercles and accessory cusps of hominoid upper and lower molars. This research also highlights the utility of the EDJ for human evolutionary studies and demonstrates that features that look similar at the external surface may be the product of different developmental patterns.

Acknowledgements

Access to specimens was kindly provided by the following institutions: Croatian Museum of Natural History, Ditsong National Museum of Natural History, Francisc Rainer Anthropology Institute, National Museums of Kenya, Musée d'Art et d'Archéologie du Périgord, Musée d'Archéologie Nationale de Saint-Germain-en-Laye, Musée d'Angoulême, Musée National de

Préhistoire des Eyzies, Musée de l'Homme, Museo Nacional de Ciencias Naturales, Max Planck Institute for Evolutionary Anthropology, Royal Museum for Central Africa, Museum für Vor und Frühgeschichte, National Museum of Ethiopia, National Museum of Natural History, American Museum of Natural History, Beaker People Project, Rockefeller Museum, Royal Belgian Institute of Natural Sciences, Senckenberg Research Institute, Germany; Sackler School of Medicine, Tel Aviv University, Leipzig University Anatomical Collection, University of Witwatersrand, Museum for Natural History, Institut National des Sciences du Patrimoine et de l'Archéologie, the Direction du Patrimoine Culturel and the Musée Archéologique de Rabat. We also thank Colin Menter for access to material from Drimolen, Bill Kimbel for access to material from Hadar, and Teku Jacob for access to material from Sangiran. We thank Heiko Temming, David Plotzki, and Lukas Westphal for technical assistance, and Susan Antón, Terry Harrison, Catalina Villamil, and Myra Laird for help and comments throughout this project. This research was supported by the National Science Foundation, the Wenner-Gren Foundation, the Leakey Foundation, the NYU GSAS James Arthur Fellowship, and the Max Planck Society.

Author Contributions

AO, SEB, MMS conceived and designed the study. JJH, MMS acquired the data; AO, MMS processed the data; AO analyzed the data. AO wrote the paper with input from all co-authors.

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Supplementary Information

Table S1. Fossil hominin upper molars used in this study including accession number locality/site and source.

Taxon	Specimen ID	Locality/Site (Country)	UM1	UM2	UM3	UM12	UM23	UM
A. anamensis	KNM-ER 30200	Koobi Fora (Kenya)	X	X				
A. anamensis	KNM-ER 30745	Koobi Fora (Kenya)	X					
A. anamensis	KNM-ER 7727	Koobi Fora (Kenya)		X				
A. anamensis	KNM-KP 30498	Kanapoi (Kenya)	X					
A. anamensis	KNM-KP 34725	Kanapoi (Kenya)		X				
A. cf. *afarensis*	KNM-WT 16003	West Turkana (Kenya)			X			
A. afarensis	AL 333x-1	Hadar (Ethiopia)			X			
A. afarensis	AL 144-23	Hadar (Ethiopia)	X					
A. cf. *afarensis*	Omo 18-1970-1799	Omo (Ethiopia)				X		
A. afarensis	AL 200-1a	Hadar (Ethiopia)	X	X	X			
A. afarensis	AL 333-86	Hadar (Ethiopia)	X					
A. africanus	MLD 28	Makapansgat (South Africa)			X			
A. africanus	STW 140	Sterkfontein (South Africa)			X			
A. africanus	STW 179	Sterkfontein (South Africa)			X			
A. africanus	STW 183	Sterkfontein (South Africa)	X	X				
A. africanus	STW 183 (STW 128)	Sterkfontein (South Africa)			X			
A. africanus	STW 188	Sterkfontein (South Africa)		X				
A. africanus	STW 189	Sterkfontein (South Africa)			X			
A. africanus	STW 204b (STW 206)	Sterkfontein (South Africa)		X				

A. africanus	STW 252	Sterkfontein (South Africa)	X	X	X	
A. africanus	STW 280 (STW 277)	Sterkfontein (South Africa)			X	
A. africanus	STW 280 (STW 283)	Sterkfontein (South Africa)	X			
A. africanus	STW 280 (STW 284)	Sterkfontein (South Africa)		X		
A. africanus	STW 449	Sterkfontein (South Africa)			X	
A. africanus	STW 498	Sterkfontein (South Africa)		X	X	
A. africanus	STW 524	Sterkfontein (South Africa)			X	
A. africanus	STW 529 (STW 530)	Sterkfontein (South Africa)		X		
A. africanus	STW 6	Sterkfontein (South Africa)			X	
A. africanus	STW 92	Sterkfontein (South Africa)			X	
A. africanus	Taung 1	Taung (South Africa)	X	X		
A. africanus	STS 1	Sterkfontein (South Africa)	X	X		
A. africanus	STS 21	Sterkfontein (South Africa)				X
A. africanus	STS 22	Sterkfontein (South Africa)		X		
A. africanus	STS 24	Sterkfontein (South Africa)	X			
A. africanus	STS 28	Sterkfontein (South Africa)		X	X	
A. africanus	STS 30	Sterkfontein (South Africa)		X		
A. africanus	STS 37	Sterkfontein (South Africa)		X	X	
A. africanus	STS 52	Sterkfontein (South Africa)	X	X	X	
A. africanus	STS 53	Sterkfontein (South Africa)		X	X	
A. africanus	STS 56	Sterkfontein (South Africa)	X	X		
A. africanus	STS 57	Sterkfontein (South Africa)	X			
A. africanus	STS 8	Sterkfontein (South Africa)	X	X	X	
A. africanus	TM 1511	Sterkfontein (South Africa)	X	X	X	
A. africanus	TM 1561	Sterkfontein (South Africa)			X	

A. africanus	STW _450	Sterkfontein (South Africa)	X				
A. africanus	STW _402	Sterkfontein (South Africa)	X				
P. boisei	KNM-CH 1	Chesowanja (Kenya)	X	X	X		
P. boisei	KNM-WT 17400	West Turkana (Kenya)	X	X	X		
P. robustus	KB 5222	Kromdraai (South Africa)			X		
P. robustus	SK 102	Swartkrans (South Africa)	X				
P. robustus	SK 105	Swartkrans (South Africa)			X		
P. robustus	SK 11	Swartkrans (South Africa)		X			
P. robustus	SK 13.14	Swartkrans (South Africa)	X	X	X		
P. robustus	SK 16.1591	Swartkrans (South Africa)	X				X
P. robustus	SK 31	Swartkrans (South Africa)			X		
P. robustus	SK 3975	Swartkrans (South Africa)			X		
P. robustus	SK 3977	Swartkrans (South Africa)			X		
P. robustus	SK 47	Swartkrans (South Africa)	X	X			
P. robustus	SK 48	Swartkrans (South Africa)	X	X	X		
P. robustus	SK 49	Swartkrans (South Africa)	X	X	X		
P. robustus	SK 52	Swartkrans (South Africa)	X	X			
P. robustus	SK 826a2	Swartkrans (South Africa)		X			
P. robustus	SK 831a	Swartkrans (South Africa)			X		
P. robustus	SK 832	Swartkrans (South Africa)	X				
P. robustus	SK 834	Swartkrans (South Africa)		X			
P. robustus	SK 836	Swartkrans (South Africa)			X		
P. robustus	SK 838a	Swartkrans (South Africa)	X				
P. robustus	SK 89a	Swartkrans (South Africa)	X				
P. robustus	SKW 14	Swartkrans (South Africa)		X			
P. robustus	SKW 33 (SK 14129a)	Swartkrans (South Africa)	X	X			
P. robustus	SKX 21841	Swartkrans (South Africa)			X		
P. robustus	TM 1517a	Kromdraai (South Africa)	X	X			

P. robustus	TM 1601e	Kromdraai (South Africa)	X			
P. robustus	DNH 1	Drimolen (South Africa)		X		
P. robustus	DNH 40	Drimolen (South Africa)			X	
P. robustus	DNH 16	Drimolen (South Africa)	X			
P. robustus	DNH 22c	Drimolen (South Africa)			X	
P. robustus	DNH 3	Drimolen (South Africa)			X	
P. robustus	DNH 54	Drimolen (South Africa)			X	
P. robustus	DNH 74	Drimolen (South Africa)		X		
P. robustus	DNH 57b	Drimolen (South Africa)	X			
P. robustus	DNH 60a	Drimolen (South Africa)	X			
P. robustus	TM 1517c	Kromdraai (South Africa)		X	X	
P. robustus	SK 829	Swartkrans (South Africa)	X			
P. robustus	SK 41	Swartkrans (South Africa)			X	
Homo sp. / *habilis s.l.*	SK 27	Swartkrans (South Africa)		X		
Homo sp. / *habilis s.l.*	KNM-ER 1813	Koobi Fora (Kenya)	X	X	X	
Homo sp. / *habilis s.l.*	KNM-ER 1590	Koobi Fora (Kenya)	X	X		
Homo sp. / *habilis s.l.*	Omo166-1973-781	Omo (Ethiopia)			X	
Homo sp. / *habilis s.l.*	DNH 39	Drimolen (South Africa)	X			
Homo sp. / *habilis s.l.*	DNH 70	Drimolen (South Africa)	X			
Homo sp. / *habilis s.l.*	SKX 268	Swartkrans (South Africa)	X			
Homo sp. / *habilis s.l.*	DNH 62	Drimolen (South Africa)	X			
H. erectus s.l.	KNM-ER 1808h	Koobi Fora (Kenya)		X		
H. erectus s.l.	Sangiran 7-3b	Sangiran Java (Indonesia)	X			
H. erectus s.l.	Sangiran 7-3c	Sangiran Java (Indonesia)		X		
H. erectus s.l.	Sangiran 4	Sangiran Java (Indonesia)	X	X	X	
H. erectus s.l.	Sangiran 11-DIJ2	Sangiran Java (Indonesia)				X
MPAE	Thomas Quarry I	Thomas Quarry (Morocco)	X		X	
MPAE	Steinheim	Steinheim an der Murr (Germany)	X	X	X	

H. neanderthalensis	SCLA 4A-3	Scladina Cave (Belgium)		X	
H. neanderthalensis	SCLA 4A-4	Scladina Cave (Belgium)	X		
H. neanderthalensis	SCLA 4A-8	Scladina Cave (Belgium)			X
H. neanderthalensis	KRP D58	Krapina (Croatia)			X
H. neanderthalensis	KRP D96	Krapina (Croatia)		X	
H. neanderthalensis	KRP D97	Krapina (Croatia)			X
H. neanderthalensis	KRP D98	Krapina (Croatia)		X	
H. neanderthalensis	KRP D99	Krapina (Croatia)			X
H. neanderthalensis	KRP D100	Krapina (Croatia)	X		
H. neanderthalensis	KRP D101	Krapina (Croatia)	X		
H. neanderthalensis	KRP D109	Krapina (Croatia)			X
H. neanderthalensis	KRP D134	Krapina (Croatia)	X		
H. neanderthalensis	KRP D135	Krapina (Croatia)		X	
H. neanderthalensis	KRP D136	Krapina (Croatia)		X	
H. neanderthalensis	KRP D162	Krapina (Croatia)			X
H. neanderthalensis	KRP D163	Krapina (Croatia)			X
H. neanderthalensis	KRP D164	Krapina (Croatia)	X		
H. neanderthalensis	KRP D165	Krapina (Croatia)		X	
H. neanderthalensis	KRP D166	Krapina (Croatia)		X	
H. neanderthalensis	KRP D167	Krapina (Croatia)	X		
H. neanderthalensis	KRP D169	Krapina (Croatia)		X	
H. neanderthalensis	KRP D170	Krapina (Croatia)			X
H. neanderthalensis	KRP D171	Krapina (Croatia)	X		
H. neanderthalensis	KRP D172	Krapina (Croatia)		X	
H. neanderthalensis	KRP D173	Krapina (Croatia)			X
H. neanderthalensis	KRP D174	Krapina (Croatia)	X		
H. neanderthalensis	KRP D175	Krapina (Croatia)		X	
H. neanderthalensis	KRP D176	Krapina (Croatia)		X	

H. neanderthalensis	KRP D177	Krapina (Croatia)		X		
H. neanderthalensis	KRP D178	Krapina (Croatia)			X	
H. neanderthalensis	KRP D180	Krapina (Croatia)			X	
H. neanderthalensis	KRP D192	Krapina (Croatia)		X		
H. neanderthalensis	KRP 45	Krapina (Croatia)	X			
H. neanderthalensis	KRP 46	Krapina (Croatia)	X			
H. neanderthalensis	KRP 47	Krapina (Croatia)	X	X		
H. neanderthalensis	KRP 48	Krapina (Croatia)	X	X		
H. neanderthalensis	La Quina H18	La Quina (France)	X	X		
H. neanderthalensis	Vi 12-1	Vindija (Croatia)		X		
H. neanderthalensis	Vi 11-46	Vindija (Croatia)		X		
H. neanderthalensis	KMH 21	Kebara Cave (Israel)	X			
H. neanderthalensis	KMH 24	Kebara Cave (Israel)			X	
H. neanderthalensis	Kebara-dumps	Kebara Cave (Israel)				X
H. neanderthalensis	La Ferrassie 8	La Ferrasie (France)	X			
H. neanderthalensis	Combe-Grenal IX	Combe-Grenal Cave (France)		X		
H. neanderthalensis	Combe-Grenal XIII	Combe-Grenal Cave (France)	X			
H. neanderthalensis	Saint-Cesaire 1	La Roche a Pierrot Saint-Cesaire (France)		X	X	
H. neanderthalensis	Roc de Marsal	Roc de Marsal (France)	X			
H. neanderthalensis	BD8	Abri Bourgeois-Delaunay La Chaise Cave (France)	X	X	X	
H. neanderthalensis	Le Moustier 1	Le Moustier (France)	X	X	X	
H. neanderthalensis	SD 1105	El Sidron (Spain)	X			
H. neanderthalensis	SD 1164	El Sidron (Spain)			X	
H. neanderthalensis	SD 332	El Sidron (Spain)			X	
H. neanderthalensis	SD 4	El Sidron (Spain)		X		
H. neanderthalensis	SD 407	El Sidron (Spain)		X		

H. neanderthalensis	SD 531	El Sidron (Spain)	X					
H. neanderthalensis	SD 551	El Sidron (Spain)		X				
H. neanderthalensis	SD 621	El Sidron (Spain)			X			
H. neanderthalensis	SD 741	El Sidron (Spain)			X			
H. sapiens (Pleistocene)	Skhul I	Skhul Cave (Israel)	X					
H. sapiens (Pleistocene)	Qafzeh 11	Qafzeh Cave (Israel)	X	X				
H. sapiens (Pleistocene)	Qafzeh 15	Qafzeh Cave (Israel)	X	X				
H. sapiens (Pleistocene)	Qafzeh 10	Qafzeh Cave (Israel)	X	X				
H. sapiens (Pleistocene/early Holocene)	Combe Capelle	Combe Capelle (France)		X	X			
H. sapiens (Pleistocene)	DES H6	Dar es Soltane II (Morocco)	X					
H. sapiens (Pleistocene)	DES H9	Dar es Soltane II (Morocco)		X				
H. sapiens (Pleistocene)	DES H10	Dar es Soltane II (Morocco)		X				
H. sapiens (Pleistocene)	Equus Cave H1	Equus Cave (South Africa)						X
H. sapiens (Pleistocene)	Equus Cave H10	Equus Cave (South Africa)						X
H. sapiens (Pleistocene)	Oberkassel D999	Oberkassel (Germany)			X			
H. sapiens (Pleistocene)	Qafzeh 9	Qafzeh Cave (Israel)	X	X	X			
H. sapiens (Pleistocene)	Skhūl X	Skhūl Cave (Israel)	X					
H. sapiens (Pleistocene)	Temara H7	Contrebandiers Temara (Morocco)	X					
H. sapiens (Pleistocene)	Temara T3b	Contrebandiers Temara (Morocco)	X					
H. sapiens (Pleistocene)	Temara IB19	Contrebandiers Temara (Morocco)	X	X				

* The X indicates which tooth/teeth are represented for each specimen. MPAE: Middle Pleistocene African and European humans

Table S2. Fossil hominin lower molars used in this study including accession number locality/site and source.

Taxon	Specimen ID	Locality/Site (Country)	LM1	LM2	LM3	LM12	LM23	LM
A. anamensis	KNM-KP 29281	Kanapoi (Kenya)		X	X			
A. anamensis	KNM-KP 29286h	Kanapoi (Kenya)	X					
A. anamensis	KNM-KP 29286i	Kanapoi (Kenya)		X				
A. anamensis	KNM-KP 29286i	Kanapoi (Kenya)			X			
A. anamensis	KNM-ER_20428	Koobi Fora (Kenya)			X			
A. anamensis	KNM-ER_35233	Koobi Fora (Kenya)		X				
A. anamensis	KNM-KP 31712j	Kanapoi (Kenya)	X					
A. anamensis	KNM-KP 29286c	Kanapoi (Kenya)	X					
A. anamensis	KNM-KP 34725r	Kanapoi (Kenya)	X					
A. anamensis	KNM-KP 34725t	Kanapoi (Kenya)		X				
A. afarensis	AL 145-35	Hadar (Ethiopia)	X	X				
A. afarensis	AL 241-14	Hadar (Ethiopia)		X				
A. afarensis	AL 128-23	Hadar (Ethiopia)	X	X				
A. afarensis	AL 333w-1a	Hadar (Ethiopia)	X	X				
A. afarensis	AL 333-43b	Hadar (Ethiopia)	X					
A. afarensis	AL 188-1	Hadar (Ethiopia)		X	X			
A. afarensis	AL 333w-32	Hadar (Ethiopia)			X			
A. afarensis	AL 333w-48	Hadar (Ethiopia)		X				
A. africanus	MLD 2	Makapansgat (South Africa)		X				
A. africanus	STW 106	Sterkfontein (South Africa)	X					
A. africanus	STW 109	Sterkfontein (South Africa)		X	X			
A. africanus	STW 123b (STW 130)	Sterkfontein (South Africa)	X					
A. africanus	STW 131	Sterkfontein (South Africa)	X					

A. africanus	STW 133	Sterkfontein (South Africa)			X
A. africanus	STW 14	Sterkfontein (South Africa)		X	X
A. africanus	STW 145	Sterkfontein (South Africa)	X		
A. africanus	STW 213	Sterkfontein (South Africa)		X	
A. africanus	STW 213 (STW 235)	Sterkfontein (South Africa)		X	
A. africanus	STW 234	Sterkfontein (South Africa)		X	
A. africanus	STW 237	Sterkfontein (South Africa)			X
A. africanus	STW 246	Sterkfontein (South Africa)	X		
A. africanus	STW 280 (STW 278)	Sterkfontein (South Africa)			X
A. africanus	STW 285b (STW 286)	Sterkfontein (South Africa)		X	
A. africanus	STW 291	Sterkfontein (South Africa)	X		
A. africanus	STW 295 (STW 322)	Sterkfontein (South Africa)			X
A. africanus	STW 3	Sterkfontein (South Africa)		X	
A. africanus	STW 308	Sterkfontein (South Africa)		X	
A. africanus	STW 309a	Sterkfontein (South Africa)	X		
A. africanus	STW 327	Sterkfontein (South Africa)	X	X	X
A. africanus	STW 353	Sterkfontein (South Africa)			X
A. africanus	STW 364	Sterkfontein (South Africa)	X		
A. africanus	STW 384	Sterkfontein (South Africa)			X
A. africanus	STW 412a	Sterkfontein (South Africa)		X	
A. africanus	STW 498c	Sterkfontein (South Africa)		X	X
A. africanus	STW 520	Sterkfontein (South Africa)			X
A. africanus	STW 529 (STW 532)	Sterkfontein (South Africa)			X
A. africanus	STW 537 (STW 540)	Sterkfontein (South Africa)		X	
A. africanus	STW 537 (STW 551b)	Sterkfontein (South Africa)			X
A. africanus	STW 555	Sterkfontein (South Africa)		X	
A. africanus	STW 586	Sterkfontein (South Africa)			X
A. africanus	STW 90	Sterkfontein (South Africa)			X

A. africanus	Taung1	Taung (South Africa)	X	X			
A. africanus	STS 18	Sterkfontein (South Africa)	X				
A. africanus	STS 24	Sterkfontein (South Africa)	X				
A. africanus	STS 52b	Sterkfontein (South Africa)	X	X	X		
A. africanus	STS 55b	Sterkfontein (South Africa)			X		
A. africanus	STS 59	Sterkfontein (South Africa)			X		
A. africanus	STS 9	Sterkfontein (South Africa)	X				
A. africanus	TM 1520	Sterkfontein (South Africa)			X		
A. africanus	STW 560a	Sterkfontein (South Africa)			X		
A. africanus	STW 560e	Sterkfontein (South Africa)			X		
A. africanus	STW 491 (STW 492)	Sterkfontein (South Africa)	X				
A. africanus	STW 491 (STW 519)	Sterkfontein (South Africa)	X				
A. africanus	STW 491	Sterkfontein (South Africa)			X		
A. africanus	STW 424	Sterkfontein (South Africa)		X			
A. africanus	STW 421a	Sterkfontein (South Africa)	X				
A. africanus	STW 412b	Sterkfontein (South Africa)		X			
A. africanus	STW 404	Sterkfontein (South Africa)	X	X	X		
A. africanus	STW 142 (STW 312)	Sterkfontein (South Africa)			X		
P. aethiopicus	L157-35	Omo (Ethiopia)		X			
P. aethiopicus	L 62-17	Omo (Ethiopia)		X			
P. boisei	KNM-ER 3230	Koobi Fora (Kenya)			X		
P. boisei	KNM-ER 15930	Koobi Fora (Kenya)		X			
P. boisei	KNM-ER 25520	Koobi Fora (Kenya)		X			
P. boisei	KNM-ER 6080	Koobi Fora (Kenya)				X	
P. boisei	L 628-3	Omo (Ethiopia)			X		
P. boisei	L 427-7	Omo (Ethiopia)		X			
P. boisei	Omo F203-1	Omo (Ethiopia)					X
P. boisei	Omo 47-1973-1500	Omo (Ethiopia)		X			

P. robustus	GDA 2	Gondolin (South Africa)		X	
P. robustus	SK 1	Swartkrans (South Africa)		X	
P. robustus	SK 104	Swartkrans (South Africa)	X		
P. robustus	SK 1587ab	Swartkrans (South Africa)	X		
P. robustus	SK 1587ab	Swartkrans (South Africa)		X	
P. robustus	SK 1588	Swartkrans (South Africa)	X		
P. robustus	SK 22	Swartkrans (South Africa)			X
P. robustus	SK 23	Swartkrans (South Africa)	X	X	X
P. robustus	SK 25	Swartkrans (South Africa)	X	X	
P. robustus	SK 34	Swartkrans (South Africa)		X	X
P. robustus	SK 3974	Swartkrans (South Africa)	X		
P. robustus	SK 3976	Swartkrans (South Africa)		X	
P. robustus	SK 3978	Swartkrans (South Africa)	X		
P. robustus	SK 5	Swartkrans (South Africa)		X	
P. robustus	SK 6	Swartkrans (South Africa)	X	X	X
P. robustus	SK 61	Swartkrans (South Africa)	X		
P. robustus	SK 62	Swartkrans (South Africa)	X	X	
P. robustus	SK 63	Swartkrans (South Africa)	X	X	
P. robustus	SK 64	Swartkrans (South Africa)	X		
P. robustus	SK 75	Swartkrans (South Africa)			X
P. robustus	SK 826b (828)	Swartkrans (South Africa)	X		
P. robustus	SK 841b	Swartkrans (South Africa)			X
P. robustus	SK 843.846a	Swartkrans (South Africa)	X	X	X
P. robustus	SK 851	Swartkrans (South Africa)			X
P. robustus	SK 880	Swartkrans (South Africa)			X
P. robustus	SK 885	Swartkrans (South Africa)			X
P. robustus	SKW 5	Swartkrans (South Africa)	X	X	X
P. robustus	SKX 10642	Swartkrans (South Africa)			X

P. robustus	SKX 10643	Swartkrans (South Africa)			X	
P. robustus	SKX 4446	Swartkrans (South Africa)	X	X		
P. robustus	SKX 5002	Swartkrans (South Africa)			X	
P. robustus	SKX 5014	Swartkrans (South Africa)			X	
P. robustus	TM 1517b	Kromdraai (South Africa)	X		X	
P. robustus	TM 1600	Kromdraai (South Africa)		X	X	
P. robustus	DNH 51	Drimolen (South Africa)		X	X	
P. robustus	DNH 21	Drimolen (South Africa)		X	X	
P. robustus	DNH 46	Drimolen (South Africa)	X			
P. robustus	DNH 8	Drimolen (South Africa)	X	X	X	
P. robustus	DNH 68	Drimolen (South Africa)		X	X	
P. robustus	DNH 12	Drimolen (South Africa)			X	
P. robustus	DNH 18	Drimolen (South Africa)			X	
P. robustus	DNH 75	Drimolen (South Africa)			X	
P. robustus	DNH 60b	Drimolen (South Africa)	X			
P. robustus	DNH 60c	Drimolen (South Africa)		X		
Homo sp. / *habilis s.l.*	SK 15	Swartkrans (South Africa)		X	X	
Homo sp. / *habilis s.l.*	SKX 258	Swartkrans (South Africa)	X			
Homo sp. / *habilis s.l.*	KNM-ER 1802	Koobi Fora (Kenya)	X	X		
Homo sp. / *habilis s.l.*	KNM-ER 2597	Koobi Fora (Kenya)		X		
Homo sp. / *habilis s.l.*	L 26-1g	Omo (Ethiopia)				X
Homo sp. / *habilis s.l.*	L 628-10	Omo (Ethiopia)				X
Homo sp. / *habilis s.l.*	Omo K7-1969-19	Omo (Ethiopia)				X
Homo sp. / *habilis s.l.*	DNH 67	Drimolen (South Africa)	X			
H. erectus s.l.	KNM-BK 67	Baringo Kapthurin (Kenya)		X	X	
H. erectus s.l.	Sangiran 6a	Sangiran Java (Indonesia)	X			
H. erectus s.l.	Sangiran 5	Sangiran Java (Indonesia)		X		
H. erectus s.l.	Sangiran 1b	Sangiran Java (Indonesia)	X	X	X	

MPAE	Mauer	Mauer (Germany)	X	X	X
H. neanderthalensis	1048/69	Weimar - Ehringsdorf (Germany)	X		
H. neanderthalensis	Scla 4A-1	Scladina Cave (Belgium)	X	X	X
H. neanderthalensis	KRP D1	Krapina (Croatia)		X	
H. neanderthalensis	KRP D2	Krapina (Croatia)		X	
H. neanderthalensis	KRP D3	Krapina (Croatia)		X	
H. neanderthalensis	KRP D4	Krapina (Croatia)			X
H. neanderthalensis	KRP D6	Krapina (Croatia)		X	
H. neanderthalensis	KRP D9	Krapina (Croatia)			X
H. neanderthalensis	KRP D10	Krapina (Croatia)		X	
H. neanderthalensis	KRP D77	Krapina (Croatia)	X		
H. neanderthalensis	KRP D79	Krapina (Croatia)	X		
H. neanderthalensis	KRP D80	Krapina (Croatia)	X		
H. neanderthalensis	KRP D81	Krapina (Croatia)	X		
H. neanderthalensis	KRP D82	Krapina (Croatia)	X		
H. neanderthalensis	KRP D84	Krapina (Croatia)	X		
H. neanderthalensis	KRP D86	Krapina (Croatia)		X	
H. neanderthalensis	KRP D104	Krapina (Croatia)		X	
H. neanderthalensis	KRP D105	Krapina (Croatia)	X		
H. neanderthalensis	KRP D106	Krapina (Croatia)			X
H. neanderthalensis	KRP D107	Krapina (Croatia)		X	
H. neanderthalensis	KRP D108	Krapina (Croatia)			X
H. neanderthalensis	KRP 52	Krapina (Croatia)	X		
H. neanderthalensis	KRP 53	Krapina (Croatia)	X	X	X
H. neanderthalensis	KRP 54	Krapina (Croatia)	X	X	
H. neanderthalensis	KRP 55	Krapina (Croatia)	X	X	
H. neanderthalensis	KRP 57	Krapina (Croatia)	X	X	
H. neanderthalensis	KRP 58	Krapina (Croatia)	X	X	X

H. neanderthalensis	KRP 59	Krapina (Croatia)	X	X	X
H. neanderthalensis	La Quina H9	La Quina (France)	X	X	X
H. neanderthalensis	Vi 11-40A	Vindija (Croatia)	X		
H. neanderthalensis	Vi 11-45	Vindija (Croatia)		X	X
H. neanderthalensis	Vi 11-39	Vindija (Croatia)	X	X	X
H. neanderthalensis	Tabun II	Tabun Cave (Israel)	X		
H. neanderthalensis	KMH 14	Kebara Cave (Israel)		X	
H. neanderthalensis	KMH 4	Kebara Cave (Israel)	X		
H. neanderthalensis	KMH 18	Kebara Cave (Israel)		X	
H. neanderthalensis	La Ferrassie 8	La Ferrasie (France)	X		
H. neanderthalensis	Combe-Grenal I	Combe-Grenal Cave (France)	X		
H. neanderthalensis	Combe-Grenal IV	Combe-Grenal Cave (France)	X		
H. neanderthalensis	Combe-Grenal XII	Combe-Grenal Cave (France)			X
H. neanderthalensis	Le Regourdou 1	Le Regourdou Montignac (France)	X	X	X
H. neanderthalensis	Saint-Cesaire 1	La Roche a Pierrot Saint-Cesaire (France)	X	X	X
H. neanderthalensis	Roc de Marsal	Roc de Marsal (France)	X		
H. neanderthalensis	BD1	Abri Bourgeois-Delaunay La Chaise Cave (France)		X	X
H. neanderthalensis	La Chaise 5	Abri Bourgeois-Delaunay La Chaise Cave (France)	X		
H. neanderthalensis	La Chaise 14-7	Abri Bourgeois-Delaunay La Chaise Cave (France)	X		
H. neanderthalensis	La Chaise 36	Abri Bourgeois-Delaunay La Chaise Cave (France)		X	X
H. neanderthalensis	La Chaise 43	Abri Bourgeois-Delaunay La Chaise Cave (France)			X
H. neanderthalensis	La Chaise 49	Abri Bourgeois-Delaunay La Chaise Cave (France)	X		

H. neanderthalensis	Le Moustier 1	Le Moustier (France)	X	X	X			
H. neanderthalensis	SD 780	El Sidron (Spain)	X					
H. neanderthalensis	SD 1135	El Sidron (Spain)			X			
H. neanderthalensis	SD 755	El Sidron (Spain)		X				
H. neanderthalensis	SD 540	El Sidron (Spain)		X				
H. neanderthalensis	SD 756	El Sidron (Spain)	X					
H. neanderthalensis	Amud 17	Amud Cave (Israel)						X
H. sapiens (Pleistocene)	Ohalo II H1	Ohalo (Israel)			X			
H. sapiens (Pleistocene)	Nahal Oren 8	Nahal Oren (Israel)		X	X			
H. sapiens (Pleistocene)	Nahal Oren 14	Nahal Oren (Israel)		X				
H. sapiens (Pleistocene)	Hayonim 17	Hayonim (Israel)		X				
H. sapiens (Pleistocene)	Hayonim 19	Hayonim (Israel)	X	X	X			
H. sapiens (Pleistocene)	Hayonim 8	Hayonim (Israel)		X	X			
H. sapiens (Pleistocene)	Hayonim 20	Hayonim (Israel)		X	X			
H. sapiens (Pleistocene)	DES H4	Dar es Soltane II (Morocco)	X	X	X			
H. sapiens (Pleistocene)	DES H5	Dar es Soltane II (Morocco)	X	X				
H. sapiens (Pleistocene)	SAM AP 6242	Die Kelders (South Africa)						X
H. sapiens (Pleistocene)	SAM AP 6277	Die Kelders (South Africa)						X
H. sapiens (Pleistocene)	SAM AP 6282	Die Kelders (South Africa)						X
H. sapiens	El Haroura	El Harhoura (Morocco)	X	X	X			

(Pleistocene)								
H. sapiens (Pleistocene)	Equus Cave H3	Equus Cave (South Africa)					X	
H. sapiens (Pleistocene)	Equus Cave H5	Equus Cave (South Africa)						X
H. sapiens (Pleistocene)	Equus Cave H8	Equus Cave (South Africa)		X				
H. sapiens (Pleistocene)	Irhoud 3	Jebel Irhoud (Morocco)	X	X				
H. sapiens (Pleistocene)	Qafzeh 10	Qafzeh Cave (Israel)	X	X				
H. sapiens (Pleistocene)	Qafzeh 11	Qafzeh Cave (Israel)	X	X	X			
H. sapiens (Pleistocene)	Qafzeh 15	Qafzeh Cave (Israel)	X	X				
H. sapiens (Pleistocene)	Qafzeh 8	Qafzeh Cave (Israel)		X	X			
H. sapiens (Pleistocene)	Temara	Contrebandiers Temara (Morocco)	X	X	X			
H. sapiens (Pleistocene)	Temara T3a	Contrebandiers Temara (Morocco)	X					
H. sapiens (Pleistocene/early Holocene)	Combe Capelle	Combe Capelle (France)		X	X			

* The X indicates which tooth/teeth are represented for each specimen. MPAE: Middle Pleistocene African and European humans

Table S3. Frequencies of UM C5 assessed at the EDJ.

Taxon	n	C5 absent	One C5 present	Two related "C5" present	Two unrelated "C5" present	Three+ "C5" present
A. anamensis	6	83.3%	0.0%	0.0%	16.7%	0.0%
A. afarensis	8	62.5%	37.5%	0.0%	0.0%	0.0%
	(6)	(83.3%)	(16.7%)	(0%)	(0%)	(0%)
A. africanus	48	58.3%	31.3%	0.0%	8.3%	2.1%
	(39)	(71.8%)	(20.5%)	(0%)	(5.1%)	(2.6%)
P. boisei	6	50.0%	33.3%	0.0%	0.0%	16.7%
	(5)	(60.0%)	(40.0%)	(0%)	(0%)	(0%)
P. robustus	50	62.0%	28.0%	6.0%	2.0%	2.0%
	(40)	(77.5%)	(10.0%)	(7.5%)	(2.5%)	(2.5%)
Homo sp./*habilis s.l.*	13	69.2%	23.1%	7.7%	0.0%	0.0%
	(11)	(81.8%)	(9.1)%	(9.1)%	(0%)	(0%)
H. erectus *s.l.*	7	85.7%	14.3%	0.0%	0.0%	0.0%
	(6)	(100.0%)	(0%)	(0%)	(0%)	(0%)
MPAE	4	25.0%	75.0%	0.0%	0.0%	0.0%
	(1)	(100.0%)	(0%)	(0%)	(0%)	(0%)
H. neanderthalensis	57	61.4%	19.3%	5.3%	7.0%	7.0%
	(46)	(76.1%)	(4.3%)	(4.3%)	(6.5%)	(8.7)%
H. sapiens (Pleistocene)	18	38.9%	55.6%	0.0%	0.0%	5.6%
	(12)	(58.3%)	(33.3%)	(0%)	(0%)	(8.3%)
H. sapiens (recent)	79	74.7%	24.1%	1.3%	0.0%	0.0%
	(64)	(92.2%)	(7.8%)	(0%)	(0%)	(0%)
P. troglodytes	67	62.7%	31.3%	1.5%	3.0%	1.5%
	(52)	(80.8%)	(15.4%)	(1.9%)	(0%)	(1.9%)
P. paniscus	6	100.0%	0.0%	0.0%	0.0%	0.0%
Gorilla sp.	34	76.5%	20.6%	0.0%	2.9%	0.0%
	(29)	(89.7%)	(10.3%)	(0%)	(0%)	(0%)
Pongo sp.	28	82.1%	7.1%	7.1%	0.0%	3.6%
	(26)	(88.5%)	(3.8%)	(3.8%)	(0%)	(3.8%)

* Data in brackets do not include "suspected" cases; MPAE: Middle Pleistocene African and European humans

Table S4. Results of the bootstrapping analysis (1000 iterations) for PPT expression.

Taxon	PPT absent		PPT shouldering		PPT faint/moderate		PPT marked	
	95% CI min	95% CI max	95% CI min	95% CI max	95% CI min	95% CI max	95% CI min	95% CI max
EA *Australopithecus**	82.91%	101.44%	0.00%	17.04%	0.00%	0.00%	0.00%	0.00%
A. africanus	86.49%	96.21%	3.83%	13.45%	0.00%	0.00%	0.00%	0.00%
P. robustus	100.00%	100.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Early *Homo***	66.10%	91.52%	3.10%	25.38%	0.00%	15.80%	0.00%	0.00%
H. sapiens (all)	65.18%	75.62%	12.56%	20.92%	5.46%	12.14%	1.70%	6.18%
H. sapiens (Pleistocene)	39.07%	64.48%	9.09%	29.34%	9.24%	28.62%	1.90%	16.87%
H. sapiens (recent)	69.57%	80.66%	11.50%	21.05%	3.24%	9.40%	0.55%	4.44%
H. neanderthalensis	0.00%	3.39%	21.56%	34.47%	39.92%	54.19%	17.10%	29.62%
P. troglodytes	84.93%	93.78%	3.62%	11.37%	0.58%	5.45%	0.00%	0.00%
Gorilla	100.00%	100.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Pongo	77.82%	93.36%	3.97%	17.36%	0.00%	0.00%	0.00%	7.68%

* EA *Australopithecus* : East African *Australopithecus* (*A. anamensis* and *A. afarensis* pooled); **Early *Homo* : *H. habilis s.l.* and *H. erectus s.l.* pooled due to small sample sizes. When present, negative percentages set to 0%

Table S5. Frequencies of LM C6 assessed at the EDJ.

Taxon	n	C6 absent	One C6 present	Two related "C6" present	Two unrelated "C6" present	Three+ "C6" present
A. anamensis	11	45.5%	27.3%	27.3%	0.0%	0.0%
A. afarensis	12	66.7%	33.3%	0.0%	0.0%	0.0%
	(11)	(81.8%)	(18.2%)	(0%)	(0%)	(0%)
A. africanus	56	57.1%	28.6%	12.5%	0.0%	1.8%
	(47)	(68.1%)	(14.9%)	(14.9%)	(0%)	(2.1%)
P. aethiopicus	2	100.0%	0.0%	0.0%	0.0%	0.0%
P. boisei	7	0.0%	85.7%	14.3%	0.0%	0.0%
P. robustus	60	18.3%	65.0%	11.7%	3.3%	1.7%
	(54)	(20.4%)	(61.1%)	(13.0%)	(3.7%)	(1.9%)
Homo sp./*habilis s.l.*	10	60.0%	40.0%	0.0%	0.0%	0.0%
H. erectus s.l.	7	85.7%	0.0%	14.3%	0.0%	0.0%
MPAE	3	66.7%	33.3%	0.0%	0.0%	0.0%
	(2)	(100.0%)	(0%)	(0%)	(0%)	(0%)
H. neanderthalensis	68	51.5%	42.6%	5.9%	0.0%	0.0%
	(56)	(62.5%)	(30.4%)	(7.1%)	(0%)	(0%)
H. sapiens (Pleistocene)	40	82.5%	17.5%	0.0%	0.0%	0.0%
	(39)	(84.6%)	(15.4%)	(0%)	(0%)	(0%)
H. sapiens (recent)	167	89.8%	10.2%	0.0%	0.0%	0.0%
	(161)	(93.2%)	(6.8%)	(0%)	(0%)	(0%)
P. troglodytes	103	32.0%	59.2%	8.7%	0.0%	0.0%
	(80)	(41.3%)	(51.3%)	(7.5%)	(0%)	(0%)
P. paniscus	25	72.0%	24.0%	4.0%	0.0%	0.0%
	(22)	(81.8%)	(13.6%)	(4.5%)	(0%)	(0%)
Gorilla sp.	35	85.7%	11.4%	2.9%	0.0%	0.0%
	(34)	(88.2%)	(8.8%)	(2.9%)	(0%)	(0%)
Pongo sp.	45	75.6%	22.2%	2.2%	0.0%	0.0%
	(41)	(82.9%)	(17.1%)	(0%)	(0%)	(0%)

* Data in brackets do not include "suspected" cases; MPAE: Middle Pleistocene African and European humans

Table S6. Frequencies of LM C7 manifestation at the EDJ following Skinner et al.'s (2008) classification.

Taxon	n	A	B	C	D	E	F	Others
A. anamensis	9	55.6%	33.3%	0.0%	0.0%	0.0%	0.0%	11.1%
A. afarensis	11	72.7%	9.1%	0.0%	9.1%	9.1%	0.0%	0.0%
A. africanus	60	48.3%	16.7%	0.0%	26.7%	3.3%	5.0%	0.0%
P. aethiopicus	2	100.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
P. boisei	7	85.7%	0.0%	14.3%	0.0%	0.0%	0.0%	0.0%
P. robustus	62	61.3%	19.4%	0.0%	14.5%	1.6%	3.2%	0.0%
Homo sp./*habilis s.l.*	8	37.5%	0.0%	12.5%	0.0%	50.0%	0.0%	0.0%
H. erectus s.l.	7	57.1%	14.3%	0.0%	14.3%	0.0%	14.3%	0.0%
MPAE	3	66.7%	33.3%	0.0%	0.0%	0.0%	0.0%	0.0%
H. neanderthalensis	77	53.2%	18.2%	2.6%	7.8%	1.3%	15.6%	1.3%
H. sapiens (Pleistocene)	42	35.7%	35.7%	4.8%	2.4%	16.7%	4.8%	0.0%
H. sapiens (recent)	169	59.2%	36.7%	0.0%	3.6%	0.6%	0.0%	0.0%
P. troglodytes	103	26.2%	53.4%	10.7%	5.8%	1.0%	1.9%	1.0%
P. paniscus	25	24.0%	44.0%	0.0%	24.0%	8.0%	0.0%	0.0%
Gorilla sp.	32	59.4%	0.0%	0.0%	6.3%	9.4%	25.0%	0.0%
Pongo sp.	48	81.3%	14.6%	0.0%	0.0%	0.0%	4.2%	0.0%

*Frequencies of origin types per taxon do not include individuals with trait absence; MPAE: Middle Pleistocene African and European humans

Table S7. Frequencies of C7 assessed at the EDJ.

Taxon	n	C7 absent	One C7 present	Two "C7" present
A. anamensis	9	88.9%	11.1%	0.0%
A. afarensis	12 (10)	83.3% (100.0%)	16.7% (0%)	0.0% (0%)
A. africanus	59 (48)	72.9% (89.6%)	27.1% (10.4%)	0.0% (0%)
P. aethiopicus	2	100.0%	0.0%	0.0%
P. boisei	7 (6)	85.7% (100.0%)	14.3% (0%)	0.0% (0%)
P. robustus	62 (58)	88.7% (94.8%)	11.3% (5.2%)	0.0% (0%)
Homo sp./*habilis s.l.*	8	37.5%	62.5%	0.0%
H. erectus s.l.	7 (6)	71.4% (83.3%)	28.6% (16.7%)	0.0% (0%)
MPAE	3	100.0%	0.0%	0.0%
H. neanderthalensis	77 (68)	74.0% (83.8%)	26.0% (16.2%)	0.0% (0%)
H. sapiens (Pleistocene)	42 (41)	73.8% (75.6%)	26.2% (24.4%)	0.0% (0%)
H. sapiens (recent)	174 (169)	96.6% (99.4%)	3.4% (0.6%)	0.0% (0%)
P. troglodytes	106 (89)	79.2% (94.4%)	19.8% (5.6%)	0.9% (0%)
P. paniscus	24 (17)	62.5% (88.2%)	37.5% (11.8%)	0.0% (0%)
Gorilla sp.	33 (28)	60.6% (71.4%)	39.4% (28.6%)	0.0% (0%)
Pongo sp.	47	95.7%	4.3%	0.0%

* Data in brackets do not include "suspected" cases; MPAE: Middle Pleistocene African and European humans

Tables

Table 1. Sample composition for hominoid upper and lower molars used in this study.

Taxon	UM1	UM2	UM3	UM	Total UM	LM1	LM2	LM3	LM	Total LM	**Total**
A. anamensis	3	3	0	0	6	4	4	3	0	11	**17**
A. afarensis	3	1	3	1	8	4	6	2	0	12	**20**
A. africanus	13	18	19	1	51	18	19	24	0	61	**112**
P. aethiopicus	0	0	0	0	0	0	2	0	0	2	**2**
P. boisei	2	2	2	0	6	0	4	2	2	8	**14**
P. robustus	17	14	17	1	49	20	20	24	0	64	**113**
H. habilis s.l.	6	3	2	0	11	3	3	1	3	10	**21**
H. erectus s.l.	2	3	1	1	7	2	3	2	0	7	**14**
MPAE	2	1	2	0	5	1	1	1	0	3	**8**
H. neanderthalensis	21	25	19	1	66	33	27	20	1	81	**147**
H. sapiens (Pleistocene)	10	8	3	2	23	10	17	11	5	43	**66**
H. sapiens (recent)	18	41	14	13	86	47	86	41	7	181	**267**
P. troglodytes	23	29	18	0	70	42	51	16	0	109	**179**
P. paniscus	5	3	0	0	8	12	14	0	0	26	**34**
Gorilla sp.	11	13	12	0	36	10	13	13	0	36	**72**
Pongo sp.	14	11	9	0	34	20	19	9	0	48	**82**
Total per tooth type	150	175	121	20	466	226	289	169	18	702	**1168**

MPAE: Middle Pleistocene African and European humans

Table 2. Spearman's correlation coefficient test for UM C5 expression at the EDJ and OES.

Taxon	n	r	*p* -value
East African *Australopithecus**	14	0.662	**<0.01**
A. africanus	38	0.638	**<0.001**
P. robustus	32	0.560	**<0.001**
early *Homo***	10	0.697	**<0.05**
H. neanderthalensis	41	0.857	**<0.001**
Pleistocene *H. sapiens*	9	0.922	**<0.01**
Recent *H. sapiens*	66	0.833	**<0.001**
P. troglodytes	54	0.829	**<0.001**
Gorilla sp.	32	0.905	**<0.001**
Pongo sp.	24	1.000	**<0.001**

* Includes *A. anamensis* and *A. afarensis*

** Includes *H. habilis s.l. and H. erectus s.l.*

Significant values bolded

Table 3. Variation in origin of UM C5 per taxon.

Taxon	n	absent	present	hypocone	metacone	distal fovea	buccal cingulum	occlusal surface	enamel
A. anamensis	5	100.0%	0 (0.0%)	-	-	-	-	-	-
A. afarensis	8	50.0%	4 (50.0%)	0.0%	0.0%	75.0%	0.0%	0.0%	25.0%
A. africanus	43	51.2%	21 (48.8%)	0.0%	4.8%	19.0%	42.9%	4.8%	28.6%
P. boisei	5	40.0%	3 (60%)	0.0%	0.0%	66.7%	0.0%	0.0%	33.3%
P. robustus	45	48.9%	23 (51.1%)	0.0%	13.0%	47.8%	0.0%	0.0%	39.1%
Homo sp./*habilis s.l.*	12	75.0%	3 (25.0%)	0.0%	33.3%	66.7%	0.0%	0.0%	0.0%
H. erectus s.l.	7	85.7%	1 (14.3%)	-	-	100.0%	-	-	-
MPAE	4	25.0%	3 (75.0%)	-	33.3%	66.7%	-	-	-
H. neanderthalensis	46	71.7%	13 (28.3%)	15.4%	0.0%	69.2%	0.0%	0.0%	15.4%
H. sapiens (Pleistocene)	17	41.2%	10 (58.8%)	10.0%	0.0%	90.0%	0.0%	0.0%	0.0%
H. sapiens (recent)	78	75.6%	19 (24.4%)	5.3%	0.0%	94.7%	0.0%	0.0%	0.0%
P. troglodytes	63	66.7%	21 (33.3%)	57.1%	9.5%	28.6%	0.0%	4.8%	0.0%
P. paniscus	6	100.0%	0 (0.0%)	-	-	-	-	-	-
Gorilla sp.	33	78.8%	7 (21.2%)	14.3%	14.3%	71.4%	0.0%	0.0%	0.0%
Pongo sp.	25	92.0%	2 (8.0%)	0.0%	0.0%	100.0%	0.0%	0.0%	0.0%

*Frequencies of origin types per taxon do not include individuals with trait absence; MPAE: Middle Pleistocene African and European humans

Table 4. Frequencies of occurrence and expression of the PPT per taxon.

Taxon	n	PPT absent	PPT shouldering	PPT faint / moderate	PPT marked
A. anamensis	5	**100.0%**	0.0%	0.0%	0.0%
A. afarensis	7	**85.7%**	14.3%	0.0%	0.0%
A. africanus	46	**91.3%**	8.7%	0.0%	0.0%
P. boisei	6	**100.0%**	0.0%	0.0%	0.0%
P. robustus	43	**100.0%**	0.0%	0.0%	0.0%
Homo sp./*habilis* s.l.	8	**87.5%**	0.0%	12.5%	0.0%
H. erectus s.l.	6	**66.7%**	33.3%	0.0%	0.0%
MPAE	5	0.0%	**60.0%**	40.0%	0.0%
H. neanderthalensis	64	1.6%	28.1%	**46.9%**	23.4%
H. sapiens (Pleistocene)	21	**52.4%**	19.0%	19.0%	9.5%
H. sapiens (recent)	80	**75.0%**	16.3%	6.3%	2.5%
P. troglodytes	66	**89.4%**	7.6%	3.0%	0.0%
P. paniscus	7	**100.0%**	0.0%	0.0%	0.0%
Gorilla sp.	35	**100.0%**	0.0%	0.0%	0.0%
Pongo sp.	28	**85.7%**	10.7%	0.0%	3.6%

Highest frequency per sample bolded; MPAE: Middle Pleistocene African and European humans

Table 5. Spearman's correlation coefficient test for LM C6 expression at the EDJ and OES.

Taxon	n	r	*p* -value
A. anamensis	11	0.975	**<0.001**
A. afarensis	11	0.981	**<0.001**
A. africanus	51	0.878	**<0.001**
P. robustus	44	0.629	**<0.001**
early *Homo* *	14	1.000	**<0.001**
H. neanderthalensis	35	0.962	**<0.001**
Pleistocene *H. sapiens*	36	1.000	**<0.001**
Recent *H. sapiens*	152	0.941	**<0.001**
P. troglodytes	89	0.900	**<0.001**
P. paniscus	22	0.788	**<0.001**
Gorilla sp.	35	1.000	**<0.001**
Pongo sp.	37	1.000	**<0.001**

* Includes *H. habilis s.l.* and *H. erectus s.l.*

Significant values bolded

Table 6. Variation in origin of LM C6 of lower molars.

Taxon	n	absent	present	distal fovea	hypoconulid	entoconid	occlusal surface	enamel
A. anamensis	8	62.5%	3 (37.5%)	100.0%	0.0%	0.0%	0.0%	0.0%
A. afarensis	12	66.7%	4 (33.3%)	100.0%	0.0%	0.0%	0.0%	0.0%
A. africanus	48	64.6%	17 (35.4%)	88.2%	0.0%	0.0%	5.9%	5.9%
P. aethiopicus	2	100.0%	0 (0.0%)	-	-	-	-	-
P. boisei	6	0.0%	6 (100.0%)	100.0%	0.0%	0.0%	0.0%	0.0%
P. robustus	50	20.0%	40 (80.0%)	97.5%	0.0%	0.0%	0.0%	2.5%
Homo sp./*habilis s.l.*	10	60.0%	4 (40.0%)	100.0%	0.0%	0.0%	0.0%	0.0%
H. erectus s.l.	6	100.0%	0 (0.0%)	-	-	-	-	-
MPAE	3	66.7%	1 (33.3%)	100.0%	0.0%	0.0%	0.0%	0.0%
H. neanderthalensis	64	54.7%	29 (45.3%)	75.9%	24.1%	0.0%	0.0%	0.0%
H. sapiens (Pleistocene)	40	82.5%	7 (17.5%)	100.0%	0.0%	0.0%	0.0%	0.0%
H. sapiens (recent)	167	89.8%	17 (10.2)%	100.0%	0.0%	0.0%	0.0%	0.0%
P. troglodytes	94	35.1%	61 (64.9%)	65.6%	31.1%	0.0%	3.3%	0.0%
P. paniscus	24	75.0%	6 (25.0)%	100.0%	0.0%	0.0%	0.0%	0.0%
Gorilla sp.	34	88.2%	4 (11.8%)	75.0%	0.0%	0.0%	25.0%	0.0%
Pongo sp.	44	77.3%	10 (22.7%)	80.0%	0.0%	10.0%	10.0%	0.0%

*Frequencies of origin types per taxon do not include individuals with trait absence; MPAE: Middle Pleistocene African and European humans

Table 7. Spearman's correlation coefficient test for LM C7 expression at the EDJ and OES.

Taxon	n	r	*p* -value
*East African Australopithecus**	20	1.000	**<0.001**
A. africanus	38	0.747	**<0.001**
P. robustus	31	0.765	**<0.001**
*early Homo***	15	0.933	**<0.001**
H. neanderthalensis	42	0.963	**<0.001**
Pleistocene H. sapiens	37	0.911	**<0.001**
Recent H. sapiens	139	0.729	**<0.001**
P. troglodytes	94	0.823	**<0.001**
P. paniscus	24	0.797	**<0.001**
Gorilla sp.	34	0.886	**<0.001**
Pongo sp.	44	0.826	**<0.001**

* Includes *A. anamensis* and *A. afarensis*

** Includes *H. habilis s.l. and H. erectus s.l.*

Significant values bolded

Table 8. Variation in origin of LM C7 of lower molars.

Taxon	n	absent	present	metaconid	lingual groove	entoconid	occlusal surface	enamel
A. anamensis	9	88.9%	1 (11.1%)	0.0%	0.0%	100.0%	0.0%	0.0%
A. afarensis	11	81.8%	2 (18.2%)	50.0%	50.0%	0.0%	0.0%	0.0%
A. africanus	60	65.0%	21 (35.0%)	76.2%	23.8%	0.0%	0.0%	0.0%
P. aethiopicus	2	100.0%	0 (0.0%)	-	-	-	-	-
P. boisei	7	85.7%	1 (14.3%)	100.0%	0.0%	0.0%	0.0%	0.0%
P. robustus	62	79.0%	13 (21.0%)	69.2%	23.1%	0.0%	0.0%	7.7%
Homo sp./*habilis s.l.*	8	37.5%	5 (62.5%)	20.0%	80.0%	0.0%	0.0%	0.0%
H. erectus s.l.	7	71.4%	2 (28.6%)	50.0%	50.0%	0.0%	0.0%	0.0%
MPAE	3	100.0%	0 (0.0%)	-	-	-	-	-
H. neanderthalensis	77	71.4%	22 (28.6%)	36.4%	59.1%	0.0%	4.5%	0.0%
H. sapiens (Pleistocene)	42	71.4%	12 (28.6%)	25.0%	75.0%	0.0%	0.0%	0.0%
H. sapiens (recent)	169	95.9%	7 (4.1%)	85.7%	14.3%	0.0%	0.0%	0.0%
P. troglodytes	103	79.6%	21 (20.4%)	81.0%	14.3%	4.8%	0.0%	0.0%
P. paniscus	25	68.0%	8 (32.0%)	75.0%	25.0%	0.0%	0.0%	0.0%
Gorilla sp.	32	59.4%	13 (40.6%)	15.4%	84.6%	0.0%	0.0%	0.0%
Pongo sp.	48	95.8%	2 (4.2%)	0.0%	100.0%	0.0%	0.0%	0.0%

*Frequencies of origin types per taxon do not include individuals with trait absence; MPAE: Middle Pleistocene African and European humans

Figure legends

Figure 1. Three-dimensional models of the EDJ of four upper molars illustrating variation in PPT expression. A) grade 0: PPT absent (extant *H. sapiens* depicted); B) grade 1: shouldering present (*H. neanderthalensis* KRP_D169 depicted); C) grade 2: faint-to-moderate tubercle present (*H. neanderthalensis* KRP_D96 depicted); and D) grade 3: marked tubercle present (*H. neanderthalensis* Scladina 4A_4 depicted).

Figure 2. *Paranthropus robustus* (SK 831a ULM3 mirror-imaged) showing one dentine horn associated with UM C5 at the EDJ (A) but three cuspules at the OES (B). The white arrows indicate the presence and location of the dentine horn and cuspules at the EDJ and OES respectively. Distal to the left.

Figure 3. Types of UM C5 development. A) UM C5 absent (EDJ of *P. t. verus* illustrated); B) hypocone type (EDJ of *P. t. troglodytes* illustrated); C) metacone type (EDJ of *A. africanus* MLD 28 URM3 illustrated); D) distal fovea type (EDJ of *P. robustus* SKX 21841 URM3 illustrated); E) buccal cingulum type (EDJ of *A. africanus* Sts 28 URM2 illustrated); F) occlusal type (EDJ of *A. africanus* Sts 52a URM3 illustrated); and G-H) enamel type (EDJ and OES of *P. robustus* SK 13.14 URM2 illustrated).

Figure 4. Buccal view of upper molars with examples of PPT expression on the distal slope of the paracone in *H. neanderthalensis* (A-F; A: Vi 11-46 M2 B: KMH 21 UM1 C: SD 407 UM1 D: KRP 46 UM1 E: KRP 171 UM1 F: SR 1164 M3) compared to the smooth surface more

commonly observed in other hominoids. G: *P. robustus* (SK 102 UM1) H: Pleistocene *H. sapiens* (Qafzeh 15 UM2) I: early Holocene *H. sapiens* (Combe Capelle UM2) J: Pleistocene *H. sapiens* (Skhul I UM1) K: Pleistocene *H. sapiens* (Qafzeh 9 UM1) and L: recent *H. sapiens*. Mesial to the left.

Figure 5. Types of LM C6 development. A) LM C6 absent (EDJ of recent *H. sapiens* illustrated); B) distal fovea type (EDJ of *P. t. verus* illustrated); C) hypoconulid type (EDJ of *P. t. verus* illustrated); D) entoconid type (EDJ of *Pongo* illustrated); E) occlusal type (EDJ of *Pongo* illustrated); and F) enamel type (EDJ of *A. africanus* STW 412a LRM2 illustrated with distal view of OES inset in bottom right corner). Lingual to the left.

Figure 6. Types of LM C7 development (lingual view). A) LM C7 absent Skinner et al.'s (2008) type A (EDJ of *P. troglodytes* illustrated); B) Skinner et al.'s (2008) type B (EDJ of *P. troglodytes* illustrated); C) Skinner et al.'s (2008) type C (EDJ of *P. troglodytes* illustrated); D) Skinner et al.'s (2008) type D (EDJ of recent *H. sapiens* illustrated); E) Skinner et al.'s (2008) type E (EDJ of *Homo* sp. DNH 67 LRM1 illustrated); F) Skinner et al.'s (2008) type F (EDJ of *H. neanderthalensis* SD 780 LLM1 illustrated mirror-imaged); G) occlusal type (EDJ of *H. neanderthalensis* Vi 11-39 LRM3 illustrated); and entoconid type (EDJ of *P. troglodytes* illustrated). Mesial to the left.

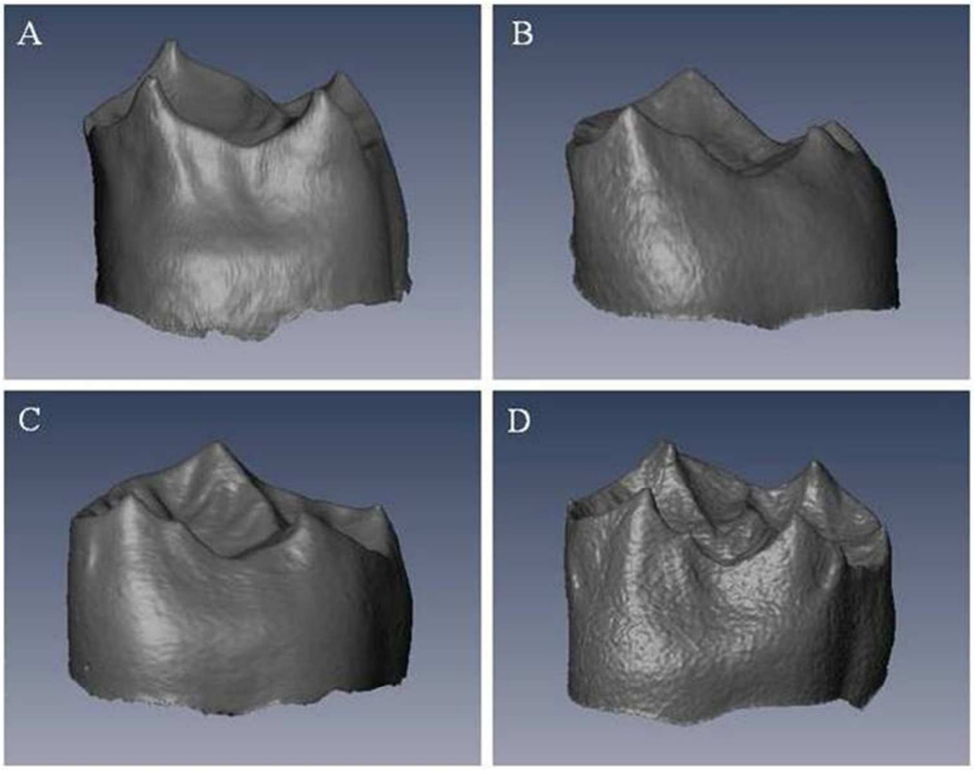

Figure 1. Three-dimensional models of the EDJ of four upper molars illustrating variation in PPT expression. A) grade 0: PPT absent (extant H. sapiens depicted); B) grade 1: shouldering present (H. neanderthalensis KRP_D169 depicted); C) grade 2: faint-to-moderate tubercle present (H. neanderthalensis KRP_D96 depicted); and D) grade 3: marked tubercle present (H. neanderthalensis Scladina 4A_4 depicted).

184x146mm (97 x 97 DPI)

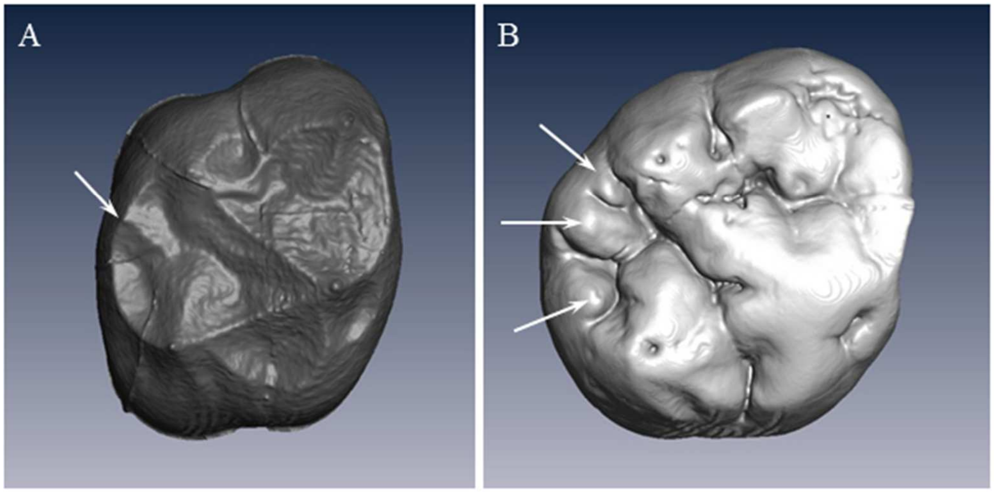

Figure 2. Paranthropus robustus (SK 831a ULM3 mirror-imaged) showing one dentine horn associated with UM C5 at the EDJ (A) but three cuspules at the OES (B). The white arrows indicate the presence and location of the dentine horn and cuspules at the EDJ and OES respectively. Distal to the left.

164x83mm (96 x 96 DPI)

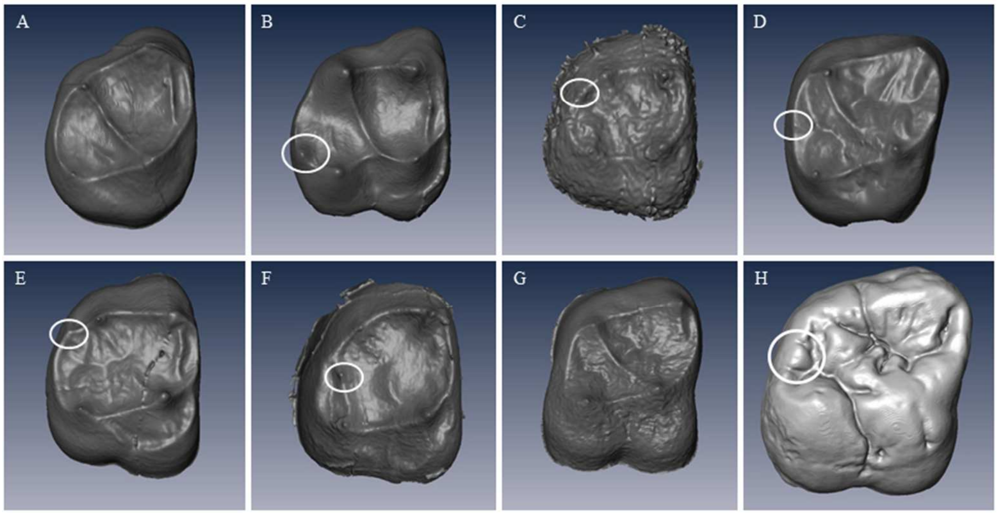

Figure 3. Types of UM C5 development. A) UM C5 absent (EDJ of P. t. verus illustrated); B) hypocone type (EDJ of P. t. troglodytes illustrated); C) metacone type (EDJ of A. africanus MLD 28 URM3 illustrated); D) distal fovea type (EDJ of P. robustus SKX 21841 URM3 illustrated); E) buccal cingulum type (EDJ of A. africanus Sts 28 URM2 illustrated); F) occlusal type (EDJ of A. africanus Sts 52a URM3 illustrated); and G-H) enamel type (EDJ and OES of P. robustus SK 13.14 URM2 illustrated).

228x116mm (96 x 96 DPI)

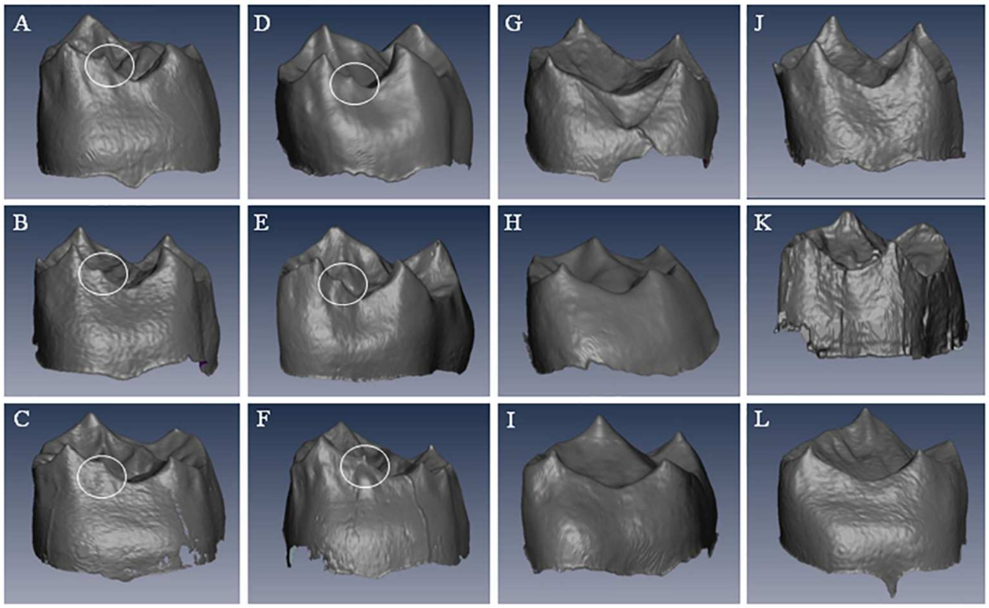

Figure 4. Buccal view of upper molars with examples of PPT expression on the distal slope of the paracone in H. neanderthalensis (A-F; A: Vi 11-46 M2 B: KMH 21 UM1 C: SD 407 UM1 D: KRP 46 UM1 E: KRP 171 UM1 F: SR 1164 M3) compared to the smooth surface more commonly observed in other hominoids. G: P. robustus (SK 102 UM1) H: Pleistocene H. sapiens (Qafzeh 15 UM2) I: early Holocene H. sapiens (Combe Capelle UM2) J: Pleistocene H. sapiens (Skhul I UM1) K: Pleistocene H. sapiens (Qafzeh 9 UM1) and L: recent H. sapiens. Mesial to the left.

203x124mm (150 x 150 DPI)

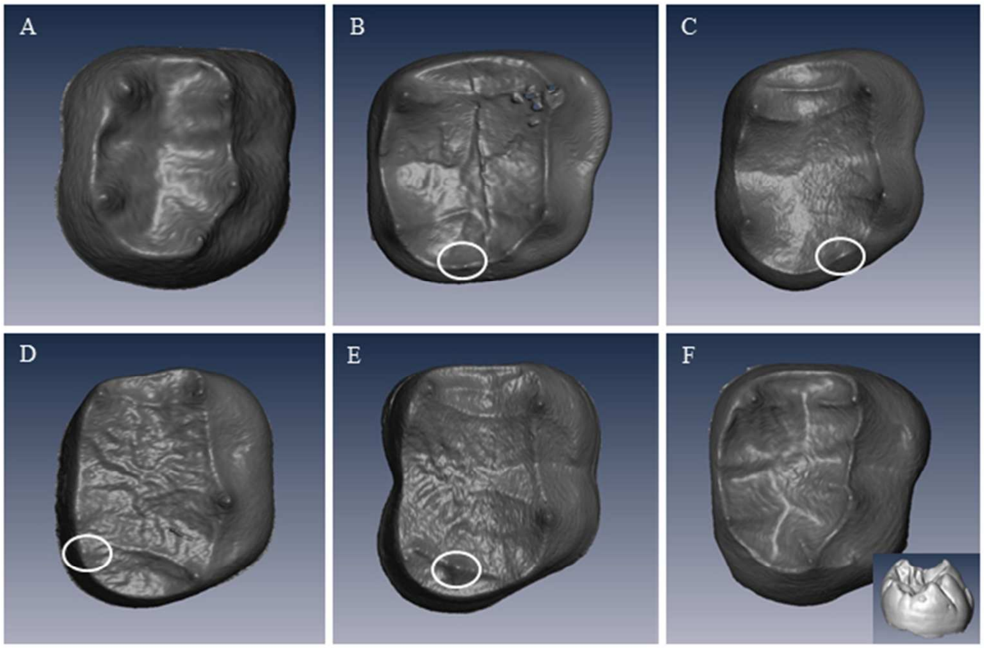

Figure 5. Types of LM C6 development. A) LM C6 absent (EDJ of recent H. sapiens illustrated); B) distal fovea type (EDJ of P. t. verus illustrated); C) hypoconulid type (EDJ of P. t. verus illustrated); D) entoconid type (EDJ of Pongo illustrated); E) occlusal type (EDJ of Pongo illustrated); and F) enamel type (EDJ of A. africanus STW 412a LRM2 illustrated with distal view of OES inset in bottom right corner). Lingual to the left.

177x118mm (96 x 96 DPI)

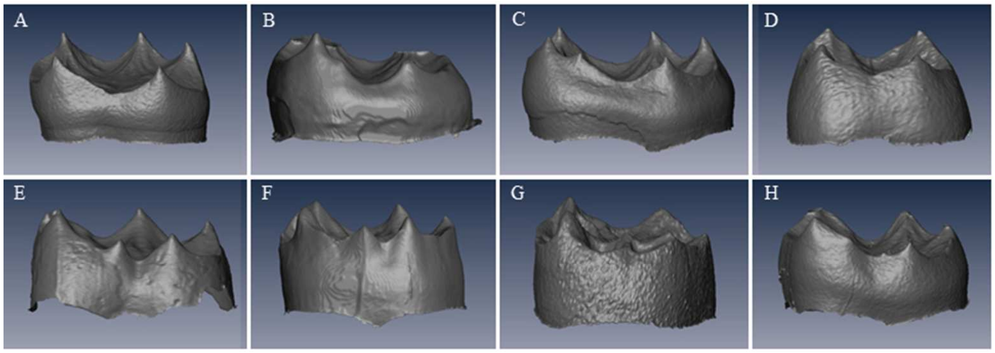

Figure 6. Types of LM C7 development (lingual view). A) LM C7 absent Skinner et al.'s (2008) type A (EDJ of P. troglodytes illustrated); B) Skinner et al.'s (2008) type B (EDJ of P. troglodytes illustrated); C) Skinner et al.'s (2008) type C (EDJ of P. troglodytes illustrated); D) Skinner et al.'s (2008) type D (EDJ of recent H. sapiens illustrated); E) Skinner et al.'s (2008) type E (EDJ of Homo sp. DNH 67 LRM1 illustrated); F) Skinner et al.'s (2008) type F (EDJ of H. neanderthalensis SD 780 LLM1 illustrated mirror-imaged); G) occlusal type (EDJ of H. neanderthalensis Vi 11-39 LRM3 illustrated); and entoconid type (EDJ of P. troglodytes illustrated). Mesial to the left.

212x74mm (96 x 96 DPI)