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Enamel thickness trends in Plio-Pleistocene hominin mandibular molars

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ABSTRACT

Enamel thickness continues to be an important morphological character in hominin systematics and is frequently invoked in dietary reconstructions of Plio-Pleistocene hominin taxa. However, to date, the majority of published data on molar enamel thickness of Pliocene and early Pleistocene hominins derive from naturally fractured random surfaces of a small number of specimens. In this study we systematically analyze enamel thickness in a large sample of Plio-Pleistocene fossil hominins ($n = 99$), extant hominoids ($n = 57$), and modern humans ($n = 30$). Based on analysis of 2D mesial planes of section derived from microtomography, we examine both average and relative enamel thickness, and the distribution of enamel across buccal, occlusal, and lingual components of mandibular molars. Our results confirm the trend of increasing enamel thickness during the Pliocene that culminates in the thick enamel of the robust *Australopithecus* species, and then decreases from early *Homo* to recent modern humans. All hominin taxa share a regional average enamel thickness pattern of thick occlusal enamel and greater buccal than lingual enamel thickness. *Pan* is unique in exhibiting the thinnest average enamel thickness in the occlusal basin. Statistical analysis indicates that among Pliocene hominins enamel thickness is a weak taxonomic discriminator. The data underlying these results are included in a table in the Supplementary Online Material.

Introduction

The thickness and distribution of enamel tissue across tooth crowns remains an important character in assessments of the taxonomy, phylogeny, and dietary reconstructions of fossil primates. Within the hominoid clade, over three decades of research has elucidated patterns of enamel thickness variation in fossil hominins (e.g., Martin, 1985; Beynon and Wood, 1986; Grine and Martin, 1988; Conroy, 1991; Macho and Thackeray, 1992; Schwartz et al., 1998; Brunet et al., 2002, 2005; Olejniczak and Grine, 2005; White et al., 2006; Smith et al., 2006b, 2009a, b; 2012a; Olejniczak et al., 2008a, b), fossil hominoids (e.g., Martin et al., 2003; Smith et al., 2003; Olejniczak et al., 2008c), and extant hominoids (Molnar and Gantt, 1977; Gantt, 1986; Grine, 1991; Schwartz, 2000; Kono, 2004; Tafforeau, 2004; Smith et al., 2005, 2006a, 2012b; Kono and Suwa, 2008; Olejniczak et al., 2008d). Many of these studies in the last decade have utilized microtomography to systematically produce homologous mesial planes of section in molars, which has led to more rigorous taxonomic comparisons (see review in Smith et al., 2012a). However, due to inherent practical and methodological difficulties in producing microtomographic scans of their dentitions, systematic analysis has not been conducted on the majority of otherwise extensively investigated Pliocene hominin taxa. In this contribution we fill in this gap for many species of the genus *Australopithecus* and complement the extensive review recently published by Smith and colleagues (2012a) for Pleistocene *Homo*.

To date, the majority of reported enamel thickness values for Pliocene hominins derive from linear measurements taken on naturally cracked surfaces of molars. For example, White et al. (1994) report linear measurements of *Ardipithecus* (*Ar.*) *ramidus* molars ranging from 1.1 to 1.2 mm and for *Australopithecus* (*Au.*)

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afarensis of 1.4–2.0 mm. Based on microtomography, Suwa et al. (2009) reported *Ar. ramidus* as having enamel thickness greater than *Pan* but thinner than later *Australopithecus*. Johanson et al. (1982) and White et al. (2000) report linear dimensions for various *Au. afarensis* specimens but do not report any measurements for mandibular molars. In the initial publication of the *Au. anamensis* specimens, linear measurements of upper and mandibular molars ranged between 1.5 and 2.0 mm (Leakey et al., 1995). Ward et al. (2001) report linear measurements of 1.0–2.1 mm based on ground thin-sections of naturally fractured (and thin-sectioned mounted) specimens (upper molar KNM-ER 30748 and mandibular molar KNM-ER 30749) in the occlusal basin, cusp tip, and lingual and buccal walls. The *Au. anamensis* finds from Asa Issie exhibit radial (i.e., measured not in a mesial plane of section but rather along a trajectory running perpendicular from the dentine surface to the enamel surface) linear measurements of 1.7–2.3 mm for functional cusps (i.e., buccal cusps on mandibular molars and lingual cusps on upper molars) and 1.3–2.0 mm for adjacent cusps (White et al., 2006). Haile-Selassie et al. (2010) assessed enamel thickness in the Woranso-Mille material from naturally fractured molars and concluded that the range (1.5–2.1 mm) falls within the range of reported measurements for *Au. afarensis, Au. anamensis*, and *Au. africanus*. In their analysis of crown formation times, Lacruz and Ramirez Rozzi (2010) report linear enamel thickness measurements of 1.95 mm (AL 333-52), 2.13 mm (AL 366-1), and 1.71 mm (Omo L2-79). Examining *Au. africanus* specimens, Grine and Martin (1988) report average enamel thickness values of 1.81 mm (Stw 284; now referred to as Stw 280) and 1.78 mm (Stw 402), and relative enamel thickness values of 21.27 (Stw 280) and 23.06 (Stw 402). Macho and Thackeray (1992) used medical CT to examine the regional distribution of enamel thickness across the crowns of *Au. robustus*, *Au. africanus*, and *Homo* sp. maxillary molars and found considerable overlap between taxa in many regions of the crown. Finally, Olejniczak et al. (2008b) published data on *Au. africanus* and *Au. robustus* from South Africa, expanding their analysis to 3D enamel distribution across the crown. Collectively, however, the limited sample size, limited assessment of enamel thickness (i.e., often linear measurements), and variation in location of measurement result in a poor characterization of enamel thickness variation along the molar row in Pliocene hominins.

Using microtomography and controlled mesial planes of section in mandibular molars, we analyze enamel thickness to assess taxonomic differences in mandibular molar crowns of *Au. anamensis*, *Au. afarensis*, *Au. africanus*, *Au. boisei*, *Au. robustus*, and specimens of early *Homo*. We compare these results to samples of *Pan*, *Gorilla*, and *Pongo*, as well as to a sample of recent humans. The goals of this study are to: 1) analyze enamel thickness variation among Plio-Pleistocene hominins using a 2D mesial plane of section; 2) characterize the distribution of lingual, occlusal, and buccal enamel among hominin taxa; 3) assess the reliability of taxonomic discrimination based on enamel thickness measured in a 2D section; 4) evaluate the affinity of taxonomically ambiguous specimens based on their enamel thickness values; and 5) provide molar-specific enamel thickness measurements for extant apes and fossil hominins for use by other researchers.

Materials

The study sample consists of mandibular molars (n = 186) belonging to both extant hominoids and fossil hominins and is detailed in full in Supplementary Online Material (SOM) Table 1. The number of first, second, and third molars of each taxon is listed in Table 1. This sample is the largest compiled to date for a systematic analysis of enamel thickness in Plio-Pleistocene hominins of Africa. Molars either derive from mandibles or are isolated specimens. In the case of the latter, the justification for assigning a molar to a particular position is also noted. Only specimens that exhibited no evidence of known pathology were chosen for study. Given that sex is unknown for the majority of fossil specimens it was not incorporated into our analysis as a variable.

Table 1
Composition of the study sample.[a]

Taxon	M1	M2	M3	Total
Pongo	9	8	3	20
Gorilla	2	5	6	13
Pan paniscus	3	5	0	8
Pan troglodytes	6	7	3	16
Australopithecus anamensis	6	4	3	13
Australopithecus afarensis	2	4	2	8
Australopithecus africanus	9	13	12	34
Australopithecus aethiopicus	0	2	1	3
Australopithecus boisei	0	4	3	7
Australopithecus robustus	6	8	10	24
Homo sp. indet.	2	2	0	4
Homo erectus	1	3	2	6
Homo sapiens	8	15	7	30
Total	54	80	52	186

[a] Not including specimens of uncertain taxonomic affinity listed in Table 4.

Hominoid taxa include *Pongo* sp., *Gorilla* sp., *Pan paniscus*, and *Pan troglodytes* ssp. Due to the small sample sizes for some molar positions, no species delineation was made for *Pongo* and *Gorilla* and no subspecies delineation for *P. troglodytes*. The Plio-Pleistocene hominin taxa include *Au. anamensis*, *Au. afarensis*, *Au. africanus*, *Au. aethiopicus*, *Au. boisei*, *Au. robustus*, *Homo* sp. indet., *Homo erectus*, and modern *Homo sapiens*. A number of specimens of uncertain taxonomic affinity were also analyzed and their taxonomic affinity assessed based on their measured enamel thickness values.

Fossil hominin specimens derive from collections housed at the following institutions: National Museum of Ethiopia, Addis Ababa, Ethiopia; National Museums of Kenya, Nairobi, Kenya; University of Witwatersrand, Johannesburg, South Africa; Ditsong National Museum of Natural History, Pretoria, South Africa. The hominoid samples derive from the Museum for Natural History (ZMB), Berlin, Germany; the Senckenberg Research Institute (SMF), Frankfurt, Germany; the Royal Museum for Central Africa (MRAC), Tervuren, Belgium; and the Max Planck Institute for Evolutionary Anthropology (MPI), Leipzig, Germany. The modern human sample derives from the Leipzig University Anatomical Collection (ULAC), Leipzig, Germany; the 'Francisc J. Rainer' Anthropology Institute (R), Bucharest, Romania; and the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

Methods

To obtain a 2D mesial plane of section each molar was non-destructively imaged using computed tomography (using either a BIR Actis 300/225 FP or SkyScan 1172 microtomographic scanner) with a resultant isometric voxel size of 15–65 μm^3. The CT data set of each specimen was rotated manually in Avizo (v6.3, FEI Inc.) into anatomical position. Next, a plane was placed perpendicular to the occlusal plane and passing through the tip of the protoconid dentine horn. This plane was then rotated to pass through the tip of the metaconid dentine horn. This slice image was then saved in TIFF format (Fig. 1). Benazzi et al. (2014) have outlined a methodology to produce repeatable 2D planes of section. This methodology was not adopted here because it is difficult to apply to many of the fragmentary hominin teeth used in this study whose cervical line is not preserved (see Discussion).

Four variables were measured on each mesial section using ImageJ (v1.47, NIH): area of the enamel cap (mm^2), area of the