A geometric morphometric analysis of hominin lower molars: Evolutionary implications and overview of postcanine dental variation

Aida Gómez-Robles [a,*], José María Bermúdez de Castro [b], María Martinón-Torres [b], Leyre Prado-Simón [c], Juan Luis Arsuaga [d]

[a] Department of Anthropology, The George Washington University, 800 22nd St. NW, Washington, DC 20052, USA
[b] Centro Nacional de Investigación sobre la Evolución Humana, Paseo de la Sierra de Atapuerca S/N, 09002 Burgos, Spain
[c] Stomatology Department, Dentistry Faculty, University of Granada, Spain
[d] Centro Mixto UCM-ISCIII de Evolución y Comportamiento Humanos, Avd. Monforte de Lemos 5, Pabellón 14, 28029 Madrid, Spain

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ABSTRACT

Lower molars have been extensively studied in the context of hominin evolution using classic and geometric morphometric analyses, 2D and 3D approaches, evaluations of the external (outer enamel surface) and internal anatomy (dentine, pulp chamber, and radicular canals), and studies of the crown and root variation. In this study, we present a 2D geometric morphometric analysis of the crown anatomy of lower first, second, and third molars of a broad sample of hominins, including Pliocene and Lower, Middle, and Upper Pleistocene species coming from Africa, Asia, and Europe. We show that shape variability increases from first to second and third molars. While first molars tend to retain a relatively stable 5-cusped conformation throughout the hominin fossil record, second and third molars show marked distal reductions in later *Homo* species. This trend to distal reduction is similar to that observed in previous studies of premolars and upper second and third molars, and points to a correlated reduction of distal areas across the whole postcanine dentition. Results on lower molar variation, as well as on other postcanine teeth, show certain trends in European Pleistocene populations from the Atapuerca sites. Middle Pleistocene hominins from Sima de los Huesos show Neanderthal affinities and strong dental reduction, especially in the most distal molars. The degree of dental reduction in this population is stronger than that observed in classic Neanderthals. *Homo antecesor* hominins from Gran Dolina-TD6 have primitive lower teeth that contrast with their more derived upper teeth. The evolutionary implications of these dental affinities are discussed in light of recent paleogenetic studies.

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Introduction

The central role of dental anthropology in the broader framework of paleoanthropology is demonstrated by the profusion of articles aiming to address taxonomic and phylogenetic questions via dental morphometry. Dental evolution is subject to several influences, ranging from developmental constraints related to the serially homologous nature of the dentition to functional constraints related to occlusion (Gómez-Robles and Polly, 2012). Nevertheless, a significant phylogenetic signal remains in dental morphology (Caumul and Polly, 2005), and this is the basis of the generally accepted utility of dental traits in the classification of specimens and species, as well as in describing possible evolutionary scenarios (Suwa et al., 1994, 1996; Bailey, 2002a, 2004; Bailey and Lynch, 2005; Guatelli-Steinberg and Irish, 2005; Kaifu et al., 2005; Moggi-Cecchi et al., 2006; Martinón-Torres et al., 2007a, b; Moggi-Cecchi and Boccone, 2007; Bailey et al., 2009; Benazzi et al., 2011b; Gómez-Robles et al., 2013). Among studies evaluating dental variation, analyses of lower molar morphology are especially common in the literature, and they range from classic morphometric analyses (e.g., Wood and Abbott, 1983; Wood et al., 1983; Bermúdez de Castro and Nicolás, 1995) to quantitative studies of form and shape variation (Benazzi et al., 2011a), sometimes based on 3D reconstructions (Skinner et al., 2008). More recently, some microCT-based studies have focused on the root morphology of mandibular molars (Kupczik and Hublin, 2010; Emonet et al., 2012).

Given the relevance of dental morphology in understanding hominin evolution, we initiated in 2006 a systematic evaluation of postcanine dental variation in crown morphology (Martinón-Torres et al., 2006). Our evaluations have included a comprehensive representation of the hominin fossil record, but they have paid special attention European Pleistocene groups. Our series of papers has provided evidence that several dental traits typify Middle and Upper Pleistocene European groups. These features include a change towards symmetry and distal reduction in upper premolars (Gómez-Robles et al., 2011b); a very characteristic skewed morphology in upper first molars that can be traced back to the late Lower Pleistocene (Gómez-Robles et al., 2007, 2011a; see also Bailey, 2004); a strong reduction of distal cusps in upper second and, especially, third molars (Gómez-Robles et al., 2012); an acquisition of nearly symmetric shape and a strong reduction of the talonid in lower first premolars (Gómez-Robles et al., 2008); and a general maintenance of an asymmetric conformation in lower second premolars (Martinón-Torres et al., 2006). Dental traits related primarily to dental reduction are shared in general terms by *Homo sapiens* and *Homo neanderthalensis* (also referred to as modern humans and Neanderthals throughout the text, respectively), although the specific features of these reductions differ in both species. These features are the ones that allow for the differentiation of these two species (and sometimes of their ancestral populations) in spite of the general reduction that drives dental evolution in both cases.

Dental morphology shows a wide range of variation within species, and its analysis across the closely related species that constitute the hominin clade does not allow for the identification of unmistakably delineated species-specific morphologies. However, several trends can be identified and linked to particular population dynamics either via random factors such as genetic drift (Weaver et al., 2007), or specific direct or indirect selective pressures (Grine, 1986; Bermúdez de Castro, 1989; Macho and Moggi-Cecchi, 1992; Bermúdez de Castro and Nicolás, 1995; Bermúdez de Castro et al., 2003b; Irish and Guatelli-Steinberg, 2003; Lozano et al., 2008). Regardless of the origin of morphological diversification, it is evident in most studies of dental morphology that the ranges of variation of different species overlap, although they can be distinguished in their mean values/morphologies. This causes taxonomic classification based on dental morphology to be a probabilistic task that will give rise to the allocation of specimens to species with certain probability (Bailey et al., 2009).

Our previous studies of upper and lower premolars, as well as upper molars, have revealed not only particular morphological patterns typical of European groups (*Homo antecessor* from Gran Dolina-TD6, European *Homo heidelbergensis*, and *H. neanderthalensis*) but also a markedly derived character state of the Middle Pleistocene population from Atapuerca-Sima de los Huesos (SH) compared with other European Middle Pleistocene groups and classic Neanderthals (Gómez-Robles et al., 2012; Martinón-Torres et al., 2012, 2013). The derived state of hominins from the SH collection is especially apparent in the most proximal premolars and the most distal molars. These morphological peculiarities are especially puzzling in light of the recent DNA analysis of one SH hominin (Meyer et al., 2014), which has revealed a higher genetic mitochondrial affinity with Denisovans (Reich et al., 2010; Meyer et al., 2012) than with Neanderthals. In terms of dental morphology, the scarce morphological information on Denisovans shows that they are morphologically different from both Neanderthals and modern humans, with metric and shape features similar to those observed in *Homo habilis* and *Homo erectus* (Reich et al., 2010).

We have previously evaluated lower second molar morphology in the context of methodological approaches useful to deal with evolutionary novelties and losses (Gómez-Robles et al., 2011c).

Nevertheless, a systematic evaluation of hominin lower molars in the context of our 2D geometric morphometric series of analyses is still lacking (Martinón-Torres et al., 2006; Gómez-Robles et al., 2007, 2008, 2011b). Therefore, the main objective of this study is to complete the geometric morphometric analysis of the postcanine dentition in order to investigate a more comprehensive scenario of hominin dental evolution during the Plio-Pleistocene. As in previous cases, our analysis is focused on the evaluation of the European fossil record and the relationship of European fossils with modern humans, although Asian and African specimens are also included to place European variation into a broader context. As the final article in our series of papers, we discuss the implications of dental variation across the whole poscanine dentition, with special emphasis on the evolutionary relationships of the Lower and Middle Pleistocene fossil samples from the Atapuerca sites of Gran Dolina-TD6 and Sima de los Huesos.

Material and methods

Material

A sample of 132 lower first molars (M_1), 126 lower second molars (M_2), and 108 lower third molars (M_3) was analyzed (Tables 1—3). The study of fossil teeth by means of 2D geometric morphometrics based on image analysis ensured the availability of

Table 1
List of lower first molars included in this study.[a]

Species	n	Specimens
A. afarensis	n = 6	AL128-23, AL145-35, AL266-1, AL288, AL333-1a, LH2
A. africanus	n = 4	MLD2, STS24, STW498, Taung
P. robustus	n = 4	SK23, SKW5, SKX4446, TM1517
P. boisei	n = 2	KNM-ER3230, KNM-ER15930
H. habilis s. l.	n = 6	KNM-ER1802, KNM-ER5431, OH7, OH13, OH16, STW151b
H. ergaster	n = 3	KNM-ER820, OH22, KNM-WT15000
Dmanisi	n = 2	D211, D2735
H. erectus	n = 11	Zhoukoudian: B3.9, 36, 137 Sangiran: S1b, S6, S7-20, S7-42, S7-43, S7-61, S7-62, S7-76
H. antecessor	n = 3	Atapuerca-TD6: ATD6-5, ATD6-93, ATD6-96
European *H. heidelbergensis*	n = 22	Arago: A13, A40, A89 Atapuerca-SH: AT-2 (Ind 2), AT-101 (Ind 3), AT-1759 (Ind 6), AT-141 (Ind 10), AT-286 (Ind 11), AT-300 (Ind 12), AT-2276 (Ind 14), AT-2779 (Ind 16), AT-829 (Ind 18), AT-576 (Ind 19), AT-4318 (Ind 20), AT-607 (Ind 23), AT-1458 (Ind 24), AT-3934 (Ind 25), AT-561 (Ind 26), AT-792 (Ind 27), AT-950 (Ind 31) Montmaurin Pontnewydd 11
H. neanderthalensis	n = 22	Arcy-sur-Cure (Grotte de l'Hyène): 3 Arcy-sur-Cure (Grotte du Renne): 35 Ehringsdorf Hortus: H1262 (Ind II), H988 (Ind V), H IV Krapina: B, C, D, E, G, J, 79 (Ind L), 84 (Ind N), 81 (Ind P), 80, 105 Le Moustier 1 Malarnaud Petit-Puymoyen (two specimens) Saint Césaire
Fossil *H. sapiens*	n = 10	Qafzeh: 4, H4 Abri Pataud Isturitz: 106 Les Rois (three specimens including Les Rois A) Saint Germain-La Rivière: B3, B4, B5
Recent *H. sapiens*	n = 37	Heidenheim (AMNH): 15 individuals La Torrecilla (LPA-UGR): 22 individuals

[a] Ind: individual; AMNH: American Museum of Natural History (New York, USA); LPA-UGR: Laboratory of Physical Anthropology, University of Granada (Granada, Spain).