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A geometric morphometric analysis of hominin upper premolars. Shape variation and morphological integration

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ABSTRACT

This paper continues the series of articles initiated in 2006 that analyse hominin dental crown morphology by means of geometric morphometric techniques. The detailed study of both upper premolar occlusal morphologies in a comprehensive sample of hominin fossils, including those coming from the Gran Dolina-TD6 and Sima de los Huesos sites from Atapuerca, Spain, complement previous works on lower first and second premolars and upper first molars. A morphological gradient consisting of the change from asymmetric to symmetric upper premolars and a marked reduction of the lingual cusp in recent *Homo* species has been observed in both premolars. Although percentages of correct classification based on upper premolar morphologies are not very high, significant morphological differences between Neanderthals (and European middle Pleistocene fossils) and modern humans have been identified, especially in upper second premolars. The study of morphological integration between premolar morphologies reveals significant correlations that are weaker between upper premolars than between lower ones and significant correlations between antagonists. These results have important implications for understanding the genetic and functional factors underlying dental phenotypic variation and covariation.

Introduction

Numerous recent studies have demonstrated the existence of morphometric differences among the dentitions of several hominin species. These differences are subtle in some cases, but in other cases morphological differences are enough to determine the specific assignment of isolated teeth (e.g., Wood and Abbott, 1983; Wood et al., 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988; Gómez-Robles et al., 2007, 2008; Bailey et al., 2009). Different teeth can be used to discriminate among different taxa, including non-hominins and hominins (e.g., Haile-Selassie et al., 2004; White et al., 2006; Suwa et al., 2009), early and late hominins (e.g., Wood and Abbott, 1983; Wood et al., 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988; Gómez-Robles et al., 2008; Quam et al., 2009), gracile and robust australopiths (e.g., Wood and Abbott, 1983; Wood et al., 1983, 1988; Wood and Uytterschaut, 1987; Moggi-Cecchi et al., 2006; Skinner et al., 2008), Eurasian and African hominins (e.g., Martinón-Torres et al., 2006, 2007a, 2008), and Neanderthals and modern humans (e.g., Bailey, 2002a, 2004; Bailey and Lynch, 2005; Gómez-Robles et al., 2007; Bailey et al., 2009). The slightly different trends impacting the morphological evolution of each tooth class stress the importance of carefully analysing dental morphology in fossil hominin species in all dental classes, and of later integrating the information obtained from different studies.

Several papers have been published with this aim using both classic morphometrics (e.g., Wood and Abbott, 1983; Wood et al., 1983, 1988; Wood and Uytterschaut, 1987; Wood and Engleman, 1988; Bailey, 2004; Quam et al., 2009) and geometric morphometric techniques (e.g., Bailey and Lynch, 2005; Martinón-Torres et al., 2006; Gómez-Robles et al., 2007, 2008; Skinner et al., 2008), with particular focus on molars and lower premolars. Upper premolars, however, have been regarded very often as teeth that do not show clear specific differences when using either the ASUDAS classification (Bailey, 2002b; Martinón-Torres, 2006; Bailey et al., 2009) or measurements of cusp base areas (Wood and Engleman, 1988; Bailey, 2002b), especially in distinguishing

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Neanderthals from modern humans. Wood and Engleman (1988) noted that the buccal cusp of the upper premolars of robust australopiths is relatively larger than the buccal cusp measured in African gracile taxa, although these differences are not significant (probably due to small sample sizes). Moreover, some multivariate characters based on landmarks (Lavalle, 1984), as well as some angular measurements (Morris, 1981), have demonstrated that upper first premolar morphology can differentiate modern human populations, so more marked differences between fossil species are expected. Hence, the reassessment of upper first and second premolar morphologies in extensive hominin samples by using geometric morphometric techniques may reveal interspecific differences previously unnoticed by using classic morphometric methods.

An increasing number of articles quantitatively analysing the three-dimensional morphology of hominin and hominoid teeth has been published recently (e.g., Skinner et al., 2008, 2009; Braga et al., 2010; Singleton et al., 2011). The advantages of 3D approaches are clear in preserving information regarding the general topography of the studied teeth, and providing an illustrative and visually appealing graphical representation of morphological differences. Nonetheless, in spite of the lack of these characteristics, 2D studies of dental morphology also present important advantages. Among them, the greater simplicity of data collection allows for greater sample sizes and for a more comprehensive study of the hominin fossil record.

A broad sample of African, Asian and European hominins has been included in this study. However, European Pleistocene specimens are clearly predominant, so inferences regarding these populations can be more accurately tackled. Although with some variants, the role of European middle Pleistocene populations in the context of hominin evolution has been summarized in two models (recently reviewed in Hublin, 2009; Endicott et al., 2010). One of them regards *Homo heidelbergensis* as a geographically widespread species giving rise to Neanderthals in Europe and to modern humans in Africa (e.g., Rightmire, 1998). The second model describes *H. heidelbergensis* as an exclusive European species directly related to Neanderthals and sharing some apomorphic traits with them (e.g., Arsuaga et al., 1997b). It is important to note that the term *H. heidelbergensis* is used in this paper with this second meaning to make reference to European middle Pleistocene populations with clear morphological affinities with classic Neanderthals (see discussion and references therein). As such, the vernacular term pre-Neanderthal is also used throughout the text to designate these populations. As far as *Homo antecessor* is concerned, this species was initially defined as ancestral to both Neanderthals and modern humans (Bermúdez de Castro et al., 1997). Nevertheless, some derived Neanderthal dental traits have been recently identified in this species (Gómez-Robles et al., 2007, 2011; Martinón-Torres et al., 2007a,b). Models describing a continuous fossil record in Europe during the Pleistocene would predict stronger morphological affinities between TD6, Sima de los Huesos and Neanderthals than between the two earlier samples and modern humans.

This manuscript continues the series of articles initiated in 2006, in which the dental morphology in a representative sample of hominin species is analysed by using Procrustes-based methods. Our first aim is to describe dental morphological variation in the hominin fossil record, determining the ability of upper premolar shape to correctly assign individuals to taxa and to reflect phylogenetic relationships among species. The second objective of the paper is to evaluate the possible coevolution of both upper premolars (also with antagonist premolars), using the toolkit provided by geometric morphometric techniques. The third objective of this manuscript is to provide a quantitative description of upper premolar morphology of both samples coming from the Sierra de Atapuerca sites: the lower Pleistocene assemblage from the TD6 level of the Gran Dolina site (Bermúdez de Castro et al., 1997, 1999) and the middle Pleistocene assemblage from the Sima de los Huesos site (Bermúdez de Castro, 1986, 1988, 1993). This morphological description will be brought into context by comparison of the Spanish fossils with African, Asian, and European Pliocene and Pleistocene specimens, as well as with recent human populations. These comparisons will enable us to provide new information to the ongoing debate about human taxonomy and phylogeny, as well as to improve current understandings of the role of European populations, especially of those from Atapuerca, in the evolutionary scenarios described by different authors (Arsuaga et al., 1997b; Bermúdez de Castro et al., 1997; Stringer and Hublin, 1999; Carbonell et al., 2005, 2008; Martinón-Torres et al., 2007a; Hublin, 2009).

Material and methods

Materials

One hundred and sixteen upper first premolars (P^3) and one hundred and twenty upper second premolars (P^4) were analysed (the detailed composition of the samples is shown in Tables 1 and 2). The majority of Eurasian fossils (with the exception of the Zhoukoudian specimens and some Neanderthals) were analysed by studying the original fossils, whereas Plio- and Pleistocene African premolars were studied by means of casts. Taxonomic grouping of individuals followed the same general guidelines as those laid out in Gómez-Robles et al. (2007, 2008). Occlusal photographs on which subsequent analyses are based were taken with a Nikon D80 digital camera fitted with an AF Micro Nikkor 105 mm, f/2.8D lens. The plane parallel to the cemento-enamel junction was placed parallel to the lens of the camera, following the same protocol described in Gómez-Robles et al. (2007, 2008). Only one antimere was analysed per individual, so left premolars were studied by default. When a given individual only preserved the right antimere (or when left premolars were not as well preserved as right ones), right antimeres were mirror-imaged.

Methods

Four landmarks and 39 sliding semilandmarks were digitized by A. G.-R, with TpsDig2 software (Rohlf, 2005) to analyse the occlusal morphology of both maxillary premolars. The four landmarks corresponded to (Fig. 1):

1. The deepest point of the mesial/anterior fovea or point where the central groove intersects the mesial foveal grooves.
2. The tip of the buccal cusp or paracone.
3. The deepest point of the distal/posterior fovea or point where the central groove intersects the distal foveal grooves.
4. The tip of the lingual cusp or protocone.

Additionally, 39 equidistant sliding semilandmarks (Bookstein, 1996) were used to analyse the dental outline. The first semilandmark was located at the point of the distal outline directly opposite to the distal fovea, and the other semilandmarks were digitized in a counterclockwise direction. These semilandmarks were slid by minimizing Procrustes distances between individual specimens and the mean shape of the sample. Additional information about sliding techniques can be found in Gunz et al. (2005), Bastir et al. (2006) and Pérez et al. (2006).

A generalized Procrustes analysis (Rohlf and Slice, 1990; Dryden and Mardia, 1998) was used to remove all of the non-morphological information (location, size, and orientation) from the sample by