Hominin lower second premolar morphology: evolutionary inferences through geometric morphometric analysis

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Abstract

Mandibular premolars are increasingly used in taxon-specific diagnostic analyses of hominins. Among the principal difficulties in these evaluations is the absence of discrete, discernible, and comparable anatomical structures for rigorous quantitative assessment. Previous research has addressed either internal crown surface features (such as cusps and fossae) or the morphology of the crown outline. In the present paper, we integrate both types of information in the examination of morphological variation of lower P4s (n = 96) among various fossil hominin species with an emphasis on genus *Homo*. We use a set of 34 2D landmarks combining coordinate data from four classical dental landmarks on the occlusal surface and 30 sliding semilandmarks of the crown outline. Our results indicate that external shape variation is closely related to the configuration of the occlusal morphological features and influenced by dental size. The external and internal shapes of P4 are polymorphic but still useful in depicting a primitive-derived gradient. The primitive pattern seems to have been an asymmetrical contour with a mesially displaced metaconid, development of a bulging talonid, and a broad occlusal polygon. The trend toward dental reduction during the Pleistocene produced different morphological variants with a reduced occlusal polygon and decreased lingual occlusal surface in later *Homo* species. *Homo heidelbergensis/neanderthalensis* have fixed plesiomorphic traits in high percentages, whereas in modern humans a symmetrical outline with a centered metaconid and talonid reduction evolved.
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Keywords: Procrustes; Sliding semilandmarks; Occlusal shape; Premolars; Asymmetry

Introduction

The morphology of mandibular premolars may be taxonomically diagnostic among hominin taxa (Ludwig, 1957; Patte, 1962; Biggerstaff, 1969; Wood and Uytterschaut, 1987; Uytterschaut and Wood, 1989; Bailey, 2002a,b; Bailey and Lynch, 2005). However, capturing premolar occlusal morphology in a way that allows rigorous quantitative comparison remains a challenge. Research on premolar crown morphology has largely relied on descriptive and qualitative assessments of

the shape of the crown and the cuspal morphology (e.g., Fraipont and Lohest, 1887; Genet-Varcin, 1962; Lumley et al., 1972; Turner et al., 1991; Irish, 1993; Scott and Turner, 1997). Recently, Elliptic Fourier Analysis (EFA) (Lestrel, 1974, 1997; Khul and Giardina, 1982; Seiffert and Kappelman, 2001) has been used to quantify the crown outline (Bailey and Lynch, 2005). While this method is useful in obtaining mean shapes for inter-hominin comparisons (Bailey and Lynch, 2005), it does not provide geometrically comparable structures for a direct comparison. In addition, EFA provides no information about size.

These analytical problems can be overcome to some degree by using recent improvements in geometric morphometric

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techniques including sliding semilandmarks (Bookstein, 1997). Semilandmarks are evenly spaced points along an outline that can be analyzed together with information about cusp morphology by common Procrustes superimposition techniques (Rohlf and Slice, 1990; Bookstein, 1991). Thus, these methods allow investigation on both shape and size (see details in Materials and methods).

The morphology of the lower second premolar (P4) has been described as particularly useful for taxonomic designations in hominins (e.g., Wood and Uytterschaut, 1987; Bailey and Lynch, 2005). For this reason, we use geometric morphometric techniques to explore the utility of P4 morphology in characterizing *Homo* species. We consider dental variation in Middle and Late Pleistocene groups and include small samples of *Australopithecus*, Pliocene, and Lower Pleistocene *Homo* for comparison.

Materials and methods

We used standardized occlusal surface pictures of 96 P4s sampled from various hominin taxa (Table 1). We focus on premolar variation in Middle and Late Pleistocene *Homo*. In order to assess the phylogenetic significance of these differences, data from small samples of *Australopithecus* and Pliocene and Lower Pleistocene *Homo* are also included. In order to investigate trait polarity, we have assumed that *Australopithecus* represents the primitive condition. For comparative purposes, we have pooled some specimens into more or less homogeneous groups relating their geographical

and chronological span: *Australopithecus* (n = 6), *Paranthropus* (n = 1), Plio-Pleistocene *Homo* (n = 6), Late Lower Pleistocene *Homo* (n = 3), African Middle Pleistocene *Homo* (n = 5), *Homo antecessor* (n = 2), European Middle Pleistocene *Homo* (n = 23), *Homo neanderthalensis* (n = 13), and *Homo sapiens* (n = 37) (Table 1). We analyze *Homo antecessor* separately from the rest of Late Lower Pleistocene specimens because their premolars display morphological differences from the other groups.

Images of each occlusal surface were taken with a Nikon® D1H camera fitted with an AF Micro-Nikon 105 mm, f/2.8D. The camera was attached to a Kaiser Copy Stand Kit RS-1® with grid baseboard, column, and adjustable camera arm. A leveling device was used to ensure that the lens was parallel to the baseboard and the cemento-enamel junction (CEJ). For maximum depth of field, we used an aperture of f/32. The magnification ratio was adjusted to 1:1, and a scale was included in each photograph and placed parallel to, and at the same distance from the lens as, the occlusal plane.

Because asymmetry in dental morphological traits tends to be minor (Trinkaus, 1978; Scott and Turner, 1997), only the right antimere was used in the analyses. In order to maximize sample sizes, when the right tooth was absent or damaged, the left tooth was mirror-imaged with Adobe® Photoshop®. Teeth with severe attritional wear and those where one or more landmarks could not be clearly identified were not used.

Geometric morphometric methods

At the core of geometric morphometrics is Kendall's (1977) definition of shape as "all geometric information that remains when location, orientation and scale have been filtered out of an object." Shape can be described by configurations of landmarks, which are points of correspondence between different objects that match between and within populations (Bookstein, 1991; O'Higgins, 2000; Zelditch et al., 2004). Landmarks have both coordinates and a biological significance (Bookstein, 1991) (Fig. 1A).

Procrustes techniques use least square methods to superimpose a given structure (target) at its corresponding landmarks (by translation, rotation, and scaling) onto a reference structure (Bookstein, 1991) (Fig. 1B). In the Generalized Procrustes Analysis (GPA) (Rohlf and Slice, 1990), all specimens (many target configurations) are aligned to their mean shape (reference configuration). The results of the generalized Procrustes superimposition are scatters of corresponding landmarks (Procrustes shape coordinates) around their means (Fig. 1B,C). The shape of a GPA superimposed landmark configuration is defined by the entirety of its residual coordinates.

During the scaling procedure of GPA, a scaling factor called "centroid size" is obtained. It is defined as the square root of the summed squared distances between the centroid (the mean of all landmark coordinates of a specimen) and each of the landmarks. It is a powerful size measurement because it

Table 1
List of the specimens included in this analysis

Australopithecus (n = 6)	AL-266, AL-333w, AL-400, Sts14, Sts52, Stw 498 (casts)
Paranthropus (n = 1)	TM1517 (cast)
Plio-Pleistocene *Homo* (n = 6)	OH-7, OH-13, OH-16 (casts) D211, D2735 (originals) KNM-ER 1802 (cast)
Late Lower Pleistocene *Homo* (n = 3)	KNM-WT 15000, KNM-ER 992, Sangiran 6 (casts)
African Middle Pleistocene *Homo* (n = 5)	Ternifine 1, 2, 3 (originals) Rabat, OH-22 (casts)
Homo antecessor (n = 2)	ATD6-4, ATD6-96 (originals)
European Middle Pleistocene *Homo* (n = 23)	Mauer (cast) Arago 13, Arago 28 (originals) Sima de los Huesos (originals): AT-792, AT-1465, AT-1467, AT-168, AT-1763, AT-1828, AT-2, AT-221, AT-2386, AT-277, AT-2780, AT-2787, AT-28, AT-300, AT-3188, AT-3942, AT-4101, AT-562, AT-607, AT-9
Homo neanderthalensis (n = 13)	Shanidar 2 (cast) Hortus II, Hortus V (originals) Krapina: 113, 118, 26, 30, 32, 50, D, E, H, J (casts)
Homo sapiens (n = 37)	Dolni Vestonice: DV 13, DV 14, DV 15 (originals) Modern human collection from Institute of Anthropology of the University of Coimbra (Portugal)