

## BRIEF COMMUNICATION

# Crown size and cusp proportions in *Homo antecessor* upper first molars. A comment on Quam et al. 2009

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## Abstract

A recent evaluation of upper first molar (M<sup>1</sup>) crown size and cusp proportions in the genus *Homo* (Quam et al. 2009) describes *Homo antecessor* as maintaining a primitive pattern of cusp proportions, similar to that identified in australopithecines and the earliest members of the genus *Homo*. These results contrast with those of Gómez-Robles et al. (2007), who described the crown shape in these molars as derived and similar to Neanderthals and European *Homo heidelbergensis*. The reassessment of these measurements following the same methodology described by Quam et al. (2009) in all the M<sup>1</sup>s that are currently part of the hypodigm of *H. antecessor* demonstrates that the fossils from TD6 not only have the same cusp proportions identified in later *Homo* species, but also a strongly reduced metacone and a large hypocone shared with Middle and Upper Pleistocene members of the Neanderthal lineage. The evolutionary significance of these features should be evaluated in light of the results provided by recently discovered dental, cranial, mandibular, and postcranial *H. antecessor* fossils.

**Key words** Atapuerca; cusp base areas; dental anthropology; dental morphometrics; TD6.

## Introduction

Several recent works have assessed the morphological differences in upper first molar morphology among different hominin species (Bailey, 2004; Gómez-Robles et al. 2007; Quam et al. 2009). Among these, Bailey (2004) found a Neanderthal-specific morphology based on the relative proportion of cusp areas and the relative size of the occlusal polygon. Gómez-Robles et al. (2007) identified similar morphologies in European Lower and Middle Pleistocene specimens by using geometric morphometric methods, and Quam et al. (2009) proposed a derived pattern of relative cusp proportions shared by most species of the genus *Homo*. Following Quam et al. (2009) *H. antecessor* maintains a primitive molar morphology, shared with the earliest members of the genus, consisting of a relative metacone area larger than the relative paracone area. However, in later *Homo* species (including *Homo ergaster*, *Homo erectus*, *Homo heidelbergensis*, *Homo neanderthalensis* and *Homo sapiens*) 'the relative area relationships have shifted so that the relative area of the paracone is now larger than

that of the metacone'. These results contrast with those of Gómez-Robles et al. (2007), who described *H. antecessor* morphology as derived and similar to that of Neanderthals and European *H. heidelbergensis*. However, Quam et al. (2009) did not directly measure the relative areas they used to infer the primitive/derived condition of the upper first molars of *H. antecessor*, but rather, relied on the mean values published in Bermúdez de Castro et al. (1999). In light of the contradiction between the results of Quam et al. (2009) and Gómez-Robles et al. (2007), a detailed quantification of the absolute and relative cusp areas of all the upper first molars that are part of the current hypodigm of the species *H. antecessor* is provided.

## Materials and methods

Five upper first molars of the species *H. antecessor* were measured by one of us (A.G.-R.). This sample includes both antimeres of the maxilla ATD6-69 (individual H3 in Bermúdez de Castro et al. 1999), both antimeres of the individual H1 (ATD6-10 and ATD6-11), and a right upper first molar (ATD6-103) not published in detail so far (but included in Gómez-Robles et al. 2007) and currently attributed to individual H5 (Bermúdez de Castro et al. 2010a; see also Bermúdez de Castro et al. 1999, 2006).

Relative and absolute cusp base areas of the molars were measured using standardized images of the occlusal surface of the original molars. As in similar works based on image analysis of the occlusal surface of teeth, photographs were taken with a Nikon D1H digital camera fitted with an AF Micro-Nikkor

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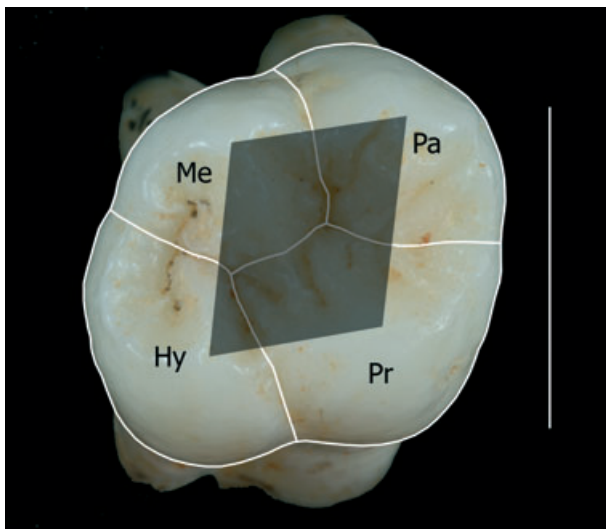
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105 mm, f/2.8D. The camera was attached to a Kaiser Copy Stand kit RS-1 with grid baseboard, column, and adjustable camera arm. For maximum depth of field, an aperture of f/32 was used. The magnification ratio was adjusted to 1 : 1, and a scale was placed parallel to and at the same distance from the lens as the occlusal plane.

IMAGEJ software was used to measure the areas from the occlusal photographs using the general methodology described elsewhere (Wood & Engleman, 1988; Bailey, 2004; Quam et al. 2009). Individual cusp base areas were measured by following the main fissures of the occlusal surface. The part of the main fissures eroded by wear were estimated by extrapolating the course of the preserved part of the fissures, but no correction was applied to interproximal wear (the TD6 molars are only minimally worn on their mesial and distal faces). However, some TD6 molars do present a *crista obliqua* connecting the metacone with the protocone that makes it difficult to separate these two cusps. In molars with this crest, the protocone and the metacone have been differentiated by continuing the course of the central groove between these two cusps (see Figs 1 and 2). The M<sup>1</sup>s of individual H3 (maxilla ATD6-69) present a c5 or metaconule (Fig. 2). Following Bailey (2004) and Quam et al. (2009), the area of this accessory cusp was measured and divided between the adjacent cusps (metacone and hypocone). The relative occlusal polygon area (area defined by the lines connecting the cusp tips divided by the total crown base area; Bailey, 2004) and cusp angles were measured in the only molar that preserves the four cusp apices due to its minimal degree of wear (ATD6-103). In general terms, the levels of interobserver measurement error in cusp base areas have been described as similar to the levels of intraobserver error and, in any case, lower than 4.5%, thus making the measurements taken by different authors comparable when they are adjusted to the same standards (Bailey et al. 2004).



**Fig. 1** Right upper first molar ATD6-103 showing the separation of the different cusp base areas (Pr: protocone; Pa: paracone; Me: metacone; Hy: hypocone), the occlusal polygon (shaded polygon) and the angles located at each cusp (angles of the occlusal polygon). Scale bar: 1 cm. Buccal: top part of the image; lingual: bottom; mesial: right; distal: left.

## Results

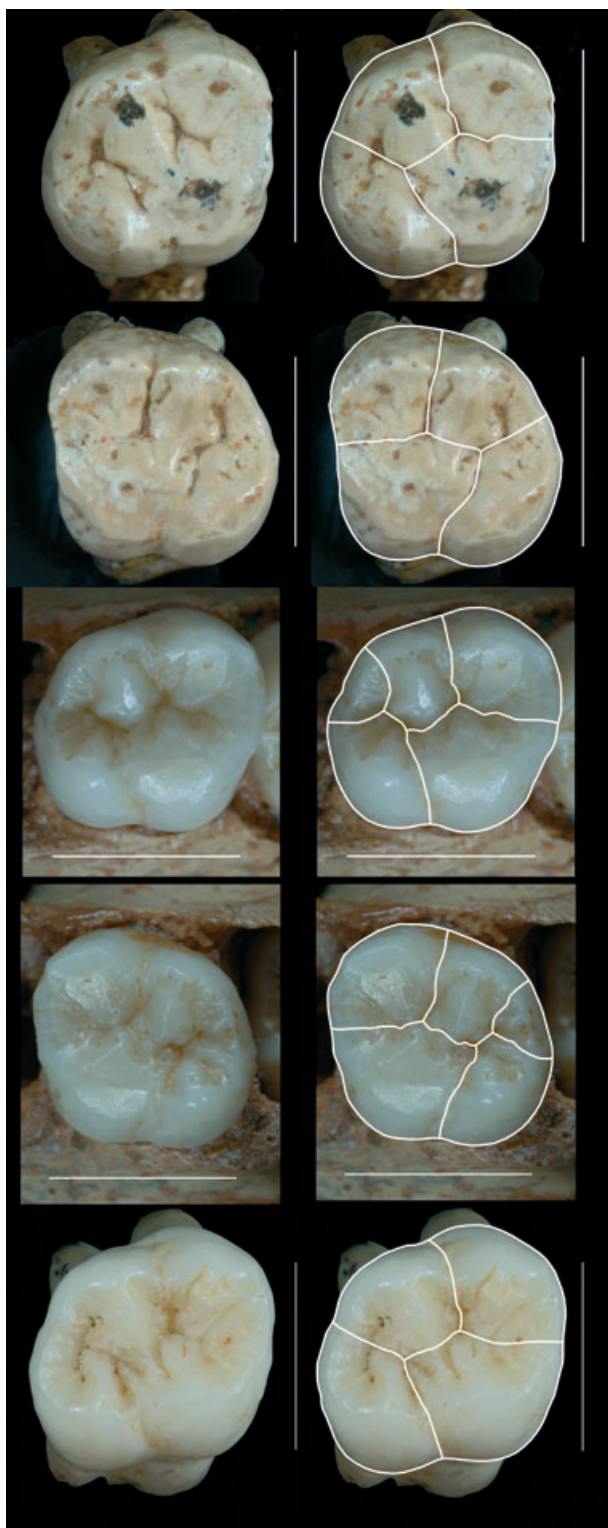
Absolute and relative cusp base areas of the five *H. antecessor* molars are provided in Table 1. Individual H5 (ATD6-103) has the largest total crown base area (TCBA), and individual H3 (ATD6-69) the smallest. The protocone is the largest cusp in the five measured molars, with an approximate size of 30% of the TCBA, but the size sequence of the other three cusps is not constant: the pattern of relative cusp size is protocone > hypocone > paracone > metacone in individuals H1 and H5, but protocone > paracone > hypocone > metacone in individual H3. In the five analysed molars, however, the metacone is the smallest cusp, with an approximate value of 21% of the TCBA, clearly smaller than the paracone.

Cusp angles and the relative occlusal polygon area (OPA) of ATD6-103 are shown in Table 2 (see also Fig. 1). Angles at the protocone and at the metacone have very similar values, approximately 106–107°, whereas angles at the paracone and metacone are also roughly coincident (≈ 70°). The relative occlusal polygon area accounts for 25.3% of the TCBA in ATD6-103.

## Discussion

The total crown base area of *H. antecessor* molars shows an intermediate value (TCBA = 123.8 mm<sup>2</sup>) between early *Homo* molars (TCBA = 134.9 mm<sup>2</sup>; Quam et al. 2009) and later *Homo* fossil molars (TCBA = 109.0 mm<sup>2</sup>; Quam et al. 2009). Nonetheless, the molars from TD6 show the cusp proportions described by Quam et al. (2009) as typical of later *Homo* taxa, consisting of a reduced metacone with respect to the paracone. These cusp proportions have been identified in later *Homo* species, including *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*.

Furthermore, not only are the TD6 M<sup>1</sup>s characterized by the derived pattern of relative cusp proportions for the genus *Homo*, they also share some characters with modern humans and, especially, with Neanderthals (see Gómez-Robles et al. 2007). Like those from other European species, *H. antecessor* upper first molars are markedly skewed (Gómez-Robles et al. 2007) and have a large hypocone and a reduced metacone, the latter accounting for 21.2% of the TCBA (relative metacone size: *H. ergaster*: 26.0%; *H. erectus*: 22.9%; *H. heidelbergensis*: 20.1%; *H. neanderthalensis*: 20.6%; *H. sapiens*: ≈ 22%; Quam et al. 2009). The pattern of relative cusp sizes typical of Neanderthals (protocone > paracone ≥ hypocone > metacone; Bailey, 2004) has been identified in one of the three *H. antecessor* individuals (H3) and in the mean value of the three individuals (protocone: 30.3% > paracone: 23.8% ≥ hypocone: 24.7% > metacone: 21.2%; note that paracone and hypocone relative sizes are considered to be equivalent because 'as a general rule, individual cusps that differ in their relative size by < 1% should be considered equal in



**Fig. 2** *Homo antecessor* upper first molars. Right half of the figure: photographs of the molars showing the cusp division used to obtain the measurements in Table 1. From top to bottom: ATD6-10: right antimeres of individual H1 (incorrectly referred to as ATD6-18 in Table 1 of Gómez-Robles et al. 2007); ATD6-11: left antimeres of individual H1; ATD6-69: right antimeres of individual H3; ATD6-69: left antimeres of individual H3; ATD6-103: right antimeres (the only preserved one) of individual H5. Scale bars: 1 cm. Buccal: top; lingual: bottom. Right antimeres: mesial – right, distal – left. Left antimeres: mesial – left, distal – right. The small cusp located between the metacone and the hypocone in the molars of ATD6-69 is the metaconule, or c5.

and bulging hypocones (larger than those from any hominin species, including *H. neanderthalensis* and *H. heidelbergensis*), together with their reduced metacone, are responsible for the skewed outline and, hence, for the location in the morphospace (in the area occupied only by Neanderthals and pre-Neanderthals) of *H. antecessor* molars described in Gómez-Robles et al. (2007).

However, cusp angles in ATD6-103 are similar to those measured in different *H. sapiens* samples (approximately 70° at the paracone and hypocone, and 105° at the protocone and metacone). The discordant patterns between relative cusp size and cusp angles in *H. antecessor* are not surprising because these two factors have moderate or low correlations and 'cusp size cannot be used to accurately predict cusp angle' (Bailey, 2004). Finally, a marked reduction of the relative occlusal polygon area has been identified in ATD6-103 (the only upper first molar of *H. antecessor* where the morphology of the occlusal polygon has not been eroded by wear, which has a relative OPA of 25.3% (relative OPA: *H. erectus*: 30.8–35.0%; Early anatomically modern humans: 29.6–36.6%; Neanderthals: 24.5–30.5%; Upper Paleolithic modern humans: 31.8–36.8%; Contemporary modern humans: 27.0–50.4%; Bailey, 2004).

These results demonstrate that the morphology of *H. antecessor* upper first molars from TD6 does not represent an exception to the rule observed in the majority of *Homo* species. Rather, these molars show the derived cusp proportions found in all later taxa within the genus *Homo*, as well as some features identified in classic Neanderthals and European *H. heidelbergensis*. The evolutionary significance of this morphology should be carefully evaluated by considering together all the traits that *H. antecessor* shares with *H. sapiens*, with *H. neanderthalensis* and with both species, taking into account that isolated characters are unlikely to provide a complete scenario of the evolution of these species. For this reason, forthcoming papers will undertake the task of re-evaluating *H. antecessor* dental and skeletal characters with the goal of shedding light on the question of its phylogenetic position, which is still debated because of its complex mixture of primitive and derived characters (e.g. Bermúdez de Castro et al. 1997, 2003; Carbonell et al. 2005). New findings of Lower Pleistocene fossils coming from the different sites located at the Sierra de Atapuerca (Bermúdez de Castro et al. 2008,

size'; Quam et al. 2009). The two remaining individuals (H1 and H5) are characterized by a very large hypocone, even larger than the paracone, which gives rise to a different pattern of cusp sizes (protocone > hypocone > paracone > metacone) that has not been identified in any species included in Quam et al. (2009). These large

**Table 1** Absolute and relative cusp base areas of the five *Homo antecessor* upper first molars.

	TCBA	Proto Abs	Para Abs	Meta Abs	Hypo Abs	Proto Rel (%)	Para Rel (%)	Meta Rel (%)	Hypo Rel (%)
ATD6-10 (R) H1	127.6	37.3	29.5	28.1	32.7	29.2	23.1	22.0	25.6
ATD6-11 (L) H1	125.8	38.2	29.3	26.7	31.6	30.4	23.3	21.2	25.1
ATD6-69 (R) H3	117.4	36.8	28.9	23.7	28.0	31.3	24.6	20.2	23.9
ATD6-69 (L) H3	112.6	34.1	27.6	24.1	26.8	30.3	24.5	21.4	23.8
ATD6-103 (R) H5	135.6	41.2	31.5	29.0	33.9	30.4	23.2	21.4	25.0
Total mean	123.8	37.5	29.4	26.3	30.6	30.3	23.8	21.2	24.7
Mean 1 antimer	124.7	37.8	29.5	26.6	30.8	30.4	23.7	21.3	24.6

TCBA, total crown base area; Proto, protocone; Para, paracone; Meta, metacone; Hypo, hypocone; Abs, absolute area; Rel, relative area; R, right; L, left; Total mean: mean of the five molars; Mean 1 antimer: mean based on left antimeres of individuals H1 and H3 and on the only preserved antimer (right) of individual H5. Absolute areas are measured in mm<sup>2</sup>. Relative areas are represented as the percentage of the TCBA.

**Table 2** Cusp angles and relative occlusal polygon area measured in the ATD6-103 M<sup>1</sup>.

	ATD6-103
Angle protocone	107.8°
Angle paracone	74.5°
Angle metacone	106.0°
Angle hypocone	71.3°
Occlusal polygon area (OPA)	34.3 mm <sup>2</sup>
Total crown base area (TCBA)	135.6 mm <sup>2</sup>
Relative occlusal polygon area	25.3%

Relative occlusal polygon area = (OPA/TCBA)\*100.

2010a,b; Carbonell et al. 2008) will help to clarify some unresolved questions about this species.

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