

Evolution of M¹ crown size and cusp proportions in the genus *Homo*

Rolf Quam,^{1,2} Shara Bailey^{3,4} and Bernard Wood⁵

¹Division of Anthropology, American Museum of Natural History, New York, NY, USA

²Centro UCM-ISCIH de Investigación sobre la Evolución y Comportamiento Humanos, Madrid, Spain

³Department of Anthropology, New York University, New York, NY, USA

⁴Max Planck Institute for Evolutionary Anthropology, Department of Human Evolution, Leipzig, Germany

⁵The George Washington University, CASHP, Department of Anthropology, Washington DC, USA

Abstract

Previous research into tooth crown dimensions and cusp proportions has proved to be a useful way to identify taxonomic differences in Pliocene and Pleistocene fossil hominins. The present study has identified changes in both M¹ crown size and cusp proportions within the genus *Homo*, with M¹ overall crown size reduction apparently occurring in two main stages. The first stage (a reduction of ca. 17%) is associated with the emergence of *Homo ergaster* and *Homo erectus sensu stricto*. The second stage (a reduction of ca. 10%) occurs in *Homo sapiens*, but the reduced modern human M¹ tooth crown size was only attained in Upper Paleolithic times. The absolute sizes of the individual cusps are highly positively correlated with overall crown size and dental reduction produces a reduction in the absolute size of each of the cusps. Most of the individual cusps scale isometrically with crown size, but the paracone shows a negative allometric relationship, indicating that the reduction in paracone size is less than in the other M¹ cusps. Thus, the phylogenetically oldest cusp in the upper molars also seems to be the most stable cusp (at least in the M¹). The most striking change in M¹ cusp proportions is a change in the relative size of the areas of the paracone and metacone. The combination of a small relative paracone and a large relative metacone generally characterizes specimens attributed to early *Homo*, and the presence of this character state in *Australopithecus* and *Paranthropus* suggests it may represent the primitive condition for the later part of the hominin clade. In contrast, nearly all later *Homo* taxa, with the exception of *Homo antecessor*, show the opposite condition (i.e. a relatively large paracone and a relatively small metacone). This change in the relationship between the relative sizes of the paracone and metacone is related to an isometric reduction of the absolute size of the metacone. This metacone reduction occurs in the context of relative stability in the paracone as crown size decreases. Among later *Homo* taxa, both *Homo heidelbergensis* and *Homo neanderthalensis* show a further reduction of the metacone and an enlargement of the hypocone. Fossil and contemporary *H. sapiens* samples show a trend toward increasing the relative size of the protocone and decreasing the relative size of the hypocone. In Europe, modern human M¹ cusp proportions are essentially reached during the Upper Paleolithic. Although some variation was documented among the fossil taxa, we suggest that the relative size of the M¹ paracone and metacone areas may be useful for differentiating the earliest members of our genus from subsequent *Homo* species.

Key words cusp proportions; hominin; *Homo*; molar.

Introduction

Studies of fossil hominin dental remains have led to the identification of species-specific patterns of dental morphology and have been useful for reconstructing the evolutionary relationships among fossil hominin taxa.

Correspondence

Rolf Quam, Division of Anthropology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024-5192, USA.
T: + 1 212 4963519; E: rquam@amnh.org

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Numerous studies have focused on tooth crown shape and on the details of occlusal and subocclusal morphology (Corruccini & McHenry, 1980; Wood & Abbott, 1983; Wood et al. 1983, 1988; Wood & Uytterschaut, 1987; Wood & Engleman, 1988; Brown, 1994; Bailey, 2004; Bailey & Lynch, 2005; Guatelli-Steinberg & Irish, 2005; Bailey & Wood, 2007; Gómez-Robles et al. 2007, 2008; Souday, 2008). Crown dimensions, as well as cusp base areas and their relative proportions have been shown to differentiate Plio-Pleistocene hominin taxa in both East and southern Africa (Wood & Uytterschaut, 1987; Wood & Engleman, 1988; Suwa et al. 1994, 1996; Boccone & Moggi-Cecchi,

2006; Moggi-Cecchi & Boccone, 2007). A number of studies have also considered the size of postcanine cusp areas in Pleistocene members of the genus *Homo* (Bermúdez de Castro & Nicolás, 1995; Bermúdez de Castro et al. 1999; Bailey, 2004; Bailey & Lynch, 2005; Trefný, 2005). The present study expands this line of research to a consideration of the M¹ cusp areas in the entire genus *Homo*.

Recent discussions of crown shape and internal cusp arrangement in both the M¹ and P₄ have led to discussion about, and sometimes conflicting interpretations regarding, the polarity of certain morphological features (Bailey, 2004; Bailey & Lynch, 2005; Martínón-Torres et al. 2006; Gómez-Robles et al. 2007). For example, Bailey & Lynch (2005) proposed that the asymmetry of the Neandertal P₄ was derived. This suggestion was based on the observation that the mean shape for contemporary modern humans was closer to that of *Homo erectus* than that of Neandertals. Unfortunately, their sample sizes precluded statistical analysis of this interpretation. In a subsequent study using larger sample sizes and a wider range of material (including *Australopithecus* and early *Homo*), Martínón-Torres et al. (2006) concluded that because asymmetry in the P₄ is observed in *Australopithecus*, as well as certain early *Homo* and *Homo erectus* individuals, it most likely represents the primitive condition within the hominin clade. Moreover, they suggested that the internal arrangement of cusp tips contributed importantly to the overall shape of the tooth.

Bailey (2004) suggested that the skewed M¹ shape found in Neandertals was likely derived for this group, but again lacked the samples of early hominins to formally test the hypothesis. Gómez-Robles et al. (2007) used a much larger sample that included *Australopithecus* and earlier *Homo*. Their assessment of polarity agreed with that of Bailey (2004), but they also found that, rather than it being exclusive to Neandertals, the same M¹ shape was also found in earlier members of the Neandertal lineage (in which they would include *Homo heidelbergensis*, represented by specimens from Sima de los Huesos, Steinheim and Pontnewydd) as well as *Homo antecessor*. Studies such as these have highlighted the need to consider the relationship between internal cusp arrangement and the shape of the crown outline and also the necessity of including larger samples of a range of earlier and later hominins.

We focused our analysis on the M¹ because, even within an individual, molars vary in both their morphological and metrical features (Bailey, 2002; Hlusko, 2002), such that combining molar types in a single analysis would not be warranted. The M¹ was chosen for this study because it is considered to be the least variable of the upper molars (Dahlberg, 1945). In modern humans, at least, it is well understood that M₃s are highly variable (Kraus et al. 1969) and the M₁ has been found to be less variable (and more diagnostic) than the M₂ in mid-late Pleistocene hominins (Bailey, 2002). Likewise, in baboons, heritability estimates

for maxillary loph angle phenotypes are higher for the M¹ than for the M² (Hlusko et al. 2004). As such, the anatomical differences in the M¹ should more closely reflect underlying genetic differentiation between populations, which is the soundest criterion for making evolutionary inferences in the fossil record (Lieberman, 1995). The recognition of consistent patterns of change in the dentition within the genus *Homo* could be useful for elucidating phylogenetic relationships among taxa and for clarifying the taxonomic identity of individual fossil hominin specimens, which are often fragmentary and/or consist only of isolated teeth.

Materials

The samples used in this study together with their sources are listed in Table 1. There is little consensus regarding the taxonomic allocations of specimens attributed to the earliest members of the genus *Homo* (Clarke & Howell, 1972; Rightmire, 1990; Tobias, 1991; Wood, 1991; Grine et al. 1993; Spoor et al. 2007). In addition, one of us (B.W.) has argued that the taxa *Homo habilis* and *Homo rudolfensis* should be removed from the genus *Homo* (Wood & Collard, 1999; Wood & Richmond, 2000; Collard & Wood, 2007). A recent study has also shown that some of the dental trends that characterize the genus *Homo* appear relatively late in human evolution (Bailey & Wood, 2007). Given the uncertainty surrounding which specimens should be included within the hypodigms of *H. habilis* and *H. rudolfensis*, we have taken a conservative approach and subsumed specimens from both East Africa and southern Africa into a pooled early *Homo* (non-*ergaster*) hypodigm.

There is also considerable disagreement regarding which specimens should be assigned to *H. erectus*. Some scholars prefer to group African and Asian specimens together into a single variable species (Rightmire, 1990, 1998; Antón, 2002, 2003; Antón et al. 2007; Spoor et al. 2007), whereas others have recognized a specific distinction between the two groups (Andrews, 1984; Wood, 1994; Wood & Collard, 1999; Tattersall, 2007). In the present study, we restrict the use of the term *H. erectus sensu stricto* to the Asian specimens from Sangiran and Zhoukoudian and prefer *H. ergaster* as the taxonomic name for the earliest of the African fossils assigned to *H. erectus*. We recognize the European middle Pleistocene specimens assigned to *H. heidelbergensis* as forming part of the Neandertal evolutionary lineage (Arsuaga et al. 1993, 1997; Hublin, 1998), and although there are differences of opinion (Vandermeersch, 1981; Tillier, 1999; Schwartz & Tattersall, 2000, 2003), we have opted to assign the entire Qafzeh sample to *Homo sapiens*.

Data for specimens attributed to early *Homo* are drawn primarily from studies where original specimens were measured (Wood & Engleman, 1988; Wood, 1991). After cross-checking the published data with measurements taken independently on high-resolution casts we found

Table 1 Sample composition used in the present study

Sample	Label	<i>n</i>	Specimens/Source
<i>Australopithecus africanus</i>	SAFGRA	7	Wood & Engleman (1988), Wood (1991)
<i>Australopithecus afarensis</i>	EAFGRA	3	Wood & Engleman (1988)
<i>Paranthropus robustus</i>	SAFROB	17	Wood & Engleman (1988), SK 14133, & SKX 3601
<i>Paranthropus boisei</i>	EAFROB	3	Wood & Engleman (1988), Wood (1991)
Early <i>Homo</i> – South Africa	SAFHOM	4	SE 255, SK 27, SKX 268 & SKW 3114
Early <i>Homo</i> – East Africa	EAFHOM	14	Wood & Engleman (1988), Wood (1991), A.L. 666-1, Omo P933-1 & Omo SH1-17
<i>Homo ergaster</i>	EAFHERG	1	Bailey (2004)
Asian <i>Homo erectus</i>	ASIAHER	5	Bailey (2004), Sangiran 4, S7-3, S7-9, & S7-37
<i>Homo antecessor</i>	HOMANT	2	Bermúdez de Castro et al. (1999)
<i>Homo heidelbergensis</i> (European Middle Pleistocene)	HOMHEID	4	Bailey (2004), Arago 31
<i>Homo neanderthalensis</i>	NEAN	21	Bailey (2004), Arsuaga et al. (2007), St. Cesaire, Obi-Rakhmat, Monsempron Petit-Puymoyen, Pinilla del Valle, Arcy sur Cure 39 & 45
Qafzeh	MPHSAP	7	Qafzeh 4, 5, 6, 9, 10, 11 & 15
European Upper Paleolithic <i>Homo sapiens</i>	UPHSAP	15	Bailey (2004), Arsuaga et al. (2007), Parpalló 5, Abri Pataud #26.224 & #26.236 Les Rois 19 & unnumbered, St. Germaine 2 & B7, Laugerie-Basse & Fontchevade
Contemporary <i>Homo sapiens</i> (Global sample)	HOMSAP	59	Bailey (2004)

only a single discrepancy (OH 21), and in this case our assessment of tooth orientation in the two photos led us to use the measurements taken on the cast. We also excluded the specimens KNM-ER 807 and KNM-ER 808 because of crown damage. We augmented our sample by including a number of specimens that were either not considered in earlier publications or discovered more recently (Table 1). From East Africa, these include A.L. 666-1, Omo P933-1 and Omo SH1-17, all of which have been attributed to *Homo* (Coppens, 1980; Howell et al. 1987; Kimbel et al. 1996). From southern Africa, we included SK 27, SKX 268 and SKW 3114 from Swartkrans and SE 255 from Sterkfontein, which have also been attributed to *Homo* (Clarke, 1977; Tobias, 1978; Grine, 1993, 2005; Grine & Strait, 1994). All of the latter data were collected on the original specimens.

Most of the data for later members of the genus *Homo* were taken from recent studies (Bermúdez de Castro et al. 1999; Bailey, 2002, 2004; Arsuaga et al. 2007). However, the present study also includes several *H. erectus* s. s. individuals ($n = 4$) from Sangiran whose cusp areas have, until now, been unpublished. In addition, the Qafzeh sample ($n = 7$), as well as those of *H. neanderthalensis* ($n = 21$) and Upper Paleolithic *H. sapiens* ($n = 15$) have been substantially augmented since an earlier study (Bailey, 2004). We have also included data from a geographically diverse sample ($n = 59$) of contemporary *H. sapiens* (Bailey, 2002). All the data was collected on original specimens.

To clarify the polarity of cusp areas and relationships within the genus *Homo*, data on early hominin specimens representing the genera *Australopithecus* and *Paranthropus* were also considered. Although there are important dental

differences between *Australopithecus* and *Paranthropus*, both show a similar trend toward trait intensification, including additional cusps on the maxillary molars (Bailey & Wood, 2007). Since our focus is on the genus *Homo*, we combined the *Australopithecus* and *Paranthropus* specimens within a single pooled early hominin sample to serve as an outgroup comparison for early *Homo*. We relied primarily on published data (Wood & Engleman, 1988; Wood, 1991) collected on original specimens. After cross-checking against measurements taken on high-resolution casts, only a single specimen (Sts 56) departed from the published measurements, and for this tooth we again used the cast measurements. We augmented the early hominin sample with data collected on the original specimens SK 14133 and SKX 3601, both of which have been attributed to *Paranthropus robustus* (Grine, 1989, 1993; Grine & Strait, 1994). We excluded some southern African specimens included in Wood & Engleman (1988): Sts 21 was judged to be too worn to reliably identify the intercusp fissures, and Sts 52a and Sts 57 show several large cracks in the enamel surface that affect the cusp base areas. We excluded TM 1512 because of damage to the crown outline and significant wear. Finally, we excluded LH 11 as in the original description of this tooth White (1977) classified it as an M².

Methods

The technique for measuring the M¹ cusp base areas has been outlined in previous studies (Wood & Engleman, 1988; Bailey, 2004). Briefly, an occlusal photograph of each tooth was taken with the cervical margin oriented perpendicular to the axis of the camera lens and a millimeter scale was included within each photo

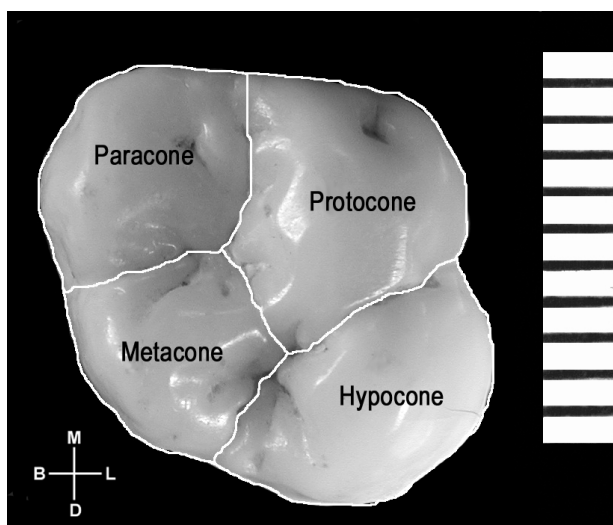


Fig. 1 Occlusal photograph of the Krapina D171 M¹ with the cusps outlined to illustrate the measurement methodology.

(Fig. 1). The scale included in each photograph was used to calibrate the image for measurement of the crown and cusp areas using either a planimeter (Wood & Engleman, 1988) or computer software (Bailey, 2004). This technique has been shown to produce reliable results between observers when applied to cusp base areas (Wood & Abbott, 1983; Bailey et al. 2004).

We measured individual cusp base areas by tracing the outline of the cusp, following the main fissures in the occlusal surface. We excluded teeth suffering from crown wear or damage that has obscured the fissure pattern or prevented an accurate assessment of crown area. Occasionally, wear obscured the course of the main fissures toward the edge of the tooth. In these cases, we estimated the course of the fissure by extrapolating a line from where the main fissure was eroded to the crown edge. The areas of accessory cusps were divided between the adjacent main cusps [e.g. the area of the metaconule (cusp 5) was divided between the metacone and the hypocone]. When both the right and left M¹ were present and equally well preserved in the same individual, the data for the left side were used. Otherwise, the tooth best preserved and least worn was used. The total crown base area (TCBA) was calculated as the sum of the absolute cusp base areas. The relative size of each cusp was determined by dividing the absolute cusp area by the TCBA.

In addition, we examined the size of each of the four main cusps relative to each other to investigate changes in cusp relationships (e.g. paracone larger or smaller than the metacone). As individual cusp sizes in some specimens may actually differ very little, characterizing one cusp as larger than the other may be overemphasizing what is in reality a minor difference. To avoid this mischaracterization, we have considered cusps that differ by less than the known interobserver measurement error (Bailey et al. 2004) to be equal in size. The difference in relative cusp sizes recorded by Bailey et al. (2004) ranged from 0.1% for both the paracone and hypocone to 1.1% for the metacone. This suggests that, as a general rule, individual cusps that differ in their relative sizes by less than or equal to 1.0% ($\leq 1.0\%$) should be considered equal in size. Thus, for example, the relative sizes of the paracone (23.7%) and metacone (24.1%) in SK 1591 (*P. robustus*) were deemed to be equal in size, as the difference between them is less than 1.0%. Throughout our

analysis, we have relied on this criterion when discussing the size of one cusp relative to another.¹ In the rest of the text we use 'area' as a proxy for the 2D areas of either the whole crown or of individual cusps.

We used basic descriptive statistics of crown and cusp base areas to investigate absolute and relative cusp size differences among hominin groups. The small sample sizes for some hominin taxa result in a higher probability that some groups depart from a normal distribution. Thus, the non-parametric Mann–Whitney test was used to determine statistical significance in the differences between groups.

The presence or absence of allometric trends in the absolute cusp areas in each *Homo* group (Table 1) was assessed following the techniques described in Hills et al. (1983). No correlation between TCBA and absolute cusp areas indicates isometry, significant positive correlation indicates positive allometry, and significant negative correlation indicates negative allometry. If changes in absolute cusp area are isometric, then relative cusp areas should remain relatively stable (apart from random variation), suggesting they are largely independent of TCBA. A value for the allometric coefficient can then be calculated from the slope and its standard error for the least squares regression line between log absolute cusp area and log TCBA (Hills et al. 1983). For the analysis of allometric trends across the genus *Homo* (i.e. between groups or taxa), mean values were used for each group due to differences in sample size.

Results

Total crown base area and absolute cusp size in the genus *Homo*

Within the pooled early *Homo* sample, the mean values for the TCBA and the absolute areas of individual cusps are larger in the southern African specimens than in their East African counterparts (Table 2). However, this difference is only significant ($P < 0.05$) for the paracone. In contrast, none of the relative cusp areas differs significantly between the southern African and East African specimens.

Although there is some overlap among specimens, the TCBA of the pooled early *Homo* sample is significantly larger ($P < 0.05$) than that of later members of the genus (Table 3). The only exception is the small *H. heidelbergensis* sample, which contains both large (Petalona = 134.5 mm²) and small (Pontnewydd 4 = 101.9 mm²) individuals. Within later archaic *Homo* (i.e. non-*Homo sapiens*) groups, the TCBA's do not differ significantly from one another, but they are significantly larger than that of most *Homo sapiens* groups (Tables 2 and 3). A notable exception is the single *H. ergaster* specimen (KNM-WT 15 000), which at 99.6 mm² falls below the lower limit of the *H. erectus s. s.* range of variation (105.2–124.1 mm²) and is similar in size to Upper Paleolithic and contemporary *H. sapiens*. In contrast to

¹Note: The single exception, LH 21, is an incomplete tooth for which crown area cannot be determined. However, the difference in absolute size between the paracone and metacone (2.7 mm²) is larger than that seen in any of the specimens deemed to have equal-sized cusps based on the above criteria. Thus, we have scored this specimen as showing a relatively large metacone area and a relatively small paracone area.

Table 2 Total crown base area (TCBA) and absolute and relative M¹ cusp areas in fossil and living hominins

Sample (n)	Total Crown Base Area (mm ²)* Mean ± SD	Protocone Area (mm ²) Mean ± SD	Paracone Area (mm ²) Mean ± SD	Metacone Area (mm ²) Mean ± SD	Hypocone Area (mm ²) Mean ± SD	Relative			
						Protocone Area (%) Mean ± SD	Paracone Area (%) Mean ± SD	Metacone Area (%) Mean ± SD	Hypocone Area (%) Mean ± SD
SAFGRA (7)	150.6 ± 17.4	45.9 ± 6.4	31.1 ± 2.6	36.6 ± 3.4	36.9 ± 8.3	30.5 ± 2.6	20.7 ± 1.2	24.5 ± 2.2	24.3 ± 2.6
EAFGRA (2)	150.9 ± 11.3	49.6 ± 4.8	34.1 ± 0.3	36.0 ± 4.3	31.3 ± 2.5	32.8 ± 0.7	22.6 ± 1.9	23.8 ± 1.0	20.7 ± 0.1
SAFROB (17)	156.7 ± 14.0	45.1 ± 4.3	34.7 ± 3.8	39.9 ± 4.9	37.1 ± 5.0	28.8 ± 1.8	22.1 ± 1.7	25.4 ± 1.8	23.6 ± 2.0
EAFROB (3)	188.7 ± 13.4	56.7 ± 4.4	41.1 ± 2.6	46.4 ± 2.9	44.1 ± 7.1	30.1 ± 0.7	21.8 ± 2.1	24.6 ± 0.4	23.3 ± 2.2
Pooled non- <i>Homo</i> (29)	158.1 ± 17.7	46.8 ± 5.9	34.3 ± 4.2	39.3 ± 5.1	37.4 ± 6.3	29.6 ± 2.2	21.8 ± 1.7	25.0 ± 1.8	23.6 ± 2.2
SAFHOM (4)	144.7 ± 8.1	43.1 ± 6.6	34.4 ± 1.5	35.4 ± 2.0	31.8 ± 1.2	29.7 ± 3.0	23.8 ± 0.7	24.5 ± 0.8	22.1 ± 2.0
EAFHOM (14)	132.1 ± 15.9	38.4 ± 4.6	30.2 ± 3.3	32.9 ± 5.1	30.5 ± 6.1	29.1 ± 1.9	23.0 ± 2.4	24.9 ± 2.2	23.0 ± 2.5
Pooled early <i>Homo</i> (18)	134.9 ± 15.3	39.5 ± 5.3	31.1 ± 3.5	33.5 ± 4.6	30.8 ± 5.4	29.3 ± 2.1	23.2 ± 2.2	24.8 ± 2.0	22.8 ± 2.4
EAFHERG (1)	99.6	29.4	27.3	25.9	17.1	29.5	27.4	26.0	17.2
ASIAHER (5)	115.5 ± 6.8	34.5 ± 3.0	28.7 ± 2.7	26.5 ± 3.2	25.8 ± 1.6	29.9 ± 2.2	24.9 ± 2.3	22.9 ± 1.7	22.3 ± 0.4
HOMANT (2)**	120.5	35.31	27.59	29.88	27.47	29.3	22.9	24.8	22.8
HOMHEID (4)	115.5 ± 17.0	34.8 ± 6.8	28.3 ± 4.8	24.2 ± 4.8	28.2 ± 3.0	31.1 ± 3.7	24.8 ± 0.9	20.1 ± 2.6	24.0 ± 1.6
NEAN (21)	112.3 ± 16.6	33.7 ± 6.1	28.8 ± 4.2	22.9 ± 3.9	26.8 ± 5.1	29.9 ± 2.4	25.8 ± 2.1	20.6 ± 1.8	23.7 ± 2.1
MPHSAP (7)	111.3 ± 12.7	34.7 ± 2.0	27.5 ± 2.4	23.7 ± 3.7	25.8 ± 7.8	31.3 ± 2.3	24.8 ± 1.6	21.3 ± 2.5	22.8 ± 5.0
UPHSAP (15)	99.6 ± 10.2	31.7 ± 3.6	25.2 ± 2.4	22.6 ± 3.3	20.3 ± 3.7	31.8 ± 1.5	25.7 ± 2.3	22.4 ± 1.7	20.1 ± 3.0
Pooled fossil later <i>Homo</i> (55)	109.0 ± 14.5	33.3 ± 4.7	27.5 ± 3.6	23.5 ± 3.8	24.8 ± 5.5	30.6 ± 2.2	25.5 ± 2.1	21.5 ± 2.0	22.5 ± 3.1
HOMSAP (59)	96.6 ± 14.0	29.9 ± 4.8	24.8 ± 3.7	22.1 ± 3.9	19.7 ± 3.8	31.0 ± 2.0	25.8 ± 2.1	22.9 ± 1.8	20.4 ± 2.5
Pooled later <i>Homo</i> (114)	102.2 ± 15.4	31.4 ± 5.0	26.0 ± 3.8	22.7 ± 3.9	22.0 ± 5.3	30.8 ± 2.1	25.6 ± 2.1	22.2 ± 2.0	21.4 ± 3.0

Sample labels follow Table 1.

*Total crown base area is equal to the sum of the individual cusp areas.

**Absolute cusp areas calculated from the relative areas and TCBA in Bermúdez de Castro et al. (1999).

Table 3 *P*-values for the comparison of the total crown base area (TCBA) in the genus *Homo* based on the Mann–Whitney–*U* non-parametric tests

Sample	Pooled early <i>Homo</i>	ASIAHER	HOMHEID	NEAN	HOMHEID + NEAN	Pooled archaic <i>Homo</i>	MPHSAP	UPHSAP
ASIAHER	**							
HOMHEID	N.S.	N.S.						
NEAN	**	N.S.	N.S.					
HOMHEID + NEAN	**	N.S.	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	**	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	**	**	N.S.	**	**	**	*	
HOMSAP	**	**	N.S.	**	**	**	**	N.S.
UPHSAP + HOMSAP	**	**	*	**	**	**	**	–
Pooled <i>Homo sapiens</i>	**	**	N.S.	**	**	**	–	–

*Significant at $P < 0.05$; **significant at $P < 0.01$. Sample labels follow Table 1. Pooled early *Homo* includes both southern and East African specimens.

Pooled archaic *Homo* includes all non-*Homo sapiens* specimens. Pooled *Homo sapiens* includes Qafzeh, Upper Paleolithic and contemporary samples.

Homo ergaster and *Homo antecessor* were not analyzed individually due to small sample size but were included in pooled archaic *Homo* sample.

these latter samples, the Qafzeh sample maintains the large TCBA of later archaic *Homo*.

The results for the absolute cusp base areas are similar to those for TCBA. The pooled early *Homo* sample shows larger mean values for each of the cusp base areas compared to later members of the genus (Table 2). Generally speaking, these differences are significant (Table 4), although they are less pronounced (only significant for a single cusp) compared to *H. erectus* and *H. heidelbergensis*. Notably, one variable – the absolute metacone size – is significantly larger in the pooled early *Homo* sample than it is in all later *Homo* taxa. Conversely, among the later *Homo* taxa this variable showed the fewest significant differences (Table 4). The European Upper Paleolithic and contemporary *H. sapiens* samples have the smallest absolute cusp areas (Table 2), and are significantly different from most of the other later *Homo* groupings, particularly with respect to the size of the hypocone.

Relative cusp size in the genus *Homo*

When the relative cusp areas of early *Homo* are compared with those of later members of the genus, the most obvious difference is that relative metacone size is significantly smaller in all the later taxa (Tables 2 and 5). Although a statistical comparison cannot be made with *H. ergaster* ($n = 1$), the single individual included in this taxon shows a large relative metacone area. Thus, the decrease in relative metacone area begins with the appearance of *H. erectus s. s.* We also note a significant increase in the relative paracone area in most *Homo* taxa that postdate *H. heidelbergensis* samples. In contrast, the relative protocone area in the early *Homo* sample is only significantly different from the

H. sapiens samples, whereas that of the hypocone differs only from Upper Paleolithic and contemporary *H. sapiens*. A notable departure from these general patterns is found in the small *H. antecessor* sample ($n = 2$), which possesses relative cusp areas that are quite similar to early *Homo* (Table 2).

There are no significant differences in relative protocone area between *H. erectus s. s.* and the *H. heidelbergensis/H. neanderthalensis* lineage (Table 5), but there is a small increase in the relative size of the protocone in the *H. sapiens* samples (Table 2). This difference is not significant when the *H. sapiens* sample is compared with *H. erectus s. s.*, but it does reach statistical significance when it is compared with both Neandertals and the pooled archaic *Homo* sample. The relative area of the paracone is considerably larger in the single *H. ergaster* specimen than in early *Homo*, and the remaining later *Homo* taxa also have a large relative paracone area (Tables 2 and 5). The only statistically significant difference in relative metacone area among later *Homo* is its small size in the *H. heidelbergensis/H. neanderthalensis* lineage. The relative area of the hypocone is largest in specimens that comprise the *H. heidelbergensis/H. neanderthalensis* lineage and smallest in Upper Paleolithic and contemporary *H. sapiens* samples.

Thus, within later *Homo*, *H. erectus s. s.* shows a reduction in the relative area of the metacone and an increase in the relative area of the paracone. With the exception of *H. antecessor*, the same pattern is seen in the other later *Homo* taxa, and a small metacone has been put forward as a possible derived feature of the *H. heidelbergensis/H. neanderthalensis* lineage (Bailey, 2004). Finally, a reduction in the relative area of the hypocone is not seen until the Upper Paleolithic and contemporary samples of *H. sapiens*.

Table 4 Significance of between-group comparisons of M¹ absolute cusp size in the genus *Homo* based on Mann–Whitney *U* non-parametric tests

Sample	Pooled early <i>Homo</i>	ASIAHER	HOMHEID	NEAN	HOMHEID + NEAN	Pooled archaic <i>Homo</i>	MPHSAP	UPHSAP
Protocone								
ASIAHER	N.S.							
HOMHEID	N.S.	N.S.						
NEAN	**	N.S.	N.S.					
HOMHEID + NEAN	**	N.S.	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	*	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	**	N.S.	N.S.	N.S.	N.S.	*	*	
HOMSAP	**	*	N.S.	**	**	**	**	N.S.
UPHSAP + HOMSAP	**	*	N.S.	N.S.	N.S.	**	N.S.	–
Pooled <i>Homo sapiens</i>	**	*	N.S.	*	*	**	–	–
Paracone								
ASIAHER	N.S.							
HOMHEID	N.S.	N.S.						
NEAN	*	N.S.	N.S.					
HOMHEID + NEAN	*	N.S.	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	*	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	**	*	N.S.	**	**	**	N.S.	
HOMSAP	**	*	N.S.	**	**	**	*	N.S.
UPHSAP + HOMSAP	**	*	N.S.	N.S.	N.S.	**	N.S.	–
Pooled <i>Homo sapiens</i>	**	*	N.S.	**	**	**	–	–
Metacone								
ASIAHER	*							
HOMHEID	*	N.S.						
NEAN	**	*	N.S.					
HOMHEID + NEAN	**	N.S.	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	**	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	**	*	N.S.	N.S.	N.S.	**	N.S.	
HOMSAP	**	*	N.S.	N.S.	N.S.	**	N.S.	N.S.
UPHSAP + HOMSAP	**	**	N.S.	*	N.S.	**	N.S.	–
Pooled <i>Homo sapiens</i>	**	*	N.S.	N.S.	N.S.	**	–	–
Hypocone								
ASIAHER	N.S.							
HOMHEID	N.S.	N.S.						
NEAN	*	N.S.	N.S.					
HOMHEID + NEAN	*	N.S.	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	**	**	*	**	**	**	N.S.	
HOMSAP	**	**	**	**	**	**	*	N.S.
UPHSAP + HOMSAP	**	**	**	**	**	**	N.S.	–
Pooled <i>Homo sapiens</i>	**	**	**	**	**	**	–	–

*Significant at $P < 0.05$; **significant at $P < 0.01$. Sample labels follow Table 1. Pooled early *Homo* includes both southern and East African specimens.

Pooled archaic *Homo* includes all non-*Homo sapiens* specimens. Pooled *Homo sapiens* includes Qafzeh, Upper Paleolithic and contemporary samples.

Homo ergaster and *Homo antecessor* were not analyzed individually due to small sample size but were included in pooled archaic *Homo* sample.

Table 5 Significance of between-group comparisons of M^1 relative cusp area in the genus *Homo* based on Mann–Whitney U non-parametric tests

	Pooled early <i>Homo</i>	ASIAHER	HOMHEID	NEAN	HOMHEID + NEAN	Pooled archaic <i>Homo</i>	MPHSAP	UPHSAP
Protocone								
ASIAHER	N.S.							
HOMHEID	N.S.	N.S.						
NEAN	N.S.	N.S.	N.S.					
HOMHEID + NEAN	N.S.	N.S.	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	*	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	**	N.S.	N.S.	**	*	**	N.S.	
HOMSAP	**	N.S.	N.S.	*	N.S.	**	N.S.	N.S.
UPHSAP + HOMSAP	**	N.S.	N.S.	*	N.S.	**	N.S.	–
Pooled <i>Homo sapiens</i>	**	N.S.	N.S.	*	N.S.	**	–	–
Paracone								
ASIAHER	N.S.							
HOMHEID	N.S.	N.S.						
NEAN	**	N.S.	N.S.					
HOMHEID + NEAN	**	N.S.	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	
HOMSAP	**	N.S.	N.S.	N.S.	N.S.	**	N.S.	N.S.
UPHSAP + HOMSAP	**	N.S.	N.S.	N.S.	N.S.	**	N.S.	–
Pooled <i>Homo sapiens</i>	**	N.S.	N.S.	N.S.	N.S.	*	–	–
Metacone								
ASIAHER	*							
HOMHEID	**	N.S.						
NEAN	**	**	N.S.					
HOMHEID + NEAN	**	**	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	**	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	**	N.S.	N.S.	**	**	N.S.	N.S.	
HOMSAP	**	N.S.	*	**	**	N.S.	N.S.	N.S.
UPHSAP + HOMSAP	**	N.S.	*	**	**	N.S.	N.S.	–
Pooled <i>Homo sapiens</i>	**	N.S.	*	**	**	N.S.	–	–
Hypocone								
ASIAHER	N.S.							
HOMHEID	N.S.	N.S.						
NEAN	N.S.	N.S.	N.S.					
HOMHEID + NEAN	N.S.	N.S.	–	–				
Pooled archaic <i>Homo</i>	–	–	–	–	–			
MPHSAP	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.		
UPHSAP	*	N.S.	*	**	**	**	N.S.	
HOMSAP	**	*	**	**	**	**	N.S.	N.S.
UPHSAP + HOMSAP	**	*	**	**	**	**	N.S.	–
Pooled <i>H. sapiens</i>	**	N.S.	*	**	**	**	–	–

*Significant at $P < 0.05$; **significant at $P < 0.01$. Sample labels follow Table 1. Pooled early *Homo* includes both southern and East African specimens.

Pooled archaic *Homo* includes all non-*Homo sapiens* specimens. Pooled *Homo sapiens* includes Qafzeh, Upper Paleolithic and contemporary samples.

Homo ergaster and *Homo antecessor* were not analyzed individually due to small sample size but were included in pooled archaic *Homo* sample.

Allometric trends in cusp size

In general, absolute cusp size is highly positively correlated with TCBA ($0.83 < r < 0.97$) across the genus *Homo*. So reductions in crown size are associated with reductions in the absolute size of each of the four main cusps. However, the changes in relative cusp size in the genus *Homo* discussed above indicate an allometric relationship between the absolute size of individual cusps and the TCBA. These allometric trends in M¹ cusp proportions were assessed within each *Homo* group.

The only significant correlation between relative cusp size and TCBA in any *Homo* taxon was a strong negative correlation ($r = -0.86$) with the protocone in the Qafzeh sample. Although the sample size is small ($n = 7$), this relationship remains significant even when a Bonferroni correction is applied. Changes in crown size appear to account for about 74% of the variation in the relative size of the protocone. Thus, smaller teeth in the Qafzeh sample are associated with relatively larger protocones. The allometric coefficient of protocone area in the Qafzeh sample (0.42 ± 0.14) was calculated from the slope and its standard error for the least squares regression line between log absolute cusp area and log TCBA. None of the remaining *Homo* taxa showed any statistically significant departures from isometry in any of the individual cusps. This was also the case in the pooled early *Homo* sample, which may include more than one taxon.

Relationships of the relative cusp areas across the genus *Homo* were similarly assessed using mean group values (Tables 2 and 6). The relative areas of the anterior cusps show negative correlations with TCBA, whereas the posterior cusps show positive correlations with crown size. However, the only significant correlation between relative cusp size and TCBA was a strong negative correlation ($r = -0.83$) with the paracone. The results for the hypocone ($r = 0.66$; $P = 0.051$) are suggestive of a positive allometric relationship, but the present sample does not allow rejection of isometry. The slope and its standard error can be calculated from the least squares regression line between log absolute paracone area and log TCBA to provide a value (0.57 ± 0.17) for the allometric coefficient of the

Table 6 Correlations (r) between tooth size and relative cusp proportions in the genus *Homo**

	Total crown base area (TCBA)
Relative protocone area	-0.54
Relative paracone area	-0.83
Relative metacone area	0.09
Relative hypocone area	0.66

*Relies on group means ($n = 9$) (Table 2).

Values in bold indicate significance at $P < 0.05$.

paracone across the genus *Homo* (Hills et al. 1983) (Table 7). Thus, as tooth size decreases, so does the absolute size of the paracone. However, the reduction in paracone size is less than in the other cusps in the M¹, resulting in an increase in the relative paracone size as tooth size decreases (Table 7).

Polarity of cusp area proportions in early *Homo*

Data for *Australopithecus* and *Paranthropus* provide some evolutionary context for interpreting differences in relative cusp areas between the early and later *Homo* samples. When the pooled non-*Homo* sample is compared with the pooled early *Homo* sample, only relative paracone size is significantly different, being larger in early *Homo* (Table 8). This suggests that, with the exception of a slight increase in the relative size of the paracone (Table 2), early *Homo* specimens preserve the likely primitive condition for the hominin clade. Later archaic *Homo* taxa further differ from the early hominins in showing a significantly smaller relative metacone area. Finally, when the pooled *Homo* and non-*Homo* samples are compared, the differences in relative cusp base area are significant ($P < 0.05$) for all four main cusps (Table 8). Compared with the non-*Homo* specimens, *Homo* has a relatively larger protocone and paracone and a relatively smaller metacone and hypocone. Of the four main cusps, temporally the paracone was the first to change its relative size, followed by the metacone, protocone and hypocone, in that order.

Table 7 Regression slopes and allometric scaling of log absolute cusp area (X) to log TCBA (M) in the genus *Homo**

Cusp	Regression Line			Correlation between		Allometry**
	Intercept	Slope	SE of Slope	X, M	X-M, M	
Protocone	-0.17	0.83	0.09	0.97	-0.63	Isometry
Paracone	0.28	0.57	0.17	0.89	-0.83	-
Metacone	-0.77	1.06	0.22	0.81	0.08	Isometry
Hypocone	-2.05	1.68	0.16	0.91	0.66	Isometry

**Homo* groups included in analysis ($n = 9$) are those listed in Table 1.

**The relationship was deemed to depart from isometry if the correlation between X-M and M was significant at $P < 0.05$.

Pooled non- <i>Homo</i> (n = 29) vs.	Pooled Early <i>Homo</i> (n = 18)	Pooled later Archaic <i>Homo</i> (n = 32)*	Pooled <i>Homo</i> (n = 131)
Relative protocone size	0.526	0.410	0.018
Relative paracone size	0.019	< 0.001	< 0.001
Relative metacone size	0.599	< 0.001	< 0.001
Relative hypocone size	0.294	0.823	< 0.001

Values in bold indicate significance at $P < 0.05$.
 *MPHSAP, UPHSAP and HOMSAP samples have been removed.

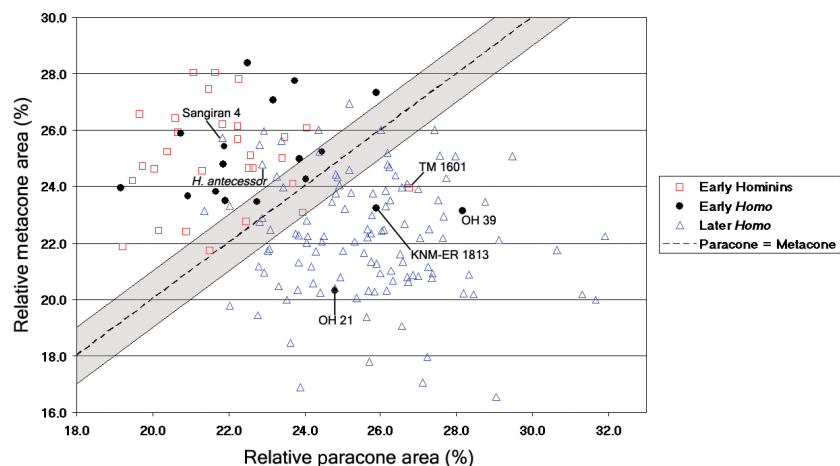


Table 8 P -values for the comparison of the relative cusp areas between the pooled non-*Homo* group and those of *Homo* based on Mann-Whitney U non-parametric tests

Fig. 2 Bivariate plot of the relative paracone area vs. the relative metacone area across the hominin sample. Specimens that fall within the shaded area between the solid lines are considered to show equal-sized cusps (see Methods). Specimens attributed to *Australopithecus*, *Paranthropus* and early *Homo* largely fall above the region of equal-sized cusps, indicating they combine a large relative metacone with a small relative paracone. In contrast, most later *Homo* taxa fall below this same region, indicating the opposite relationship. The positions of a few specimens which depart from this general pattern are indicated.

The paracone/metacone shift

The early hominin genera *Australopithecus* and *Paranthropus* show a relative paracone area which is smaller than that of the metacone (Table 2). Despite a slight increase in the relative paracone area, early *Homo* specimens also generally show this same relationship. Thus, this would appear to represent the primitive condition for the genus *Homo*. In later taxa, including the single *H. ergaster* individual KNM-WT 15 000 and *H. erectus s. s.*, the relative area relationships have shifted so that the relative area of the paracone is now larger than that of the metacone. We refer to this change in cusp proportions as the ‘paracone/metacone shift’. Figure 2 illustrates this shift by plotting these two variables against one another. Specimens attributed to *Australopithecus* and *Paranthropus* and the pooled early *Homo* sample generally fall above the region of equal-sized cusps, indicating a relative metacone area that is larger than that of the paracone. In contrast, the vast majority of specimens from later *Homo* taxa fall below the region of equal-sized cusps, indicating the opposite relationship. Thus, there appears to be a fairly clear division within the genus *Homo* when the relative areas of the paracone and metacone are compared with one another.

We scored each *Homo*, *Australopithecus* and *Paranthropus* specimen as having: (1) a larger relative paracone area, (2) a larger relative metacone area or (3) relative paracone and metacone areas that are approximately equal (see

Methods). Within the pooled early hominin sample (i.e. *Australopithecus* and *Paranthropus*) 83% of the specimens show the primitive condition of a relative metacone area that is larger than the relative paracone area (Table 9). Only a single individual (TM 1601) shows the derived condition of a relative paracone area that is larger than the metacone, while 13% of the specimens show equal-sized cusps.

Within the pooled early *Homo* sample, 67% of the specimens show the primitive condition. Derived cusp proportions are found in three East African individuals (KNM-ER 1813, OH 21 & OH 39) (Fig. 2), and equal-sized paracone and metacone are found in three of the southern African specimens (SE 255, SKX 268 & SKW 3114) (Table 9). In contrast, the pooled later *Homo* sample shows an overwhelming predominance (c. 82%) of the derived condition, while the primitive cusp proportions are still present in just less than 10% of the specimens and ~9% of the specimens have equal-sized cusps. Thus, the primitive cusp proportions can still occasionally be found in later *Homo* samples, including ca. 12% of modern humans. Among the later archaic *Homo* specimens, both *H. antecessor* and the *H. erectus s. s.* specimen Sangiran 4 retained the primitive condition (Fig. 2).

The effects of tooth size

To investigate whether the paracone/metacone shift is related to differences in overall crown area (TCBA) or the absolute size of any individual cusps, the relative sizes of

Table 9 Relationship between the relative areas of the M¹ paracone and metacone in fossil and living hominins

Sample (n)	Relative metacone larger than relative paracone % (n)	Relative metacone smaller than relative paracone % (n)	Cusps equal in size* % (n)
SAFGRA (7)	85.7 (6)	0.0 (0)	14.3 (1)
EAFGRA (3)	66.7 (2)**	0.0 (0)	33.3 (1)
SAFROB (17)	82.3 (14)	5.9 (1)	11.8 (2)
EAFROB (3)	100.0 (3)	0.0 (0)	0.0 (0)
Pooled non- <i>Homo</i> (30)	83.3 (25)	3.3 (1)	13.3 (4)
SAFHOM (4)	25.0 (1)	00.0 (0)	75.0 (3)
EAFHOM (14)	78.6 (11)	21.4 (3)	0.0 (0)
Pooled Early <i>Homo</i> (18)	66.7 (12)	16.7 (3)	16.7 (3)
EAFHERG (1)	0.0 (0)	100.0 (1)	0.0 (0)
ASIAHER (5)	20.0 (1)	80.0 (4)	0.0 (0)
HOMANT (2)	100.0 (2)	0.0 (0)	0.0 (0)
HOMHEID (4)	0.0 (0)	100.0 (4)	0.0 (0)
NEAN (21)	0.0 (0)	100.0 (21)	0.0 (0)
Pooled archaic Later <i>Homo</i> (33)	9.1 (3)	90.9 (30)	0.0 (0)
MPHSAP (7)	0.0 (0)	85.7 (6)	14.3 (1)
UPHSAP (15)	6.7 (1)	80.0 (12)	13.3 (2)
Pooled fossil later <i>Homo</i> (55)	7.3 (4)	87.3 (48)	5.4 (3)
HOMSAP (59)	11.9 (7)	76.3 (45)	11.9 (7)
Pooled later <i>Homo</i> (114)	9.6 (11)	81.6 (93)	8.8 (10)

Sample labels follow Table 1.

*Cusps were considered to be equal in size if their relative areas differed by ≤ 1.0 (see text for discussion).

**Includes specimen LH 21 based on absolute cusp areas (see text for discussion).

the paracone and metacone were expressed as a 'paracone/metacone index' (relative paracone area \times 100/relative metacone area). Lower values for this index indicate a relatively large metacone or a relatively small paracone and are generally associated with the primitive condition for the hominin M¹.

A strong significant negative correlation ($r = -0.85$) was found only with the absolute size of the metacone, indicating that changes in the absolute size of this cusp can explain about 72% of the variation in the paracone/metacone index. None of the other individual absolute cusp areas, or the TCBA, showed significant correlations with the paracone/metacone index. This would suggest that higher values for this index (associated with the derived condition) are not related to overall tooth size, but appear mainly due to a reduction in the absolute size of the metacone across the genus *Homo*.

Discussion

The preceding analyses have demonstrated significant variation in M¹ crown size and cusp proportions within the genus *Homo*.

Cusp proportions in early *Homo* – maintenance of a primitive pattern

In 83% of *Australopithecus* and *Paranthropus* specimens the relative area of the metacone exceeds that of the

paracone, whereas the opposite configuration only occurs in a single *P. robustus* individual (TM 1601). Johanson et al. (1982) also noted that three of four *Au. afarensis* individuals (75%) possessed a metacone larger than the paracone; the fourth individual had subequal cusps. Moggi-Cecchi & Boccone (2007) showed that metacone > paracone is the predominant M¹ pattern in their sample of southern African early hominins.

Despite a slight increase in the relative size of the paracone, this same size relationship (relative metacone > relative paracone) is found in two-thirds of the early *Homo* specimens in the present study. It is present in each of the three earliest (> 2.0 Ma) specimens attributed to the genus *Homo* (A.L. 666-1, Omo SH1-17 & Omo P933-1). Among younger (< 2.0 Ma) early *Homo* specimens, this primitive pattern is recognized in seven of nine Olduvai Gorge specimens, one from Koobi Fora (KNM-ER 1590), and one (SK 27) from Swartkrans. In contrast, in three early *Homo* individuals from East Africa (KNM-ER 1813, OH 21 and OH 39) the relative paracone area is larger than that of the metacone. The high prevalence of the relative metacone > relative paracone pattern in *Australopithecus* and *Paranthropus* suggests that teeth belonging to fossils assigned to early *Homo* preserve the likely primitive condition for the hominin clade.

The opposite pattern of the relative metacone area larger than that of the paracone (i.e. relative paracone > relative metacone) is seen in most later *Homo* taxa, and this shift is the most striking change in M¹ cusp proportions

within the genus *Homo*. These derived cusp proportions are found in 80% of Asian *H. erectus s. s.* specimens from Sangiran and Zhoukoudian as well as nearly all later members of the genus *Homo*. Teeth belonging to the *H. heidelbergensis/H. neanderthalensis* lineage show a 100% occurrence of this derived morphology, but the primitive condition is found in low frequencies in both Upper Paleolithic and contemporary *H. sapiens*.

Cusp proportions in *H. ergaster* – emergence of a derived pattern?

Compared to early *Homo* the M¹ of the single *H. ergaster* specimen, KNM-WT 15 000, has a relatively larger paracone area and a relatively smaller hypocone area, whereas there is less difference in the relative areas of the protocone and metacone. Nevertheless, this specimen already shows the derived relative paracone > relative metacone condition (Fig. 2; Table 9). Although the shift in the relative sizes of the paracone and metacone apparently marks a reasonably clear division within the genus *Homo*, the Konso Gardula M¹ (KGA11-350), dated to around 1.4 Mya and attributed to *H. erectus* (Suwa et al. 2007), has been described as having a metacone larger than the paracone (i.e. it possesses the primitive condition for *Homo*). Thus, it may be premature at this point to assume that *H. ergaster* shows a predominance of the derived condition of this trait. Alternatively, the presence of primitive cusp proportions in the isolated M¹ from Konso Gardula (KGA11-350) may indicate that the closest affinities for this specimen lie with early *Homo* rather than *H. ergaster*. Neither of these specimens (KNM-WT 15 000 or KGA11-350) shows the relatively reduced metacone that characterizes later *Homo* taxa.

Cusp proportions in *H. erectus s. s.*

In a description of the *H. erectus s. s.* teeth from Sangiran, Grine & Franzen (1994) reported the absolute cusp size order of the M¹'s. Four of the seven specimens were described as having the paracone larger than the metacone. Two additional specimens were said to show cusps that were approximately equal in size, while the size order in one specimen was not clear due to wear. Although measurements of the relative cusp areas in the Sangiran specimens were not presented by Grine & Franzen (1994), the absolute and relative cusp areas measured in these specimens for the present study generally agree with these observations. The one exception to this pattern is Sangiran 4 (see below), which was not considered by Grine & Franzen (1994). Thus, the derived cusp proportions (relative paracone > relative metacone) are present in four of five *H. erectus s. s.* specimens.

The relative sizes of the protocone and the paracone in *H. erectus s. s.* are similar to those observed in other later *Homo* groups (Table 8). In contrast, significant differences

were found mainly in the relative area of the metacone, which is significantly smaller than in early *Homo* and significantly larger than in *H. neanderthalensis*. The hypocone is significantly larger than in contemporary *H. sapiens*, but no significant differences were found from either the Qafzeh or Upper Paleolithic *H. sapiens* samples for any of the relative cusp areas (Table 8). Only Sangiran 4 (see above) departs from the rest of the sample in resembling early *Homo* specimens, which show a relatively small paracone and relatively large metacone.

Early *Homo* cusp proportions in *H. antecessor*

Our results agree with those of Bermúdez de Castro et al. (1999) who suggested that *H. antecessor* resembles early *Homo* specimens in all its cusp proportions. This suggests that the evolutionary origins for *H. antecessor* may be traced from a population(s) that had not undergone the paracone/metacone shift that characterizes later *Homo*.

Metacone reduction and hypocone enlargement in *H. heidelbergensis/H. neanderthalensis*

Bailey (2004) has previously reported that the combination of a small relative metacone and large relative hypocone may be a derived feature of *H. neanderthalensis*, and the expanded sample in the present study confirms this pattern. The same morphology is also seen in *H. heidelbergensis* and this would be an additional character state of the *H. heidelbergensis/H. neanderthalensis* lineage (Tables 2 and 8). In fact, these specimens show the smallest relative metacone area and largest relative hypocone area of any of the hominin samples.

Protocone increase and hypocone reduction in *H. sapiens*

The fossil and contemporary *H. sapiens* samples have a larger relative protocone and a smaller relative hypocone than the other taxa in later *Homo* (Table 2), but they are not significantly different from each other (Table 8). While following the pattern of other *H. sapiens* in relative protocone size, the Qafzeh sample maintains a larger relative hypocone compared to later *H. sapiens*. In general, there appears to be a shift in emphasis toward the mesial M¹ cusps with the emergence of our own species, a trend that was continued in Upper Paleolithic and contemporary populations.

Crown size, shape and cusp proportions

Early members of the genus *Homo* show a ca. 10–16% smaller M¹ overall crown area compared with *Australopithecus* and *Paranthropus*, respectively (Table 2). Subsequent M¹ crown reduction within the genus *Homo*

apparently occurred in two main stages. The first stage (a reduction of ca. 17%) is associated with the emergence of more derived forms of the genus, including *H. ergaster* and *H. erectus s. s.* Thereafter came a period of little or no change in M¹ crown area during most of the Pleistocene. The second stage (a reduction of ca. 10%) occurs after the appearance of our own species *H. sapiens*. This reduction is not seen in the Qafzeh sample, but in Europe it may plausibly be associated with the advent of Upper Paleolithic tool technology.

Crown reduction in early *Homo* is associated with a slight increase in the relative size of the paracone compared with *Australopithecus* and *Paranthropus*. Further crown reduction beginning with *H. ergaster* and *H. erectus s. s.* coincides with the appearance of the derived (relative paracone > relative metacone) condition for the paracone/metacone shift. In addition, crown reduction in Upper Paleolithic and contemporary *H. sapiens* is associated with a further reduction in the relative size of the hypocone and an increase in the relative size of the protocone. Thus, the major changes in the M¹ cusp proportions in the genus *Homo* are broadly associated with dental reduction.

Within individual *Homo* groups, cusp size generally scales isometrically with crown size (TCBA). The correlations between the relative sizes of the individual cusps and the TCBA in the contemporary *H. sapiens* sample in the present study ($0.01 < r < -0.23$) were lower than those reported previously for the M₁ in modern humans (Hills et al. 1983). An isometric relationship between crown size and cusp size was also generally found across the genus *Homo* based on group means, suggesting that as crown size reduces, the absolute sizes of the individual cusps also reduce. However, this reduction is less pronounced in the paracone. Thus, the phylogenetically oldest cusp in the upper molars also seems to be the most stable cusp in the M¹. Regarding the relative areas of the individual cusps, a strong negative correlation was found only between the relative area of the paracone and TCBA (Table 6). Thus as crown size reduces, the relative contribution of the paracone to overall crown area increases. The other cusps reduce their area at a more rapid rate because their relationship to overall crown area is isometric as opposed to the negative allometry of the paracone.

Changes in the paracone/metacone index are not related to changes in either overall crown size (TCBA) or the absolute size of the paracone. Rather, a strong relationship ($r = -0.85$) was found only with the absolute size of the metacone. This suggests that the emergence of the derived condition (relative paracone > relative metacone) in the genus *Homo* is primarily related to an isometric reduction of the metacone. This metacone reduction occurs in the context of the relative stability in absolute paracone area as overall crown area decreases. This is because the relative size relationships of the paracone differ from those of the other cusps (see above).

The results for cusp proportions in the present study agree with those based on the shape of the crown outline. The external crown shape of the hominin M¹ has recently been quantified using 3D geometric morphometrics (Gómez-Robles et al. 2007), and the results suggest that early *Homo* shares the presumably primitive crown shape with *Australopithecus* and *Paranthropus*, whereas the *H. heidelbergensis/H. neanderthalensis* M¹ crown outline is distinctive. The present study has documented a relatively large hypocone in the *H. heidelbergensis/H. neanderthalensis* lineage, and this may contribute to their distinctive crown outline (Gómez-Robles et al. 2007; Souday, 2008). In addition, the reduction in the relative size of the metacone in the M¹ in later *Homo* taxa seen in the present study is consistent with the suggestion that M¹ crown size reduction in later *Homo* species involved the protocone/metacone axis (Gómez-Robles et al. 2007).

Possible taxonomic implications of M¹ cusp proportions in the genus *Homo*

Despite considerable change in both the TCBA and absolute metacone area in the M² and M³ in the hominin clade, nearly all taxa show a paracone that predominates over the metacone in both these molars (Macho & Moggi-Cecchi, 1992; Grine & Franzen, 1994; Kimbel et al. 1996; Bermúdez de Castro et al. 1999; Bailey, 2002; Schwartz & Tattersall, 2003; Trefný, 2005; Moggi-Cecchi & Boccone, 2007; Suwa et al. 2007). This suggests that the pattern of variation in the relative sizes of these two cusps seen in the M¹ in the present study may have some taxonomic significance. Thus, although there is some variation within fossil *Homo* taxa, we suggest that the relative size of the M¹ paracone and metacone may be a useful taxonomic tool within the genus *Homo*.

Specifically, the results are consistent with the suggestion that the early *Homo* taxa *H. habilis* and *H. rudolfensis* lack some of the features shared by more derived members of the genus *Homo* (Wood & Collard, 1999; Wood & Richmond, 2000; Bailey & Wood, 2007). The M¹ cusp proportions in these early *Homo* specimens are more similar to those of early hominin taxa such as *Australopithecus* and *Paranthropus* than they are to *H. erectus s. s.* The derived M¹ proportions seen in three early *Homo* individuals from East Africa, KNM-ER 1813, OH 21 and OH 39, may be interpreted as a manifestation of the polymorphism we have seen in other groups of hominin taxa, or it could be evidence that the taxonomic allocation of these specimens warrants revision.

Relevant to the latter interpretation, other researchers (Hublin, 1983; Schwartz & Tattersall, 2003) have suggested that KNM-ER 1813 may belong to *H. erectus* or *H. ergaster*. In addition, one of the main reasons provided by Tobias (1991) for assigning OH 39 (which consists of isolated teeth) to *H. habilis*, the small mesiodistal length of the I²,

may not be a valid way of differentiating this taxon from later forms of *Homo*. Similarly, small I² dimensions are also found in some later *Homo* specimens from Olduvai (OH 29) (Tobias, 1991) and Sangiran (Grine & Franzen, 1994). Finally, the OH 21 isolated specimen represents a surface find from deposits which were subsequently shown to be disturbed, so its provenience remains uncertain (Tobias, 1991).

At the same time, *H. antecessor* appears to have retained the primitive condition (i.e. metacone > paracone) for the genus *Homo*. The same can be said of the Sangiran 4 specimen from Java, and the primitive character of the dentition in these specimens has been highlighted previously by other researchers (Weidenreich, 1945; Rightmire, 1990; Bermúdez de Castro et al. 1999). The presence of a primitive feature in both Sangiran 4 and *H. antecessor* cannot necessarily be taken to indicate a close evolutionary relationship between them. However, the M¹ cusp proportions in *H. antecessor* most likely represent a primitive retention in this taxon from their Plio-Pleistocene ancestors. The source area for this ancestral population can perhaps be found in Africa, but the lack of published information on the M¹ cusp proportions in the Dmanisi hominins leaves this question currently unresolved.

Conclusions

The M¹ crown areas of the earliest *Homo* specimens are smaller than those of the early hominin genera *Australopithecus* and *Paranthropus*, and this overall reduction is associated with a slight increase in the relative size of the paracone. Nevertheless, the same size relationship between the paracone and metacone (i.e. relative paracone > relative metacone) is found in the majority of early *Homo* specimens and the early hominin M¹s sampled in this study. We hypothesize that this metacone > paracone 2D relative cusp area relationship is the primitive condition for the later part of the hominin clade. Subsequent changes in cusp proportions within the genus *Homo* appear to be broadly associated with two main stages in M¹ crown size reduction.

All later *Homo* taxa, except for *H. antecessor*, show the derived condition of a relatively large paracone and relatively small metacone, and we have called this change in cusp proportions the paracone/metacone shift. Although there is some variation in this feature, all of the hominin groups in the present study showed a clear dominant condition, with some groups reaching 100% expression of one condition. Although the paracone/metacone shift is associated with the first stage in M¹ crown size reduction within the genus *Homo*, it can be more clearly related to an isometric reduction of the metacone. This metacone reduction occurs in the context of relative stability in the paracone area as the overall size of the crown decreases. The presence of the derived cusp proportions in KNM-ER

1813, OH 21 and OH 39 differentiates these individuals from other fossils assigned to early *Homo*. At the same time, both *H. antecessor* and the *H. erectus s. s.* specimen Sangiran 4 show the primitive cusp proportions, and this is consistent with previous suggestions of a primitive dental anatomy in these specimens.

The enlarged *H. neanderthalensis* sample in the present study has confirmed previous suggestions (Bailey, 2004) that this group of hominins is characterized by a derived pattern of cusp proportions, showing a reduced metacone and enlarged hypocone. This same pattern is also seen in the small *H. heidelbergensis* sample, suggesting that this feature appears early in the Neandertal evolutionary lineage.

The early modern human sample from Qafzeh shows a slight increase in the relative protocone area, but maintains a large hypocone like that of the earlier taxa. Crown size in the Qafzeh sample is unchanged from that seen in earlier *Homo* taxa. The second stage in M¹ crown size reduction only occurs during Upper Paleolithic times and is associated with a further reduction in the size of the hypocone. Modern human M¹ cusp proportions, then, emerged very late in the human lineage.

The reasons behind these changes in cusp proportions in the genus *Homo* appear to be some combination of dental reduction and allometry, and the pattern of cusp proportions in different hominin taxa appears to have some taxonomic significance. Additional studies in larger and taxonomically more diverse samples and the consideration of other tooth classes may reveal further distinctions in cusp proportions in the hominin clade and offer new insights into the evolutionary process.

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