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A comparative dental metrical and morphological analysis of a Middle Pleistocene hominin maxilla from Chaoxian (Chaohu), China

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ABSTRACT

A hominin maxilla, discovered in 1983 in Chaoxian County, Anhui Province, eastern China represents one of several Asian hominins dating to the late Middle Pleistocene. Although the maxilla and associated occipital have been described, no detailed study of the dentition has been made. This study provides metrical and morphological information on the Chaoxian dentition and places it into a larger Middle to Late Pleistocene context. Implications for the taxonomy of Middle Pleistocene hominins are discussed.

1. Introduction

There are a number of well-known Middle Pleistocene hominin fossils in China that have been assigned to either *Homo erectus* (e.g., Zhoukoudian), or archaic *Homo sapiens* (e.g., Dali). The fossil evidence has been reviewed broadly by Etler (1996) and in more detail by Wu and Poirier (1995). The craniodental remains from Chaoxian County, Anhui Province (Fig. 1) represent one of several hominins that date to the Late Middle Pleistocene (250–130 ka). This is an important time period during which Neandertals were evolving in Europe (Condemi, 2001; Huxtable and Aitken, 1988) and anatomically modern humans were evolving in Africa (McDougall et al., 2005; White et al., 2003).

As is the case with other archaic *H. sapiens*, the Dali and Jinniushan crania are more advanced (i.e., more *sapiens*-like) than *H. erectus* (Wu and Poirier, 1995). However, they lack many facial features observed in the African and European Middle Pleistocene hominins (Rightmire, 2001). Those from Europe are known to possess cranial and dental characters (at least in low frequencies) that link them to Neandertals (Bailey, 2002; Dean et al., 1998; Gómez-Robles et al., 2007; Hublin, 1996), although the extent to which these characters are unique to the European fossils is unclear (Rightmire, 2001). In this regard, it is of interest to investigate how the Chaoxian hominin compares to that of its contemporaries in Europe and Africa, especially in light of the current favoring of reassigning fossils once attributed to "archaic *H. sapiens*" to one (*Home heidelbergensis*) or more (*H. heidelbergensis* + *Homo rhodesiensis*) species (see Rightmire, 1998 for a review). Because there is still considerable debate about how many taxa are represented by these Middle Pleistocene fossils, throughout this paper we will refer to regional groups of archaic *H. sapiens* (e.g., African, European, and Asian) rather than separate taxa.

Unfortunately, only a few well-preserved crania span the entire Middle Pleistocene period, a problem that has made a worldwide comparative study difficult. Dental remains are particularly useful in this context since they preserve well in the fossil record and because they are useful in the taxonomic assessment of Middle to Late Pleistocene hominins (Bailey, 2002).

The Chaoxian maxilla preserves the right and left lateral incisors, the right P^3 and P^4 and the right M^1. Three isolated maxillary teeth discovered with the cranial remains – a P^4, M^1 and M^2, all from the left side – were assigned to the same individual (Xu and Zhang, 1986). We have no reason to doubt this association since the wear on P^4 and M^1 antimeres is consistent with them belonging to the same individual. The teeth have been placed in their inferred anatomical positions in a reconstruction by the second author and Zhang Yinyun (Fig. 2a).

The original description of the Chaoxian dentition focused primarily on the robusticity of the postcanine teeth (Xu and Zhang, 1986). A later paper described the specimen's marked anterior tooth wear (Zhang, 1989). However, a detailed description of the dentition, one placing the morphology and metrics in a comparative context, has not been undertaken. The following study provides greater details of the dental morphology and makes morphological and metrical comparisons with Middle to Late Pleistocene hominins.

2. Background

In 1983 a hominin maxilla was discovered in Chaoxian County in a locality 50 km southwest of the Hexian site. The maxilla, together

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Fig. 1. Map China indicating location of the Chaoxian site.

with an occipital discovered in 1982, is derived from a limestone fissure (or cave deposit) at Yinshan Hill near Yinshan Village, Diashan region, Chaoxian County, Anhui Province, eastern China (Wu and Poirier, 1995: 134). No artifacts were recovered from the site; however, faunal correlations placed both fossils a bit later than *H. erectus* from Hexian and equal to or later than layers 1–4 of *H. erectus* from Zhoukoudian (Xu et al., 1984). Chen et al. (1987) published uranium series dates obtained from faunal remains in the hominin bearing deposit (Layer 2) ranging from 160 to 200 ka, although they did not exclude the possibility that the age may be older. Subsequent uranium series dating from eight samples of stalagmite carbonate and three bone samples collected from the upper part of Layer 2 gave ages older than 310 ka (Shen et al., 1994).

A description of the occipital and maxilla can be found in Wu and Poirier (1995). Both have been described as generally attributable to “early” *H. sapiens*, lacking some of the derived features of Asian *H. erectus* and being more robust than anatomically modern *H. sapiens* (Xu and Zhang, 1986; Xu et al., 1984). The occipital is said to have a weak occipital torus, to lack both an external occipital protuberance and distinct supratoral sulcus. It is also said to possess a “depression similar to fossa supratoralis” (Xu et al., 1984: 209), which Wu and Poirier describe as a “small fovea corresponding to the suprainionic (sic) fossa above the middle of the torus” (page 134). And yet, the estimated large occipital angle and thin bone are said to resemble most closely that of “early” *H. sapiens* (Xu et al., 1984).

The maxilla is slightly convex in lateral view and lacks a canine fossa. The nasal aperture is wide (>21 mm at the base) and the nasal floor is depressed so that the anterior portion is higher than the posterior (SEB personal observation). This is a feature seen in high frequency in Neandertals but is present in Middle Pleistocene African specimens as well (Franciscus, 2003).

Aging the Chaoxian individual is not straightforward. Wear on the distal aspect of the M^2 suggests that the M^3 had been in functional occlusion at the time of death, indicating adult status (Zhang, 1989). Once adulthood has been reached, it is possible to refine an age estimate based on tooth wear, but only if the rate of wear for

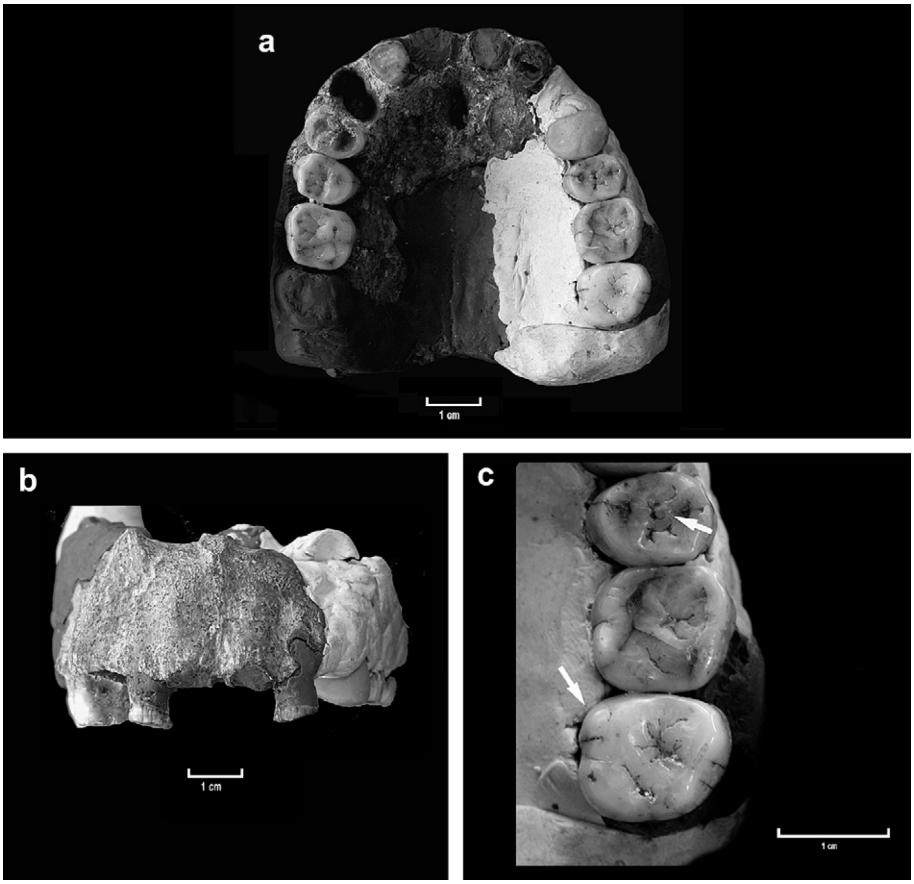

Fig. 2. The Chaoxian maxilla and dentition. (a) Inferior view (b) anterior view (c) close up view showing morphological details of the P^4 bifurcated essential crest (arrow) and the M^2 Carabelli’s cusp (arrow). Note also the relatively square shape of the M^1, the nearly equal-sized hypocone and metacone of M^1 and the large M^2 hypocone.

a population is known (e.g., Brothwell or Miles methods: Hillson, 1996). Unfortunately, estimating the rate of tooth wear in fossil populations is a difficult task. Bermúdez de Castro et al. (2003) attempted to do so based on anterior tooth wear in hominins from Sima de los Huesos. However, the degree to which the rates they derived are applicable to other fossil populations is unknown. The occlusal surface of the M^2 of Chaoxian is smoothed by wear and shows only a pin point of dentine exposure on three of the four cusps. The M^3 was, no doubt, even less worn. Therefore, the molars of this individual suggest a young adult age. However, an older assessment might be inferred from the marked wear on the anterior teeth (incisors and P3). According to the estimates worked out by Bermúdez de Castro et al. (2003), the individual would more likely be in their 4th decade. Because we do not know if the Middle Pleistocene hominins in Asia wore their teeth at the same rate as those in Europe, perhaps the best we can do is estimate that the Chaoxian individual was a young to middle-aged adult.

3. Materials and methods

Keeping in mind that accurately dating Middle Pleistocene sites in China is notoriously difficult, the Chaoxian hominin is likely to be between 160,000 and 200,000 years old (Chen et al., 1987). However, it may be as old as 300,000 years or even older (Shen et al., 1994). Based on these estimates, the maxilla and dentition can be compared to a number of similarly aged specimens from China including: Jinniushan (230–280 ka), Changyang (170–220 ka), Xujiayao (100–125 ka), Zhoukoudian: New Cave or Locality 4 (135–175 ka), Dingcun (160–210 ka), and Tongzi (102–191 ka) (Etler, 1996). Similarly aged well-preserved specimens from Europe and Africa are sparse, particularly those that preserve the same teeth as Chaoxian. Because of the dearth of available later Middle Pleistocene material, we expanded "the comparative samples" to include all of the Middle Pleistocene, as well as *H. erectus* specimens from the Early Pleistocene. Table 1 provides a list of these samples and the sources for the morphological and metrical information. Morphological and metrical observations of most non-Asian Middle Pleistocene hominins were made by SEB. Casts from Zhoukoudian, and teeth from Sangiran, Changyang and Yunxian were also examined first hand by SEB. The remaining data were gleaned from photographs, descriptions and dental measurements available in Wu and Poirier (1995), Bermúdez de Castro (1993), Weidenreich (1937), Grine and Franzen (1994), and Wolpoff (1979).

Morphology was assessed using the standards outlined by the Arizona State University Dental Anthropology System (Turner et al., 1991), as well as additional traits determined by Bailey (2002, 2004) to be useful in assessing fossil hominin relationships. All tooth measurements made by SEB were made using Mitatuyo digital calipers.

4. Results

4.1. Metrics

Basic measurements and indices for the Chaoxian teeth are presented in Table 2. Table 3 presents the Chaoxian length and breadth data in a comparative context. Where data were collected from the literature and the authors provided both corrected and uncorrected measurements (e.g., Bermúdez de Castro, 1993), only uncorrected measurements of unworn to moderately worn teeth were used. In some cases (e.g., the Krapina teeth) it is unclear whether or not the measurements provided were corrected for wear (Wolpoff, 1979). However, after examining photographs of the teeth (Bailey, unpublished data) and/or reviewing the reported wear status of the teeth (e.g., Radovcic et al., 1988), severely worn teeth were excluded from the analysis. It is the mesiodistal lengths (rather than buccolingual breadths) that are most affected by (interproximal) wear, and this should be kept in mind when evaluating the positions of specimens in Fig. 4.

The mesiodistal lengths of the I^2 crowns represent minimums due to excessive wear. However, the buccolingual breadths are fairly accurate, since this measurement usually reaches its maximum near the base of the crown (personal observation). The minimum lengths (which are certainly underestimates) place the Chaoxian I^2s closest to the archaic *H. sapiens* and *H. erectus* means, but they were likely at the higher end of these ranges during life. The I^2 breadths are within the range of all the Middle Pleistocene samples but closest to the *H. erectus* mean. The rest of the dentition is large relative to the means of other Pleistocene hominins. The breadth of the P^3 is the same as the Chinese *H. erectus* mean, while the length is equal to the early *Homo neanderthalensis* mean. The size of the P^4 is larger than the means of all other samples and the breadth is at the high end of the range for Chinese *H. erectus*. Likewise, the M^1 and M^2 breadths are larger than the comparative sample means (although within most of their ranges).

Fig. 3(a–e) plots crown length against breadth for each tooth. When plotted, the Chaoxian I^2s fall between other Middle Pleistocene hominins and early *H. neanderthalensis*, being closer to the former than the latter (Fig 3a). As noted, due to wear the mesiodistal lengths of the I^2s is certainly underestimates. If unworn their placement in this figure would be somewhat higher on the *y*-axis; however, their position relative to other fossil hominins would not change much. The P^3 is not particularly close to its Asian contemporaries, but is closer to *H. erectus* from Zhoukoudian and European archaic *H. sapiens* (Fig 3b). The size of the P^4 is remarkable: in length and breadth it is most closely aligned with *H. erectus* specimens from Sangiran and Zhoukoudian (Fig 3c). The length and breadth measurements of the upper molars vary considerably in the comparative sample with no clear clustering based on time or geography. The Chaoxian M^1 falls among *H. erectus* individuals but both larger and smaller M^1s can be found in the archaic *H. sapiens* and early *H. neanderthalensis* samples (Fig 3d). The length and breadth measurements of the M^2 also vary considerably in the comparative sample. The Chaoxian M^2 is closest to one *H. erectus* molar from Zhoukoudian, to the Petralona M^2 and one M^2 from Krapina (Fig 3e).

The relative sizes of teeth in the same tooth field may also be of interest. In Chaoxian, the breadth of the P^4 is larger than that of the P^3. This relationship is also observed in other Middle Pleistocene hominins, including some early *H. neanderthalensis*, whereas a majority of Late Pleistocene hominins (including *H. neanderthalensis* and *H. sapiens*) tend to possess P^4 breadths that are smaller on average than that of the P^3s (Fig 4). A similar observation can be made of the first and second molars. In Chaoxian, the breadth of the M^2 is larger than that of the M^1. This pattern is typical of *H. erectus*, *H. neanderthalensis* and archaic *H. sapiens*. It is not until the evolution of anatomically modern *H. sapiens* (with few exceptions) that this pattern is typically reversed (Fig. 5).

The absolute and relative cusp areas for the Chaoxian molars and those for the comparative samples are presented in Table 4. The M^1 has proven to be the most diagnostic of the molars in this regard (Bailey, 2002). As in all samples, the M^1 protocone is the largest of the cusps, although the relative size of the Chaoxian protocone is somewhat smaller than that of other samples. In addition, the relative size of the metacone is somewhat larger than most of the comparison samples. However, like most of the comparison samples (*H. antecessor* excluded), the metacone is relatively smaller than the paracone. The metacone is relatively larger than the hypocone, which contrasts with the condition observed in European archaic *H. sapiens* and *H. neanderthalensis*.

Table 1
Comparative samples used in this study.

Samples	Approximate ages	Source of metric/morphological data
Indonesian *Homo erectus*		
Sangiran (kabuh)	.8–1.5 Ma[b]	Grine and Franzen (1994), Bailey (unpublished data)
Sangiran (Pucangan)	1.6–1.8 Ma[c]	Grine and Franzen (1994), Bailey (unpublished data)
Chinese *Homo erectus*[a]		
Zhoukoudian (Loc 1)	800–400 ka[d]	Bailey (2002), Bailey (unpublished data), Weidenreich (1937)
Hexian	190–150 ka[e]	Wu and Poirier (1995)
Yiyuan	Middle Pleistocene[f]	Wu and Poirier (1995)
Luonan	? None reported	Wu and Poirier (1995)
Xichuan	? No context	Wu and Poirier (1995)
Yunxian (Meipu)	? None reported	Wu and Poirier (1995)
African *Homo erectus*		
KNM-ER 15000	1.6 Ma[g]	Brown et al. (1985), Bailey (unpublished data)
Homo antecessor	>780 ka[h]	Bermúdez de Castro et al. (1997)
Archaic *Homo sapiens*		
Asia		
Jinniushan	>220 ka[i]	Jianing (2000)
Changyang	194–196 ka[j]	Wu and Poirier (1995)
Xujiayao	104–125 ka[k]	Wu and Poirier (1995)
Tongzi	113–181 ka[j]	
Zhoukoudian Loc 4	120–300 ka[l]	Wu and Poirier (1995)
Europe		
Arago	455–350 ka[m,n,o]	Bailey (2002), Bailey (unpublished data), Quam et al. (in press)
Petralona	240–160 ka[p]	Bailey (2002), Bailey (unpublished data)
Sima de los Huesos	530–600 ka[q]	Bermúdez de Castro (1993)
Africa		
Sidi Abderrahman	~400 ka[r]	Bailey (unpublished data)
Teghenif	~400 ka[r]	Bailey (unpublished data)
Rabat	<450 ka[r]	Bailey (unpublished data)
Early *Homo neanderthalensis*		
Krapina	~130 ka[s]	Bailey (2002), Wolpoff (1979)
Pontnewydd	200 ka[t]	Bailey (2002), Bailey (unpublished data)

[a] Note: taxonomic designations of Asian hominins are from Wu and Poirier (1995) and based on assessments of the original publications. Some of these assessments were based solely on tooth size (e.g., Yunxian).
[b] Ages per: Day (1986).
[c] Ages per: Swisher et al. (1994).
[d] Ages per: Shen et al. (2001).
[e] Ages per: Chen et al. (1987).
[f] Ages per: Lu et al. (1989).
[g] Ages per: Brown and Feibel (1985).
[h] Ages per: Parés and Pérez-Gonzáles (1999).
[i] Ages per: Chen and Yuan (1988).
[j] Ages per: Yuan et al. (1986).
[k] Ages per: Chen et al. (1984).
[l] Ages per: Shen et al. (2004).
[m] Ages per: Falgueres et al. (2004).
[n] Ages per: Yokoyama and Nguyen (1981).
[o] Ages per: Yokoyama et al. (1985).
[p] Ages per: Hennig et al. (1981).
[q] Ages per: Bischoff et al. (2007).
[r] Ages per: Hublin (1985).
[s] Ages per: Rink et al. (1995).
[t] Ages per: Green et al. (1981).

4.2. Morphology

4.2.1. Right and left lateral incisors

Both crowns are severely worn and the functional surface is within 3.5 mm of the cervical line. Only about 0.5 mm thickness of enamel rings each tooth. The remaining enamel of the right I^2 is ivory-colored with some darker staining on the labial aspect. The left I^2 is more strongly stained and grayish in color. Dentin, secondary dentin, and very small patch of the pulp chamber are exposed on both teeth. The tooth wear is oriented labio-lingually (more labial than lingual) and disto-mesially (more distal than mesial) and is slightly greater on the left incisor than it is on the right (Fig. 1b). Both mesial and distal aspects of the crown are flattened from interproximal wear. Enamel damage obscures interproximal wear facets so it is not possible to detect whether or not subvertical grooves (Villa and Giacobini, 1996) are present. The incisal surfaces are etched with multiple striations and small chips.

No crown morphology is preserved; however, at the base of each tooth a projection of the mesial marginal ridge is preserved, suggesting that moderate-to-well-developed shoveling (grade 3 or above in the ASUDAS system) was once present. The concavity of the lingual surface, which is still preserved, supports this assessment. Around 5 mm of root is exposed and it is robust (~8.5–9 mm in buccolingual diameter).

4.2.2. Right third premolar (P^3)

The buccal and lingual cusps are nearly worn off and the only remaining occlusal enamel is that found along the longitudinal axis

Table 2
Dental metrics, calculated areas (CA) and crown indices (CI) of Chaoxian.

Tooth	BL	MD	CA (MD × BL)	CI (MD/BL × 100)
R UI2	8.2	(7.5)		
L UI2	8.0	(7.7)		
RUP3	12.1	(8.7)	(105.2)	(71.9)
RUP4	12.6	8.7	109.6	69.0
LUP4	12.2	8.3	101.3	68.0
RUM1	13.5	(11.7)	(158.0)	(86.7)
LUM1	13.5	(11.6)	(156.6)	(85.9)
LUM2	14.1	11.6	163.6	82.2

All metrics are actual measurements taken directly from the tooth. Those in parentheses are likely underestimates due to interproximal wear and/or difficulty in manipulating the calipers to accurately measure the teeth. CA and CI are not presented for the incisors since the MD measurements are substantially underestimated given that most of the crown is missing.

of the crown. Secondary dentin is visible on both buccal and lingual cusps. The lingual cusp exhibits cupped wear, while the less worn buccal cusp is flat. A small fovea distal to the midline of the tooth suggests that the essential crest of the paracone was once well developed. There is a ~2.5 mm wide chip from the mesial border. A ~7 mm wide interproximal facet extends lingually and buccally from the chip. Enamel is chipped from mesial and distal surfaces such that the extent of the interproximal facets is not visible. There is a hypoplastic horizontal furrow about midway down the crown (buccally).

Due to wear there is little observable morphology. The cusps are nearly equal in area but the buccal cusp is slightly wider than the lingual. The buccal surface presents a moderate mesial groove. Both buccal and lingual crown faces are vertical, and lack any cingular swelling. Both lingual and buccal cervical lines are straight with no apical enamel extension. Unfortunately, it was not possible to observe the number of roots on these (or, in fact, any) teeth.

Table 3
Average buccolingual and mesiodistal diameters of Chaoxian and comparative samples with ranges. Numbers in parentheses are underestimates due to tooth wear.

		Middle Pleistocene				Early Pleistocene
		Chaoxian	*H. neanderthalensis*	Archaic *H. sapiens*	Chinese *H. erectus*	Indonesian *H. erectus*
Tooth						
I^2	BL	**8.1**	8.9	7.5	8.2	7.7[a]
		(8.0, 8.2)	*7.75–9.9*	*6.0–8.8*	*8.0–8.4*	
	MD	**(7.6)**	8.25	7.8	7.9	7.5
		(7.5, 7.7)	*7.4–9.1*	*7.0–8.5*	*7.7–8.1*	*7.2–7.7*
P^3	BL	**12.1**	11.0	10.8	12.1	11.4
			8.8–11.9	*7.7–12.1*	*10.5–12.8*	*10.4–12.65*
	MD	**(8.7)**	8.7	9.0	8.2	8.2
			7.5–11.3	*7.4–10.9*	*7.4–8.7*	*7.8–9.1*
P^4	BL	**12.4**	10.9	11.1	11.5	10.8
		12.2, 12.6	*9.8–11.7*	*10.1–11.8*	*9.9–12.7*	*10.2–12.25*
	MD	**8.5**	8.0	7.9	8.0	8.1
		8.3, 8.7	*6.8–8.8*	*7.0–8.4*	*7.2–9.2*	*7.3–9.0*
M^1	BL	**13.5**	12.4	12.8	11.6	13.1
			11.4–14.2	*10.7–14.8*	*10.0–13.1*	*12.0–13.9*
	MD	**(11.7)**	12.2	11.7	11.6	12.1
		(11.6, 11.7)	*11.0–13.5*	*9.4–13.4*	*10.0–13.1*	*11.0–13.6*
M^2	BL	**14.1**	12.8	13.3	12.9	13.6
			11.8–14.2	*11.3–16.3*	*12.3–13.9*	*12.5–15.4*
	MD	**11.6**	11.25	11.4	10.6	12.9
			10.0–13.1	*10.1–12.4*	*10.2–11.4*	*11.6–13.6*

Note: Sample compositions as in Table 1.

[a] Measurement is from one individual.

4.2.3. *Right and left fourth premolars (P^4)*

Both right and left P^4s are considerably less worn than the P^3. The cusps of the right P^4 are flattened by occlusal wear and present large occlusal facets. In contrast to the P^3, only small pinpoints of dentine are exposed on the protocone and paracone. The left P^4 exhibits slightly more wear than the right P^4, with exposed dentine facets that are ~1.8 mm wide. The contrast in wear between the more anterior teeth (I^2s and P^3) and more posterior teeth is remarkable.

The right and left P^4s are morphologically very similar. The bulk of the protocone is mesially positioned relative to crown's midline. Both mesial and distal marginal ridges are present and moderately developed. The essential (median) crests of the two cusps are well developed and meet at the sagittal sulcus, but do not form an enamel bridge. The essential crests of the buccal cusps in both P^4s are bifurcated. The lingual cusp of the right P^4 possesses a trifurcated essential crest, while the lingual cusp on the left P^4 is bifurcated (Fig. 1c). In addition, both teeth appear to have had well-developed accessory ridges (MxPAR: Burnett, 1998) mesially and distally on both cusps. The lingual and buccal cervical lines are straight with no apical enamel extension. Buccal and lingual faces are nearly vertical having only a minimal inward slope and no bulging cingulum.

4.2.4. *Right and left first molars (M^1)*

The occlusal surface of the right M^1 is smoothed by wear and small dentine pits are exposed on the protocone, paracone and metacone. The left M^1 is more worn, with a large (~5.5 mm) patch of dentine exposed on the protocone, and smaller patches on the paracone and metacone. Only a pit of dentine is exposed on the hypocone.

The morphology of both right and left M^1s is very similar. While some of the minor occlusal morphology is obscured, the essential crest of the paracone is distinct. Two grooves extend mesially from the sagittal sulcus, one traverses lingually the other buccally, following the essential crests of the protocone and paracone respectively. A mesial accessory ridge is visible on the metacone. Both teeth possessed an undivided crista obliqua connecting the protocone and metacone. The protocone and paracone have well-developed essential crests that are separated by the sagittal sulcus. The paracone has a moderately developed mesial ridge and distal groove on the buccal surface. Cusp 5 appears to be absent from both teeth based on the lack of fissures on the distal margin of the crown. The hypocone and metacone are large and the cusp size sequence is protocone > paracone > metacone ≥ hypocone (Table 4). The distal aspect of the right tooth is somewhat narrower than the mesial aspect, while the left tooth is squarer. The cusp tips are not preserved well-enough to assess cusp angles, which have been shown to be taxonomically informative in Middle to Late Pleistocene hominins (Bailey, 2004). While there is a slight skew to the crowns, the teeth (especially the left) appear to lack the marked skew so prevalent in *H. neanderthalensis* M^1s (Gómez-Robles et al., 2007).

Although the teeth are worn, there appears to be some remnant of a Carabelli's cusp on the lingual surface of both M^1s (most likely a Y-shaped depression, which translates to ASUDAS: grade 3 or 4). Both teeth have a well-developed lingual groove associated with the hypocone. The moderately developed lingual groove is visible at the occlusal rim where it spills over to the lingual surface, and continues to the cervical line. Both lingual and buccal cervical lines are straight with no apical enamel extension.

4.2.5. *Left second molar (M^2)*

The M^2 crown was once broken and has now been glued on to the root. The cusps are flattened somewhat by wear but the

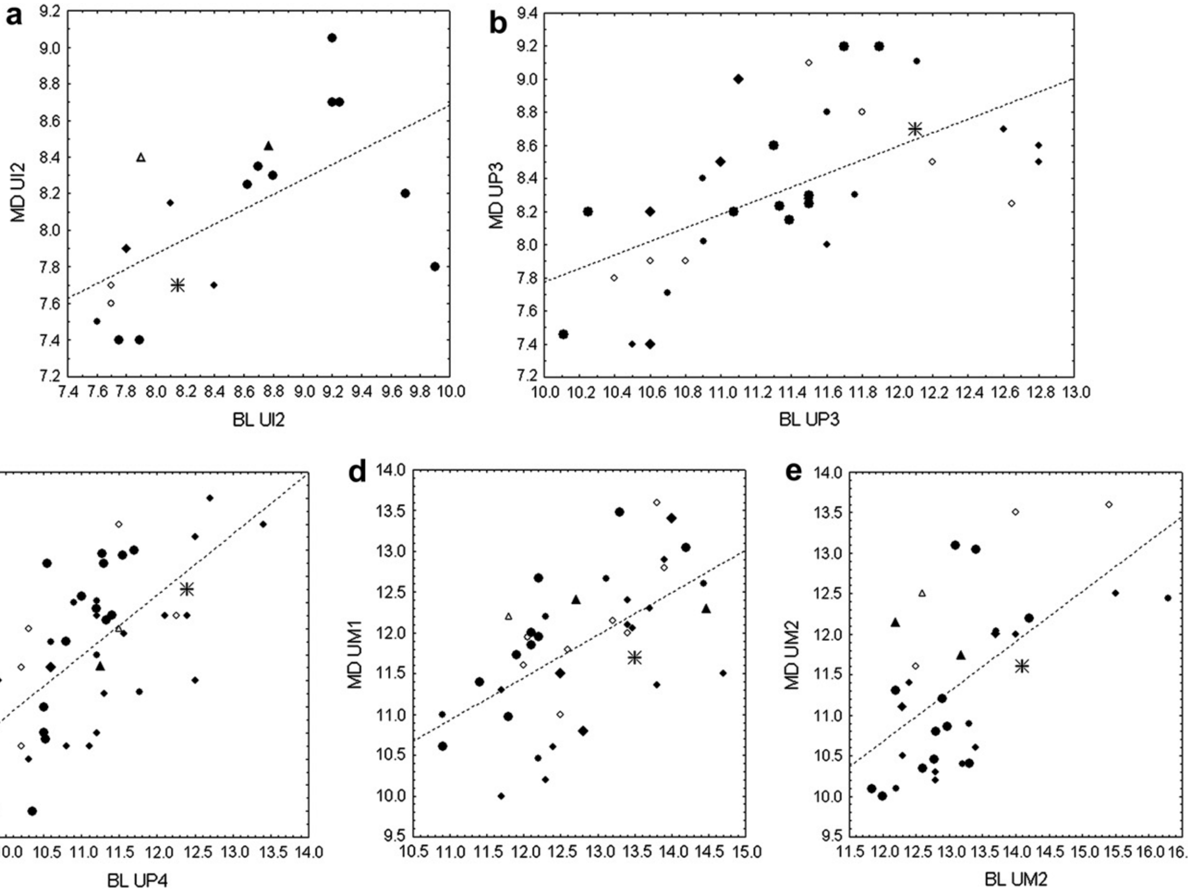

Fig. 3. Lengths plotted against breadths for I^2 (a), P^3 (b), P^4 (c), M^1 (d) and M^2 (e). Symbols: ◇ Indonesian *H. erectus*, ◆ Chinese *H. erectus*, ◆ Chinese archaic *H. sapiens*, △ African *H. erectus*, ▲ African archaic *H. sapiens*, ○ *H. antecessor*, • European archaic *H. sapiens*, ● Early European Neandertals, ∗ Chaoxian.

buccal cusps maintain some apical topography. The protocone, paracone and metacone exhibit only small points of dentine exposure. There is a ~5 mm wide distal facet that is 1.5 mm from the occlusal surface, indicating that M^3 had been in functional occlusion at the time of death, as suggested previously by Zhang (1989).

The crown area of the M^2 is approximately 9% larger than the M^1. This difference is in the mesial cusps – protocone and paracone

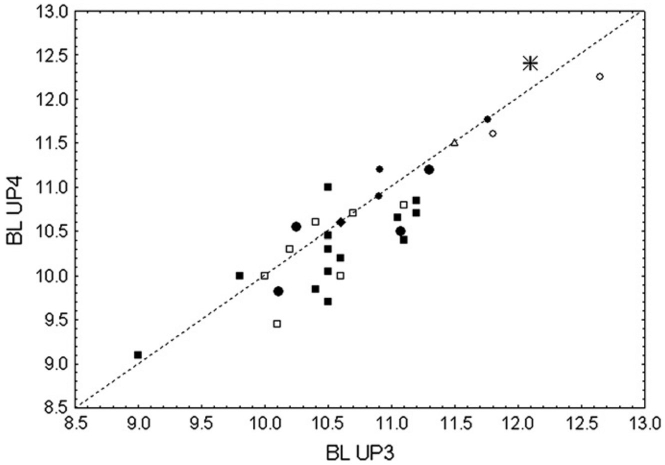

Fig. 4. Buccolingual breadths of upper premolars plotted. Dotted line represents P^3 and P^4 of equal breadth. Symbols: ◇ Indonesian *H. erectus*, ◆ Chinese archaic *H. sapiens*, △ African *H. erectus*, ○ *H. antecessor*, • European archaic *H. sapiens*, ● Early European Neandertals, ■ Late Pleistocene Neandertals, □ Late Pleistocene *H. sapiens*, ∗ Chaoxian. Note: Late Pleistocene *H. sapiens* sample is comprised of specimens from Qafzeh and Skhul and Late Pleistocene Neandertals sample is comprised of specimens from: Amud, Shanidar, Arcy-sur-Cure, Châteauneuf, Le Ferrassie, Genay, Kulna, Marilla, Monsempron, Le Moustier, La Quina, Spy.

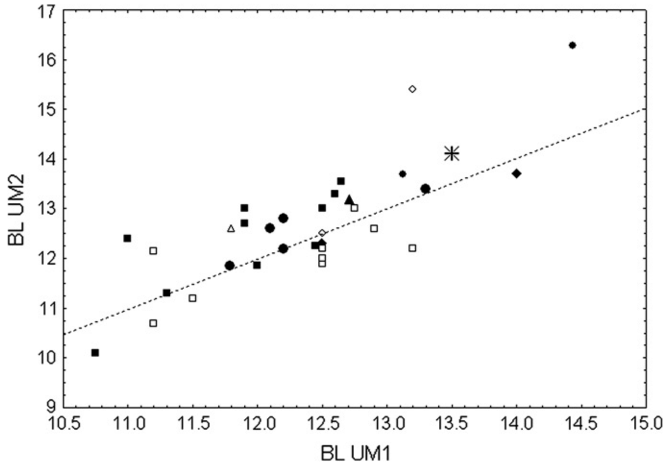

Fig. 5. Buccolingual breadths of upper molars plotted. Dotted line represents M^1 and M^2 of equal breadth. Symbols: ◇ Indonesian *H. erectus*, ◆ Chinese archaic *H. sapiens*, △ African *H. erectus*, ▲ African archaic *H. sapiens*, • European archaic *H. sapiens*, ● Early European Neandertals, ■ Late Pleistocene Neandertals, □ Late Pleistocene *H. sapiens*, ∗ Chaoxian. Note: Late Pleistocene *H. sapiens* sample is comprised of specimens from Qafzeh and Skhul and Late Pleistocene Neandertal sample is comprised of specimens from: Amud, Shanidar, Arcy-sur-Cure, Châteauneuf, Monsempron, Le Moustier, La Quina, Spy, Petit Puy.

Table 4
Total crown base areas (TCBA), Measured (Meas.) and Relative (Rel.) Cusp areas[a] (average of three measurements) of Chaoxian and a comparative sample. Comparative M^1 data are from Quam et al. (in press)[b], M^2 data are from Bailey (2002) and Bailey (unpublished data). Numbers in parentheses represent sample sizes.

	Tooth	TCBA	Protocone		Paracone		Metacone		Hypocone	
			Meas.	Rel.%	Meas.	Rel.%	Meas.	Rel.%	Meas.	Rel.%
Chaoxian	$\mathbf{M^1}$	**131.8**	**35.0**	**26.6**	**33.1**	**25.1**	**31.9**	**24.2**	**31.8**	**24.1**
	$\mathbf{M^2}$	**141.2**	**47.4**	**33.6**	**41.1**	**29.1**	**25.3**	**17.9**	**27.4**	**19.4**
H. erectus	M^1 (5)	115.5	34.5	29.9	28.7	24.9	26.5	22.9	25.8	22.3
	M^2 (3)	101.1	31.3	33.6	27.4	22.7	23.0	22.7	19.4	19.1
H. antecessor	M^1 (2)	120.5	35.3	29.3	27.6	22.9	29.9	24.8	27.5	22.8
	M^2	–	–	–	–	–	–	–	–	–
H. heidelbergensis	M^1 (4)	115.5	34.8	31.1	28.3	24.8	24.2	20.1	28.2	24.0
	M^2 (2)	122.3	43.8	35.5	31.5	26.0	25.8	20.9	21.2	17.6
H. neanderthalensis	M^1 (21)	112.3	33.7	29.9	28.2	25.8	22.9	20.6	26.8	23.7
	M^2 (11)	112.6	35.5	31.7	31.5	28.4	23.7	21.2	21.9	19.2

[a] Relative cusp areas are calculated by dividing each measured cusp areas by the total crown base area.
[b] Sample composition of Quam et al. (in press) is not the same for other analyses in this study: *H. erectus* includes Asian specimens from the Early to Late Pleistocene. *H. heidelbergensis* includes only European representatives. *H. neanderthalensis* includes both Middle and Late Pleistocene specimens.

– which are about 40% and 30% larger, respectively, in the M^2. The metacone and hypocone, on the other hand, are 23% and 10% smaller, respectively, in the M^2 than they are in the M^1. The relative cusp sizes are protocone > paracone > hypocone > metacone (Table 3). Both metacone and hypocone cusp apices are lingual to those of the protocone and paracone. Together with the slight reduction of the metacone tooth takes on a shape that is more skewed than observed in the M^1s. While the shape of the M^1 appears to be highly diagnostic, Bailey (2002) found that the shape of the M^2 was much more variable and, therefore, not particularly useful for diagnosing Middle to Late Pleistocene taxa.

Much of the fissure pattern is still visible revealing what was once a complex occlusal pattern. Small fissures delineate the essential crest, the mesial and distal accessory ridges of the protocone and paracone, and a mesial accessory ridge of the metacone. There appears to have been a well-developed, cusp-like Carabelli's trait (grade 5 or 6), based on a groove on the lingual aspect of the protocone that curves distally at the occlusal surface and a distal groove that nearly intersects with it (where the grooves would have met to form a cusp is missing due to wear). The lingual occlusal groove separating protocone and hypocone spills over on to the lingual face of the crown and becomes a deep groove that traverses vertically to the cervical line. The buccal occlusal groove separating the paracone and metacone is shallower and fades into the buccal face as it crosses the occlusal rim. There is a well-developed crista obliqua connecting the metacone and protocone that was likely divided, but is somewhat obscured by wear. Both lingual and buccal cervical lines are straight with no apical enamel extension.

5. Discussion

5.1. Tooth wear

As noted, there is a marked discrepancy in the wear of the lateral incisors and P^3, on the one hand, and the P^4 and molars on the other. Marked anterior tooth wear is commonly associated with *H. neanderthalensis*, although it can also be observed in at least some archaic *H. sapiens* specimens (Fig. 6). In these hominins, it is not uncommon to find in the same jaw anterior tooth crowns that are completely obliterated by wear and only lightly worn molars. The pattern is generally thought to be due to paramasticatory use of the anterior teeth such as using them as tools (Brace, 1962, 1979; Brose and Wolpoff, 1971; Puech, 1981; Smith, 1976a,b; Trinkaus, 1978; Zhang, 1989). The labio-lingually oriented tooth wear of the I^2s (Fig. 1b) is typically seen in *H. neanderthalensis* and may result from a combination of factors including tooth procumbancy and/or mid-facial morphology (Ungar et al., 1996).

5.2. Dental metrics and morphology

Overall, when compared to other Pleistocene hominins the dentition of Chaoxian is unremarkable. Metrically the teeth fall within the range of all Asian Middle Pleistocene hominins (Table 5). The incisors and premolars are somewhat closer to the *H. erectus* mean and the molars are somewhat closer to the mean of archaic *H. sapiens* (Table 3).

Like the dental metrics, the dental morphology of Chaoxian is unremarkable, as all of the morphological features observed are common in Middle and Late Pleistocene hominins (Bailey, 2006). Moreover, the dentition is generally primitive, as it is similar to that observed in other (earlier) fossil hominins (Bailey, 2002; Brown and Walker, 1993; Johanson et al., 1982; Martínon-Torres et al., 2007; Robinson, 1956), and lacks derived features observed in Neandertals. That some contemporary humans possess certain primitive traits as well (Burnett, 1998; Scott and Turner, 1997), does not undermine the primitive nature of the Chaoxian dentition. In addition to being large in size, the morphology is complex as exemplified by the (inferred) shoveling of the lateral incisors, the

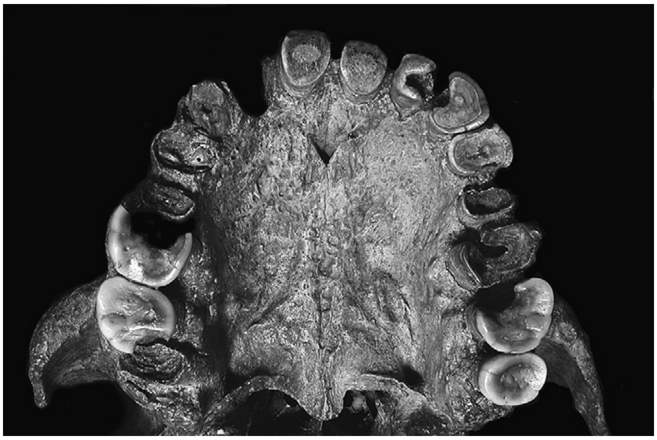

Fig. 6. African archaic *H. sapiens* (a.k.a. *H. rhodesiensis*) from Kabwe showing marked differences between anterior and posterior tooth wear. (Note: several of the post-canine tooth crowns are destroyed by carious lesions.)

Table 5
Chaoxian compared to other Asian Middle Pleistocene hominins.

	I^2		P^3		P^4		M^1		M^2	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
Chaoxian (average)	**(7.6)**	**8.1**	**8.7**	**12.1**	**8.3**	**12.4**	**(11.7)**	**13.5**	**11.6**	**14.1**
Archaic *H. sapiens*										
Jinniushan[a]	7.9	7.8	8.2	10.6	8.2	10.6	11.3	12.7	11.2	12.2
Xujiayao[b]	–	–	–	–	–	–	13.4	14.0	12.0	13.7
Changyang[c]	–	–	8.0	11.0	–	–	–	–	–	–
Zhoukoudian PA537[b]	–	–	8.5	11.0	–	–	–	–	–	–
Tongzi[b]	–	–	9.0	11.1	–	–	(11.4)	14.0	–	–
H. erectus										
Hexian[b,d]	–	–	–	–	9.0	13.4	12.3	13.7	12.5[e]	15.0[e]
Zhoukoudian[b]	8.1	8.2[e]	8.0[e]	11.6[e]	8.0[e]	11.4[e]	11.3[e]	12.7[e]	10.6[e]	12.6[e]
Luonan[b]	–	–	–	–	–	–	12.4	13.4	–	–
Xichuan[b]	–	–	–	–	8.0[e]	11.2[e]	–	–	–	–
Yiyuan[b,d]	–	–	8.6[e]	12.8[e]	7.8[e]	11.9[e]	11.5[e]	14.7[e]	–	–
Yunxian[b]	7.7	8.4	–	–	9.2	12.7	12.9	13.9	–	–

[a] From Jianing (2000).
[b] From Wu and Poirier (1995).
[c] Collected by SEB.
[d] Based on several isolated teeth representing one or more individuals.
[e] Average of >1 of the same tooth.

developed P^4 accessory ridges (MxPAR), the bifurcated essential crests on both premolars, as well as the accessory fissures and crests on the molars.

The few Asian Late Middle Pleistocene hominins that can be compared to Chaoxian show similar morphology. For example, the incisors from Jinniushan, Xujiayo, Tongzi and Dingcun are all shovel shaped (Wu and Poirier, 1995). Likewise, the P^3 from Changyang possesses a bifurcated essential crest on the buccal cusp (SEB observation) and those from Tongzi also show complex (e.g., MxPAR or bifurcated essential crests) occlusal morphology (Wu and Poirier, 1995). Finally, like Chaoxian the M^1 and M^2 of Xujiayo show complex occlusal morphology (extra fissures and crests), a hypocone and metacone about equal in size and the presence of Carabelli's trait (M^1) (inferred from photos in Wu and Poirier, 1995).

In occlusal outline, both M^1 and M^2 of Chaoxian are only slightly skewed and are similar in this respect to the M^1 of Changyang (SEB observation). Unfortunately, it was impossible to quantify the outline shape for either individual using cusp angles because of occlusal wear. The M^1 of *H. neanderthalensis* is known to show a skewed outline that is also present in earlier members of their lineage (e.g., European archaic *H. sapiens*) but this shape is absent in *H. sapiens* and *H. erectus* (Gómez-Robles et al., 2007). The right tooth of Chaoxian is slightly more skewed than the left but visual assessment of the occlusal outline suggests that both would likely fall with other Middle Pleistocene hominins with regard to shape (Gómez-Robles et al., 2007). The M^1 of Xujiayo is not skewed but is oddly trapezoidal in shape, with the distal half of the tooth quite a bit narrower than the mesial half (Wu and Poirier, 1995: 130). The occlusal polygon area (a measure of the internal placement of the cusp tips) of the M^1 is also known to show diagnostic differences in Middle to Late Pleistocene hominins (e.g., small relative occlusal polygon area is a *H. neanderthalensis* trait: Bailey, 2004). Unfortunately, wear precludes an analysis of the M^1 occlusal polygon area in Chaoxian.

It is possible, however, to observe the relative cusp areas of the Chaoxian molars. M^1 cusp areas have been shown to be useful for diagnosing Plio-Pleistocene (Quam et al., in press; Wood and Engleman, 1988) and Middle to Late Pleistocene hominins (Bailey, 2004). The Chaoxian M^1 possesses a paracone/metacone relationship (paracone > metacone) that is the derived condition observed in most later *Homo* (*H. antecessor* excluded) (Quam et al., in press). In addition, the M^1 lacks the extremely small metacone that is distinctive of *H. neanderthalensis* and members of their lineage (Bailey, 2002; Quam et al., in press).

6. Conclusions

The Chaoxian dentition is comparable in size and morphology to other Pleistocene hominins. The teeth are large and the occlusal morphology preserves primitive features observed in other fossil hominins. The distinctive asymmetry in wear between the anterior and posterior teeth has often been cited as a 'Neandertal' feature; however, it is not exclusive to *H. neanderthalensis* and is observed in other Middle Pleistocene hominins as well. Of the preserved morphology, no derived morphological characters link the teeth of Chaoxian (or any of the other Asian Middle Pleistocene hominins examined here) specifically with *H. neanderthalensis*. From the small sample examined here we do not detect any dental characters that are 'unique' to the Asian Late Middle Pleistocene hominins.

It is clear from the dentition that Chaoxian is no Neandertal. This may not be surprising given that Weidenreich's (1943) hypothesis, which envisioned humans throughout the world undergoing a Neandertal stage of evolution, has not withstood the test of time. However, seeing that *H. neanderthalensis* is now known to be present as far east as central Asia and Siberia, at least by the late Pleistocene (Bailey et al., 2008; Krause et al., 2007), it is not unreasonable to ask if *H. neanderthalensis* evolution may have occurred more broadly than is usually presumed. While there has been some speculation regarding the alleged Neandertal-like affinities of the Maba calotte (Pope, 1992), the dental data discussed here do not support this hypothesis. Instead, it still appears that European archaic *H. sapiens* (*H. heidelbergensis sensu stricto*) is unique in its possession, albeit in low frequencies, of emergent Neandertal dental traits.

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