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Hominin diversity in East Asia during the Middle Pleistocene: A premolar endostructural perspective

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Abstract

Following the recent studies of East Asian mid-Middle to early Late Pleistocene hominin material, a large spectrum of morphological diversity has been recognized and the coexistence of archaic (*Homo erectus*-like) and derived ('modern-like') dental morphological patterns has been highlighted. In fact, for most of these Chinese fossils, generally categorized as 'archaic *Homo sapiens*' or 'post-*H. erectus* *Homo*', the

taxonomic attribution is a matter of contention. With the help of μ CT techniques and a deformation-based 3D geometric morphometric (GM) approach, we focused on the morphological variation in the enamel-dentine junction (EDJ) of 18 upper and lower premolars from Chinese Middle Pleistocene hominins. We then compared our results with a number of fossil and modern human groups, including Early Pleistocene *H. erectus* from Sangiran; late Early Pleistocene hominins from Tighenif, Algeria; classic Neanderthals; and modern humans. Our results highlight an evolutionary/chronological trend of crown base reduction, elevation of EDJ topography, and EDJ surface simplification in the hominin groups studied here. Moreover, this study brings insights to the taxonomy/phylogeny of six late Middle Pleistocene specimens whose evolutionary placement has been debated for decades. Among these specimens, Changyang premolars show features that can be aligned with the Asian *H. erectus* hypodigm, while Panxian Dadong and Tongzi premolars are more similar to Late Pleistocene *Homo*. Compared with early to mid-Middle Pleistocene hominins in East Asia, late Middle Pleistocene hominins evince an enlarged morphological variation. A persistence of archaic morphotypes and possible admixture among populations during the late Middle Pleistocene are discussed.

1. Introduction

Dental evidence suggests that Eurasian Early and Middle Pleistocene hominins, including those from Central Asia (Martín-Torres et al., 2008), continental East Asia

(Bailey and Liu, 2010; Liu et al., 2013, 2017; Xing et al., 2014, 2016, 2018; Zanolli et al., 2018) and insular Southeast Asia, had a relatively independent evolutionary course compared with African hominins (Martín-Torres et al., 2007; Bermúdez de Castro and Martín-Torres, 2013; Kaifu, 2017). From the early to mid-Middle Pleistocene, hominin remains found in the Asian continent are mostly assigned to *Homo erectus* (Kaifu et al., 2005; Martín-Torres et al., 2008; Zanolli, 2013; Xing et al., 2014, 2016). However, the high-degree of morphological variation of the Asian dental remains (Zanolli et al., 2012, 2018a; Liu et al., 2013; Xing et al., 2018, 2019) suggests the (co)existence of derived (modern *H. sapiens*-like) and archaic morphotypes in the Middle Pleistocene. This complex scenario gives rise to a number of questions regarding the routes of dispersal, possible interactions and gene flow between lineages in the mid-Middle to early Late Pleistocene, before the attested presence of anatomically modern humans (Liu et al., 2015).

In the late Pleistocene Chinese hominin fossil record, the taxonomic status and phylogenetic relationships with earlier, contemporaneous and later human lineages remains unclear. Part of this is probably due to the limited sample size and the heterogeneity of expression of archaic and derived traits in the mid- to late Middle Pleistocene ‘non-*H. erectus*’ human record. For instance, the late Middle Pleistocene dental remains from Panxian Dadong, even if limited to four isolated teeth, retain some archaic traits in the anterior dentition, including a weakly expressed finger-like tuberculum dentale on the upper central incisor and robust incisor and canine crowns,

in association with derived features in most teeth (symmetrical canine crown without cingulum, modern-like premolar crown morphology; Liu et al., 2013). Similarly, the late Middle Pleistocene teeth from Tongzi, even if penecontemporaneous with late representatives of *H. erectus*, differ from the typical condition seen in the latter group and show a series of derived traits that are more commonly seen in Late Pleistocene *Homo*, including: the absence of tuberculum dentale on the upper incisor, simplified and symmetrical premolar crowns without grooves and ridges on the buccal aspect, and mesiodistally compressed upper molars (Wu, 1984; Xing et al., 2019). Conversely, dental remains from other late Middle to early Late Pleistocene populations such as Chaoxian, Changyang and Xujiayao express a degree of archaic, *H. erectus*-like features—see external crown morphology in Xing et al. (2015, 2016) and Bailey and Liu (2010), and root canal configuration in Pan et al. (2019). Taphonomic factors and occlusal wear have also erased parts of the external tooth morphology, thus adding to the confusion concerning the evolutionary interpretations of these specimens (Liu et al., 2013; Xing et al., 2015, 2019; Pan and Zanolli, 2019). However, even if the external morphology is altered, diagnostic taxonomic and phylogenetic information may still be preserved in the internal structure of teeth, and their internal signature can still be extracted using the methods developed in virtual paleoanthropology (Skinner et al., 2008b; Xing et al., 2014, 2016, 2018; Weber, 2015; Zanolli et al., 2018; Pan and Zanolli, 2019).

We used X-ray μ CT scanning and 3D image processing techniques to investigate

the inner structure of six late Middle Pleistocene premolar specimens from the sites of Changyang (PA76, PA81), Tongzi (PA873), Panxian Dadong (PA 1577 and PA 1578) and Chaoxian (Chaoxian), whose taxonomic attribution is controversial. In order to characterize these specimens, we focus here on the enamel-dentine junction (EDJ) morphology. This interface results from the membrana praeformativa that configures the outer enamel surface (OES) during tooth growth (Corruccini, 1987). In mature teeth, it preserves diagnostic morphological information, even when the occlusal enamel is worn. It is thus recognized as a reliable taxonomic proxy to distinguish between hominid taxa (even at the subspecies level) and can also bring hominid phylogenetic insights (Weber, 2001; Skinner, 2008; Skinner et al., 2008a; Braga et al., 2010; Macchiarelli et al., 2013; Pan et al., 2016; Zanolli et al., 2019).

Comparing with a number of fossil and modern human specimens/samples, including Chinese early to mid-Middle Pleistocene *H. erectus* from the sites of Zhoukoudian, Hexian, Xichuan and Yiyuan, the aims of this study are: (1) to examine the ability of premolar EDJ morphological information to discriminate among a selection of fossil and modern human premolar samples; (2) to document the morphological variability of mid- to late Middle Pleistocene human premolars in East Asia; and (3) to re-evaluate the taxonomic affinities of six late Middle Pleistocene specimens.

2. Materials and methods

2.1. Study sample

The Chinese Middle Pleistocene hominin sample consists of two groups; a map of their location is shown in Supplementary Online Material (SOM) Figure S1. The first group includes early to mid-Middle Pleistocene *H. erectus* (HEC, $n = 12$) from the sites of Zhoukoudian, Hexian, Xichuan and Yiyuan, with a chronological range from 800 to 282 ka (Table 1). Note that the specimens from Xichuan County, Hubei Province lack accurate stratigraphic context, but their morphological signature a priori places them close to Zhoukoudian *H. erectus* (Wu and Wu, 1982; Wu and Poirier, 1995). The allocation of Xichuan hominins to East Asian *H. erectus* is further supported by a recent comparative study (Xing et al., 2018) on the dental inner structure of Chinese Middle Pleistocene *H. erectus*. The second group is represented by six premolars from three mid- to late Middle Pleistocene sites (Changyang, Tongzi, Panxian Dadong and Chaoxian). These specimens do not have a clear taxonomic attribution, as in previous studies they were classified as archaic or premodern *H. sapiens*, or were categorized as non-*H. erectus* *Homo* (Xing et al., 2019) (and are thus regarded here a priori as *Homo* sp. from China, HSPC). We compared the Chinese specimens with 56 fossil and extant human specimens (Table 1), including Javanese Early Pleistocene *H. erectus* (HEJ) specimens from Sangiran (Grine, 1994; Kaifu et al., 2005); North African late Early Pleistocene hominins (HNA) from Tighenif (Zanolli and Mazurier, 2013); Neanderthals (NEA) from Krapina and La Chaise (Macchiarelli et al., 2006; NESPOS database, 2020), and modern *H. sapiens* (MHS) from Africa and Eurasia (Pan et al., 2017).

127

128 2.2 Methods

129 Tooth wear stages were scored according to the standard proposed by Smith (1984).
130 For the Neanderthal and modern *H. sapiens* specimens, we selected only premolars
131 without dentine exposure on the occlusal surface. However, for the Chinese Middle
132 Pleistocene specimens, because of the limited available sample, we included all
133 specimens with wear degree less than stage 3 (“full cusp removal and/or moderate
134 dentine patches”; Smith, 1984:45).

135 Information on the crown outer and inner morphology—non-metric features, 2D
136 geometric morphometrics (GM) on the OES—has been reported for most of the HEC
137 and HSPC specimens in previous studies (Black et al., 1933; Chia, 1957; Wu and Wu,
138 1982; Chen et al., 1987; Bailey and Liu, 2010; Xing, 2012; Liu et al., 2013; Xing et al.,
139 2014, 2016, 2018, 2019; Liu et al., 2017; Zanolli et al., 2018a). The dental remains
140 from Xichuan (PA524, PA525, PA526, PA527, PA528) and Changyang (PA76, PA81)
141 are reported and their internal structure (as well as that of the Chaoxian specimen)
142 analyzed here for the first time. The terms employed for the morphological descriptions
143 are from Weidenreich (1937), Turner et al. (1991) and Scott and Turner (1997).

144 Microcomputed tomography and processing of the 3D data All Chinese fossil
145 specimens (except for two Zhoukoudian *H. erectus* specimens housed at Uppsala
146 University) were scanned using a 225 kV micro-XCT scanner at the Institute of
147 Vertebrate Paleontology and Paleoanthropology, China according to the following

parameters: 120–140 kV voltage, 100–120 mA current, angular step of 0.5° over a scan angle of 360°. The final volumes were reconstructed with an isotropic voxel size ranging from 40 to 70 µm. The fossil premolars PMU M3887 and M3549, housed at Uppsala University, were scanned at the Multidisciplinary Laboratory of the The Abdus Salam International Centre for Theoretical Physics (ICTP), Trieste, Italy (Zanolli et al., 2018a).

Image stacks were imported into Avizo 9.0 (FEI Visualization Sciences Group), and the images were segmented using semiautomatic procedures and an adaptation of the half-maximum height method (Fajardo et al., 2002; Coleman and Colbert, 2007); the EDJ surfaces were generated using the ‘unconstrained smoothing’ option. For 11 out of 18 Chinese human fossil specimens (marked in Table 1), some cusp tips were worn, so we manually reconstructed the dentine horn tips based on the curvature and orientation of the EDJ at each side of the dentine horns (Smith et al., 2012; Zanolli et al., 2018b). Our reconstructions are depicted in SOM Figure S2.

Geometric morphometric analysis We used a recently developed diffeomorphic surface matching (DSM) method to compare the EDJ shapes among hominin groups. This landmark-free, mesh-based approach relies on the construction of average surface models, and the difference between surfaces is interpreted as the amount of deformation needed to align them by using diffeomorphic shape matching (Glaunes and Joshi, 2006; Durrleman et al., 2014). Then deformations between surfaces are mathematically modeled as smooth and invertible functions (i.e., diffeomorphisms; Glaunes and Joshi,

2006; Durrleman et al., 2014). From a set of surfaces, an atlas of surfaces is created. The method estimates an average object configuration or mean shape from a collection of object sets, here the EDJ surfaces, and computes the deformations from the mean shape to each specimen. In addition, a set of initial control points located near its most variable parts, and a set of momenta parameterizing the deformations of the mean shape to each individual are estimated (Durrleman et al., 2012a, b; Beaudet et al., 2016a). This method has been successfully employed in a number of paleontological/paleoanthropological investigations (Beaudet et al., 2016b, 2018; Zanolli et al., 2018; Braga et al., 2019; Pan et al., 2019; Urciuoli et al., 2020). A recent study comparing the discriminative power of 3D landmark-based GM and DSM demonstrated that DSM has the potential to better capture the geometric details that describe tooth shape (Braga et al., 2019).

To perform this analysis, as a previous step, at each dental position the EDJ surfaces were manually oriented, then superimposed using the rigid and uniform scale option of the ‘align surface’ module in Avizo 9.0 (Visualization Sciences Group Inc.). This was done by minimizing the root mean square distance between the points of each specimen to corresponding points on the reference surface using an iterative closest point algorithm.

We used the Deformetrica software (<https://www.deformetrica.org>; Durrleman et al., 2014) to generate a global mean shape (GMS) with a set of diffeomorphisms from the GMS to each individual and the output (control points and deformation momenta)

used to perform the statistical analyses to explore the EDJ shape variation. An example of the original EDJ surface, the simplified EDJ surface imported in Deformetrica v. 4.3 and the output virtual models generated by DSM process is shown in SOM Figure S3 (see also SOM Fig. S4 for the output surfaces of all the Chinese fossil specimens after deformations). Using the packages ade4 1.7-13 (Dray and Dufour, 2007) and Morpho v. 2.6 (Schlager et al., 2018) for R v. 3.5.1 (R Development Core Team, 2012), we checked the shape variation of the fossil and recent human groups in a principal component analysis (PCA). Even if the first two components of the PCA account for approximately 40 to 65% of the total variance in these analyses, there is still some information in the following components. However, visualizing and interpreting a complex space in multiple dimensions is difficult. We computed between-group principal component analyses (bgPCA) to evaluate the degree of shape variation between hominin groups. We used both PCA and bgPCA as the former is mostly a means to explore the morphospace, with the variance spread over multiple axes, whereas bgPCA, through projection of the data onto the principal components of the group averages, represents a viable alternative to discriminant analyses (Mitteroecker and Bookstein, 2011). Nonetheless, when sample size is small and groups are few, the results of bgPCA must be interpreted with care and a number of tests are needed to confirm that group separation is not spurious (Bookstein, 2019; Cardini et al., 2019). As a result, we checked and confirmed that group separation preexisted in the PCA and bgPCA was used to assess group affinity of target specimens. Following the

recommendations of Cardini and Polly (2020), we also computed the cross-validated bgPCA (CV-bgPCA) to confirm that the group distribution is not spurious. The six Chinese late Middle Pleistocene *Homo* sp. specimens were then projected a posteriori in the bgPCA plot to assess their morphological affinities.

The residual of allometric signals were tested using the coefficient of determination (R^2) of a multiple regression (Bookstein, 1991) in which the explicative variable is the EDJ area as proxy for size and the dependent variables are the (bg)PC scores.

3. Results

3.1. Description of enamel-dentine junction morphologies

Here we describe the morphological features on the EDJ of previously unreported material from Xichuan, Changyang and Chaoxian and compared it with a number of Pleistocene and Holocene hominin specimens (see Figs. 1A–V and 2A–S for EDJ surfaces in occlusal view). The Chinese fossil specimens are ordered and described below with regard to dental position.

Left maxillary third premolar (P³, PA524, Xichuan) See Figure 1B. Viewed from the occlusal surface, the crown contour is oval and slightly asymmetrical, the width of the buccal aspect is slightly larger than the lingual aspect, the transverse crest is pronounced and connects the buccal and lingual cusps, forming a small and deep anterior fovea and a larger posterior fovea, and a small tubercle is visible at the mesial aspect of the buccal

231 cusp base. Along the marginal ridge, no accessory ridge is identified.

232 Left maxillary third premolar (P³, PA76, Changyang) See Figure 1D. The occlusal
233 outline of the marginal ridges is elliptical and slightly asymmetrical, two faint accessory
234 ridges (one of which is bifurcated at the end) can be seen at the base of the buccal cusp
235 but interrupted in the middle of the small occlusal basin, and no continuous transverse
236 crest is formed. One mesial accessory ridge is identified. Two weakly developed
237 tubercles are visible at the base of the lingual cusp.

238 Right maxillary fourth premolar (P⁴, Chaoxian) See Figure 1O. This P⁴ is attached to a
239 maxilla, whose right P³–M¹ and left P⁴–M² are preserved (Bailey and Liu, 2010). The
240 occlusal basin of this P⁴ is relatively small compared with the crown base, similar to
241 the condition in *H. erectus* (Fig. 1M, N, P, Q). The crown contour is ovorectangular.
242 The transverse crest is not well expressed and is interrupted by the occlusal basin. In
243 all, compared with the highly crenulated EDJ surface that is expressed at East Asian *H.*
244 *erectus* (e.g., Xing et al., 2016, 2018; this study), the EDJ of Chaoxian P⁴ is more similar
245 to the less complex morphology of Indonesian *H. erectus* from Sangiran. Weakly-
246 expressed accessory tubercles are found at the mesial and distal part of the occlusal
247 basin.

248 Left mandibular third premolar (P₃, PA526, Xichuan) See Figure 2C. The crown outline
249 of PA526 is asymmetrical and mesiodistally elongated in occlusal view. The transverse
250 crest is well developed and continuous. The mesial fovea is slightly smaller than the
251 distal one, as the latter is born by a wide talonid. An accessory ridge can be found at

the mesial aspect of the lingual cusp, but it does not reach the mesial marginal ridge. At the buccal surface, the mesial vertical groove is better developed than the distal one.

Right mandibular third premolar (P₃, PA527, Xichuan) See Figure 2D. The morphology of PA527 is very similar to that of PA526; however, instead of an accessory ridge, a faint wrinkled line is present at the mesial side of the lingual cusp. Like PA526, the mesial vertical groove at the buccal surface is better expressed than the distal one.

Right mandibular fourth premolar (P₄, PA525, Xichuan) See Figure 2L. The outline of the marginal ridge is ovorectangular with a protruding mesiobuccal angle. The transverse crest is moderately expressed and interrupted. At the occlusal basin, two small, weakly expressed wrinkles are presented at the mesial marginal ridge and the distal side of the lingual cusp. Moreover, a weakly expressed accessory cusp is seen at the distal side of the buccal cusp. On the buccal surface, two vertical grooves are clearly detected.

Left mandibular fourth premolar (P₄, PA528, Xichuan) See Fig. 2M. The morphology of PA528 is slightly different from that of PA525, but resembles that of the *H. erectus* specimen M3887 from Zhoukoudian. The occlusal outline of its marginal ridge is also ovorectangular. The transverse crest is well developed and uninterrupted, and the mesial fovea is clearly smaller than the distal fovea. Several accessory cusps can be seen at the distal marginal ridge, and a moderately expressed accessory crest is present at the distal side of the lingual cusp. A moderately expressed wrinkled line is visible at the mesial marginal ridge. On the buccal surface, two vertical grooves are well expressed.

Left mandibular fourth premolar (P₄, PA81, Changyang) See Figure 2N. The crown contour is ovorectangular, the distal part of the crown being wider than the mesial one. The transverse crest is interrupted by a deep groove and is weakly developed. Mesial and distal accessory ridges for the lingual cusp can be identified, three accessory cusps are seen at the distal part of the fovea posterior, and an accessory ridge is present distally to the buccal cusp and deflects at the center of the occlusal basin. On the buccal surface, the distal vertical groove is more pronounced than the mesial one.

The East Asian mid-Middle Pleistocene *H. erectus* (PA67, 68, 110, 524, 525, 526, 527, 528, 832, M3887 and Shy071) consistently show a complex morphology, with vertical ridges and crests on the buccal aspect of the EDJ, together with a wrinkled occlusal basin and accessory cusps and crests. In the latter half of the Middle Pleistocene, more variation is observed.

For the upper premolars, the P³ PA76 (Fig. 1D) from Changyang retains archaic traits, as it exhibits multiple accessory crests running in the occlusal basin. In comparison with PA76, the P³ PA873 from Tongzi (Fig. 1E) displays a simple morphology, with a proportionally larger and smoother occlusal basin and three faint occlusal crests running on the internal aspect of the paracone. The mesial and distal marginal ridges of PA873 are more protruding, with numerous small cuspule-like features. A similarly simplified and enlarged occlusal basin than in PA873 is also shown in the P³ PA1577 (Fig. 1F) from Panxian Dadong. The P⁴ from Chaoxian (Fig. 1O) has

a smaller occlusal basin compared with the crown base, similar to East Asian *H. erectus* from Zhoukoudian (PA68, Fig. 1M; Shy071, Fig. 1N). However, unlike the ‘dendrite-like’ EDJ that is shown in *H. erectus*, the occlusal surface relief of Chaoxian is less complex (but is not comparable to PA873 and 1577, which are more simple and smooth) with a weakly-expressed, interrupted transverse crest.

As for the lower premolars, a previous study on the crown morphology (Liu et al., 2013) showed that the P₃ PA1578 (Fig. 2E) from Panxian Dadong exhibits weakly expressed archaic traits and a derived general configuration with respect to the condition in *H. erectus*. The EDJ outline is more symmetrical in PA1578 than in Early to mid-Middle Pleistocene specimens from Africa and Asia (including the North African specimen Tighenif 2, Indonesian and Chinese *H. erectus*), but is more asymmetrical than in recent modern humans. Previous analyses of crown geometric morphometrics place the Panxian Dadong premolars close to modern humans (Liu et al., 2013). Studies of the root structure show that, compared with modern humans, PA1578 has a robust morphology, although it is more gracile than the root complex usually found in *H. erectus* (Pan et al., 2019; Pan and Zanolli, 2019). On the other hand, the P₄ PA81 (Fig. 2N) from Changyang exhibits a wrinkled occlusal basin, with vertical ridges expressed on the buccal aspect of the EDJ (similar to *H. erectus*; Fig. 2K–M). The talonid of PA81 is mesiodistally elongated with a minute hypoconid dentine horn (Fig. 2N). In sum, from the six premolar specimens dated to late Middle Pleistocene, despite a small sample size, greater morphological variability (i.e., primitive, *H. erectus* like

and derived, modern-human like) is observed compared with East Asian *H. erectus*.

3.2. Geometric morphometric analyses

The results of GM analyses using DSM are shown in Figures 3–4 (see also SOM Fig. S4, which illustrates the output surfaces after DSM analyses). Taking into account that some authors have issued cautions about the interpretation of bgPCA results (Bookstein, 2019; Cardini et al., 2019), we present in Figures 3 and 4 the results from both PCA and bgPCA. Results of CV-bgPCA are illustrated in the SOM Figure S5, showing that the groups are separated in a similar way than in the bgPCA (even if inversion of the distribution of points between the negative and positive space along the axes may occur) and that group separation is not spurious. A mild allometric signal is observed along some of the (bg)PCs (SOM Table S1). While size-related component is present, the variation observed in the PCA and bgPCA thus mostly represents shape differences.

PCA and bgPCA yielded consistent results with *H. erectus*, Neanderthals and modern humans roughly distributed in a similar way along the first two axes, even if as expected the bgPCA better separates them (Figs. 3 and 4). In any case, even if slightly more overlapping, the groups identified when observing the morphospace obtained with bgPCA are already present in the PCA. The extreme shape changes along each (bg)PC are shown at the extremities of each axis. Even if comparative late Early to mid-Middle Pleistocene, Late Pleistocene and Holocene *Homo* groups are closer in the PCA

336 of P⁴ (Fig. 3C), *H. erectus* (including the North African specimen Tighenif 2,
 337 Indonesian and Chinese *H. erectus*) is discriminated from later groups along (bg)PC1
 338 (Figs. 3 and 4). (bg)PC1 reflects a chronoevolutionary trend, with lower EDJ in *H.*
 339 *erectus* than in the two other groups, as shown by the extreme shapes at the end of the
 340 axes (Figs 3 and 4; see also Figs. 1 and 2). For P³ and P⁴, *H. erectus* shows a narrower
 341 occlusal basin (buccolingually compressed and small with respect to the crown base)
 342 and more internally-positioned dentine horns than in Neanderthals and modern humans
 343 (Fig. 3 A–D). As seen in the bgPCA, Neanderthal upper premolars differs from those
 344 of modern humans by their mesiodistally wider EDJ and deeper occlusal basin (Fig. 3B,
 345 D). For the P₃ EDJ, as seen along (bg)PC1, *H. erectus* exhibits a proportionally more
 346 expanded talonid (resulting in a protruding distolingual angle of the crown) than in
 347 Neanderthals and modern humans that show more equally developed mesial and distal
 348 foveae. Along bgPC2, Neanderthal P₃ are separated from those of modern humans due
 349 to their smaller occlusal basin (Fig. 4A–B). PC1 and bgPC1 of the P₄ EDJ analyses
 350 show that *H. erectus* has low lateral aspects and short dentine horns, with a more
 351 buccolingually compressed occlusal basin (and more internally-set metaconid) than in
 352 Neanderthals and modern humans (Fig. 4 C, D). bgPC2 discriminates Neanderthals
 353 from modern humans, the latter having a lingually-positioned metaconid and
 354 buccolingually expanded occlusal basin and more equally developed mesial and distal
 355 foveae than in the former (Fig. D). In this context, the Changyang specimens (PA76 P³
 356 and PA81 P₄) and the P⁴ from Chaoxian unambiguously fall close to the late Early

Pleistocene to mid-Middle Pleistocene human groups, showing low EDJ, large crown base and complex surface relief with relatively small occlusal basin—as supported by previous observations on the EDJ surfaces (Figs. 1D, O and 2N). Conversely, the P³ PA873 from Tongzi, P³ PA1577 and P₃ PA1578 from Panxian Dadong are placed within or very close to the variability of Neanderthals and modern humans (Figs. 3A, B and 4A, B).

Results of the cross-validation tests performed on the bgPC scores shows that predictive accuracy is robust (Table 2). Correct classification of 88–100% is obtained in most analyses, except for the P⁴ analysis, which exhibits slightly more confusion for Neanderthals and modern humans (80% of correct classification; but *H. erectus* teeth show 100% discrimination). The P³ PA76, the P⁴ Chaoxian and the P₄ PA81 are classified as *H. erectus*. The P³ PA873 and the P₃ PA1578 are both classified nearly equally as belonging to either modern humans or Neanderthals, while the P³ PA1577 is classified as a Neanderthal.

4. Discussion

Increasing evidence from the morphological study of fossil hominins from China suggests remarkable morphological variability toward the end of the Middle Pleistocene (Bailey and Liu, 2010; Liu et al., 2013, 2017; Xing et al., 2014; Chang et al., 2015; Martínón-Torres et al., 2018). Similarly, recent advances in the fields of paleoproteomics and paleogenetics confirm the diversity of hominin groups that

coexisted in this chronogeographic interval, including a sister group of Neanderthals: the Denisovans (Chen et al., 2019). However, taxonomic attributions of late Middle to early Late Pleistocene specimens and their interpretation in an evolutionary perspective remain unclear (Bae, 2010; Liu et al., 2013; Kaifu, 2017). For the first time, through a novel geometric morphometric approach we analyzed the EDJ shape of a sample of hominin premolars from China spanning the Middle Pleistocene and compared this sample with other fossil and recent human groups.

At a large scale, our study reported at least two morphotypes in EDJ shape expressed in this time period: one displaying a *H. erectus*-like condition and the other showing a morphology that is closer to Late Pleistocene humans, sharing traits with both Neanderthals and modern humans. Irrespective of the taxon, in this timeframe, we also document a general trend towards a reduction of the crown base in relation to the occlusal basin, narrowing of the lingual aspect, and increasing of EDJ relief.

From the late Early to mid-Middle Pleistocene, we found a proportionally broadened crown base associated with a smaller occlusal basin and low EDJ relief in hominin premolars from Indonesia (Sangiran), Algeria (Tighenif) and China (Zhoukoudian, Hexian, Xichuan and Yiyuan). This is also compatible with previous studies suggesting a possible retention of Early Pleistocene hominin features (as seen in Sangiran 4 for example) in Chinese Middle Pleistocene *H. erectus* (Xing et al., 2014, 2016; Liu et al., 2017; Zanolli et al., 2018). Thus, until the mid-Middle Pleistocene, only one human group, likely related to *H. erectus* can be identified in China from the

available evidence. Toward the late Middle Pleistocene, the Chinese fossils express at least two morphotypes. The first one is characterized by large crown base, centrally-positioned dentine horn tips and low EDJ topography, together with a set of crown-complexifying non-metric traits as seen in the specimens from Changyang (PA76 and 81) and Chaoxian. It is noteworthy that the Chaoxian P⁴ expresses *H. erectus*-like features at the EDJ level that are in agreement with precious observations made on the outer crown morphology (Bailey and Liu, 2010). In light of these results, together with the similarities in EDJ shape of these specimens with *H. erectus* (Figs. 1 and 2), we interpret the Changyang and Chaoxian hominins as a late representative of an East Asian *H. erectus* lineage.

The second morphotype, represented by the fossils from Panxian Dadong and Tongzi, is characterized by a series of derived features generally found in Late Pleistocene hominins, like Neanderthals and modern humans, as already suggested by previous studies of the external tooth morphology (Liu et al., 2013; Pan et al., 2019; Pan and Zanolli, 2019). The EDJ shape of PA873 and PA1578, even if intermediate between the Neanderthal and modern human conditions, tends to show more affinities with the Neanderthal general pattern. Even if there is no evidence for such an early onset of dispersion into Asia, the recent finding from Misliya in Israel (Hershkovitz et al., 2018) indicates that we cannot rule out the possibility that they may represent a biogeographical variation of early modern humans in China. It is also possible that these non-*H. erectus* *Homo* may sample a distinct lineage, possibly Denisovans. In fact,

predictions from paleogenetics that Denisovans were a group of Neanderthal-like humans that lived from the Altai to East and South Asia (Meyer et al., 2012, 2016; Jacobs et al., 2019; Mondal et al., 2019), were recently reaffirmed by the combined morphological and molecular analyses of a mandible fragment from Xiahe, on the Tibetan Plateau (Chen et al., 2019). As archaic Denisovans probably occupied a broad geographical range, admixture between Denisovans and early modern humans probably occurred not only in Siberia and Southeast Asia but also in Southern China (Reich et al., 2011; Cooper and Stringer, 2013). Even if no Denisovan premolar is known yet, given the current evidence, it is possible that the Panxian Dadong and Tongzi hominins could belong to this taxon, as it was also proposed for other late Middle Pleistocene specimens from Asia, like the human remains from Xujiayao (Xing et al., 2015, Chen et al., 2019) and Penghu (Chang et al., 2015). Another possibility is that these specimens sample representative from both Denisovans and Pleistocene modern humans.

5. Conclusions

The present study suggests the existence of time-related evolutionary changes in the premolar EDJ morphology in a number of Early and Middle Pleistocene hominin groups, with special reference to mid- and late Middle Pleistocene populations in China. A general trend towards a reduction of crown base in relation to occlusal aspects, narrowed lingual aspects, heightened EDJ relief and a surface simplification is found

through time. The current analysis expands our knowledge on the dental inner morphology of Middle Pleistocene hominins, supports the coexistence of archaic (*Homo erectus*-like) and derived (Late Pleistocene *Homo*-like) dental morphological patterns and, through a dental perspective, suggest the preservation of plesiomorphic, *H. erectus*-like morphology during the Middle Pleistocene. New fossil discoveries and/or molecular analyses will be critical to explore further the past diversity and to shed light on the dispersal and interaction of hominin populations in East Asia.

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Table 1

Composition of the study specimens from China and of the comparative samples.

Chinese Pleistocene specimens	P ³	P ⁴	P ₃	P ₄	Provenance	Chronological range ^a	Citations ^b
Middle Pleistocene <i>Homo erectus</i> from China (HEC)							
PA67	1				Zhoukoudian Loc. 1 (Layer 11)	800–770 (A)	1–3
PA68		1			Zhoukoudian Loc. 1 (Layer 11)	800–770 (A)	1–3
PMU M3549			1		Zhoukoudian Loc. 1 (Layer 5)	550–500 Ka (B)	2, 4
PMU M3887				1	Zhoukoudian Loc. 1 (Layer 5)	550–500 Ka (B)	2, 4
PA110 ^c			1		Zhoukoudian Loc. 1 (Layer 3)	320–282 ka (C, D); 500 ka (E)	1–3
PA832 ^c	1				Hexian	437–387 ka (B)	5, 6
Shy071 ^c		1			Yiyuan	420–320 ka (F)	7–9
PA524 ^c	1				Xichuan	Unknown	10
PA525 ^c				1	Xichuan	Unknown	10
PA526 ^c			1		Xichuan	Unknown	10
PA527 ^c			1		Xichuan	Unknown	10
PA528				1	Xichuan	Unknown	10

Late Middle Pleistocene <i>Homo</i> sp. from China (HSPC)									
PA76 ^c	1				Changyang	196–194 ka (A)			11
PA81 ^c				1	Changyang	196–194 ka (A)			11
PA873 ^c	1				Tongzi	192–172 ka (A); 240 ka (G)			12
PA1577	1				Panxian Dadong	182–160 ka (H)			13
PA1578 ^c				1	Panxian Dadong	296–233 ka (H)			13
Chaoxian	1				Chaoxian	200–160 ka (I)			14
						360–310 ka (J)			
Comparative samples									
Early Pleistocene <i>H. erectus</i> from Java (HEJ)									
Sangiran 4	2	2			Sangiran (Pucangan Fm).	1.8–1.6 Ma (K)			4
Sangiran 7-3a				1	Sangiran (Pucangan Fm).	~1.3 Ma (L)			15
Early Pleistocene <i>Homo</i> from North Africa (HNA)									
Tighenif 2				1	Tighenif	~1.0 Ma (M)			16
Neanderthals (NEA)	5	4	4	4	Krapina (Level 8)	140–120 ka (N)			17, 18

	1	2	1	La Chaise-de-Vouthon (Abri Bourgeois-Delaunay)	146–106 ka (O)	18, 19
Recent modern humans (RMH)	10	6	11	8	Asia/ Europe/South Africa	20

^a Age references: A = Yuan et al. (1986); B = Grün et al. (1998); C = Grün et al. (1997); D = Huang et al. (1993); E = Shen et al. (2001); F = Han et al. (2016); G = Shen and Jin (1991); H = Karkanas et al. (2008); I = Chen et al. (1987); J = Shen et al. (2010); K = Huffman (2001); L = Matsu'ura et al. (2020); M = Sahnouni and Van der Made (2009); N = Rink et al. (1995); O = Macchiarelli et al. (2006).

^b Citations reporting descriptions of the morphology of the specimens : 1 = Xing (2012); 2 = Xing et al. (2018); 3 = Black et al. (1933); 4 = Zanolli et al. (2018a); 5 = Xing et al. (2014); 6= Liu et al. (2017); 7 = Chen et al. (1987); 8= Wu and Wu (1982); 9 = Xing et al. (2016); 10 = Wu and Wu (1982); 11 = Chia (1957); 12 = Xing et al. (2019); 13 =Liu et al. (2013); 14 = Bailey and Liu (2010); 15 = Grine (1994); 16 = Zanolli and Mazurier (2013); 17 = Radovčić et al. (1988); 18 = NESPOS database (2020); 19 = Macchiarelli et al. (2006); 20 = Pan et al. (2017).

^c Worn crown, reconstructed dentine horn tips. For the reconstruction see SOM Figure S1.

1 **Table 2**

2 Results of the cross-validation analyses performed on the between-group principal component scores.
 3 The posterior probabilities that the Chinese specimens are closer to any group were then calculated. The
 4 highest probabilities are indicated in bold (the greater the number, the higher the probability).

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Dental position	Specimen	Predictive accuracy of comparative specimens	Classification of the investigated Chinese fossils
P ³	PA76	HE: 100%; NEA: 100%, MHS: 100%	HE: 0.061 ; NEA: <0.001; MHS <0.001
	PA873	HE: 100%; NEA: 100%, MHS: 100%	HE: <0.001; NEA: 0.001 ; MHS: 0.002
	PA1577	HE: 100%; NEA: 100%, MHS: 100%	HE: <0.01; NEA: 0.104 ; MHS: <0.001
P ⁴	Chaoxian	HE: 100%; NEA: 80%, MHS: 80%	HE: 0.334 ; NEA: 0.001; MHS: <0.001
P ₃	PA1578	HE: 100%; NEA: 100%, MHS: 91%	HE: <0.001; NEA: 0.004 ; MHS: 0.026
P ₄	PA81	HE: 100%; NEA: 100%, MHS: 88%	HE: 0.808 ; NEA: <0.001; MHS: <0.001

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14 Abbreviations: HE = *Homo erectus* from Asia and late Early Pleistocene *Homo* from North Africa; NEA
 15 = Neanderthals; MHS = modern *Homo sapiens*.

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Figure captions

Figure 1. Volume rendering of upper premolar EDJ of *Homo erectus* from China (HEC), late Middle Pleistocene *Homo* sp. from China (HSPC), Javanese *H. erectus* (HEJ), Neanderthals (NEA) and modern *Homo sapiens* (MHS). Occlusal view (right) and mesial view (left), with dentine horn tips restored. The 3D models of left teeth (marked by an asterisk) were mirrored to the right side for comparison. Abbreviations: b = buccal; l = lingual; m = mesial.

Figure 2. Volume rendering of lower premolar EDJ of *Homo erectus* from China (HEC), late Middle Pleistocene *Homo* sp. from China (HSPC), late Early Pleistocene *Homo* from North Africa (HNA), Neanderthals (NEA) and modern *Homo sapiens* (MHS). Occlusal view (right) and mesial view (left), with dentine horn tips restored. The 3D models of left teeth (marked by an asterisk) were mirrored to the right side for comparison. Abbreviations: b = buccal; l = lingual; m = mesial.

Figure 3. Principal component analysis (PCA) and between-group principal component analysis (bgPCA) of the P³ (A, B) and P⁴ (C, D) enamel-dentine junction (EDJ) morphology using diffeomorphism surface matching (DSM) approach. The extreme shapes are illustrated in occlusal and mesial views at the end of each axis. Abbreviations: HEC = *Homo erectus* from China; HEJ = Javanese *H. erectus*; NEA = Neanderthals;

38 MHS = modern *Homo sapiens*.

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40 **Figure 4.** Principal component analysis (PCA) and between-group principal component
41 analysis (bgPCA) of the P₃ (A, B) and P₄ (C, D) enamel-dentine junction (EDJ)
42 morphology using diffeomorphism surface matching (DSM) approach. The extreme
43 shapes are illustrated in occlusal and mesial views at the end of each axis. Abbreviations:
44 HEC = *Homo erectus* from China; HNA = late Early Pleistocene *Homo* from North
45 Africa; NEA = Neanderthals; MHS = modern *Homo sapiens*.