



# Hominin diversity in East Asia during the Middle Pleistocene: A premolar endostructural perspective 1 2

Lei Pan, Jean Dumoncel, Arnaud Mazurier, Clément Zanolli

## ► To cite this version:

Lei Pan, Jean Dumoncel, Arnaud Mazurier, Clément Zanolli. Hominin diversity in East Asia during the Middle Pleistocene: A premolar endostructural perspective 1 2. *Journal of Human Evolution*, 2020, 148, pp.102888. 10.1016/j.jhevol.2020.102888 . hal-03002831

**HAL Id: hal-03002831**

**<https://hal.science/hal-03002831>**

Submitted on 12 Nov 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Lei Pan <sup>a, b, 1</sup>, Jean Dumoncel <sup>c</sup>, Arnaud Mazurier <sup>d</sup>, Clément Zanolli <sup>e, \*</sup>

<sup>a</sup> *Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, CAS, Beijing, China*

<sup>b</sup> *State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China*

<sup>c</sup> *Laboratoire AMIS, UMR 5288 CNRS, Université Toulouse III - Paul Sabatier, France*

<sup>d</sup> *Institut de Chimie des Milieux et Matériaux, UMR 7285 CNRS, Université de Poitiers, 86073 Poitiers, France*

<sup>e</sup> *Laboratoire PACEA, UMR 5199 CNRS, Université de Bordeaux, France*

\* Corresponding author.

E-mail address: [clement.zanolli@gmail.com](mailto:clement.zanolli@gmail.com) (C. Zanolli).

<sup>1</sup> Deceased May 2020

## 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  $\mu$ 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  $\mu$ 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)

190 used to perform the statistical analyses to explore the EDJ shape variation. An example  
191 of the original EDJ surface, the simplified EDJ surface imported in Deformetrica v. 4.3  
192 and the output virtual models generated by DSM process is shown in SOM Figure S3  
193 (see also SOM Fig. S4 for the output surfaces of all the Chinese fossil specimens after  
194 deformations). Using the packages ade4 1.7-13 (Dray and Dufour, 2007) and Morpho  
195 v. 2.6 (Schlager et al., 2018) for R v. 3.5.1 (R Development Core Team, 2012), we  
196 checked the shape variation of the fossil and recent human groups in a principal  
197 component analysis (PCA). Even if the first two components of the PCA account for  
198 approximately 40 to 65% of the total variance in these analyses, there is still some  
199 information in the following components. However, visualizing and interpreting a  
200 complex space in multiple dimensions is difficult. We computed between-group  
201 principal component analyses (bgPCA) to evaluate the degree of shape variation  
202 between hominin groups. We used both PCA and bgPCA as the former is mostly a  
203 means to explore the morphospace, with the variance spread over multiple axes,  
204 whereas bgPCA, through projection of the data onto the principal components of the  
205 group averages, represents a viable alternative to discriminant analyses (Mitteroecker  
206 and Bookstein, 2011). Nonetheless, when sample size is small and groups are few, the  
207 results of bgPCA must be interpreted with care and a number of tests are needed to  
208 confirm that group separation is not spurious (Bookstein, 2019; Cardini et al., 2019).  
209 As a result, we checked and confirmed that group separation preexisted in the PCA and  
210 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 (P<sup>3</sup>, 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 (P<sup>3</sup>, 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 (P<sup>4</sup>, Chaoxian) See Figure 1O. This P<sup>4</sup> is attached to a  
239 maxilla, whose right P<sup>3</sup>–M<sup>1</sup> and left P<sup>4</sup>–M<sup>2</sup> are preserved (Bailey and Liu, 2010). The  
240 occlusal basin of this P<sup>4</sup> 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 P<sup>4</sup> 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 (P<sub>3</sub>, 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 (P<sub>3</sub>, 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 (P<sub>4</sub>, 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 (P<sub>4</sub>, 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 (P<sub>4</sub>, 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 P<sup>3</sup> PA76 (Fig. 1D) from Changyang retains archaic traits, as it exhibits multiple accessory crests running in the occlusal basin. In comparison with PA76, the P<sup>3</sup> 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 P<sup>3</sup> PA1577 (Fig. 1F) from Panxian Dadong. The P<sup>4</sup> 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 P<sub>3</sub> 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 P<sub>4</sub> 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 P<sup>4</sup> (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 P<sup>3</sup> and P<sup>4</sup>, *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 P<sub>3</sub> 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 P<sub>3</sub> are separated from those of modern humans due  
 349 to their smaller occlusal basin (Fig. 4A–B). PC1 and bgPC1 of the P<sub>4</sub> 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 P<sup>3</sup>  
 356 and PA81 P<sub>4</sub>) and the P<sup>4</sup> 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 P<sup>3</sup> PA873 from Tongzi, P<sup>3</sup> PA1577 and P<sub>3</sub> 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 P<sup>4</sup> analysis, which exhibits slightly more confusion for Neanderthals and modern humans (80% of correct classification; but *H. erectus* teeth show 100% discrimination). The P<sup>3</sup> PA76, the P<sup>4</sup> Chaoxian and the P<sub>4</sub> PA81 are classified as *H. erectus*. The P<sup>3</sup> PA873 and the P<sub>3</sub> PA1578 are both classified nearly equally as belonging to either modern humans or Neanderthals, while the P<sup>3</sup> 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 P<sup>4</sup> 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.

## Acknowledgements

This study is dedicated to the memory of our dear friend and coworker Pan Lei, who passed away while this paper was being peer-reviewed. For access to specimens, we sincerely thank C. Argot, O. Kullmer, E.N. L'Abbé, H. Lelièvre, W. Liu, A. Oettlé, F. Schrenk, C. Thèves, J.F. Tournepiche, S. Xing, and C.K. Sun. The Musée of Angoulême kindly granted access for study and scanning to the specimens from La Chaise Abri Bourgeois-Delaunay; for this, we are indebted to J.F. Tournepiche. These specimens were scanned by A. Mazurier and R Macchiarelli at the ESRF beamline ID 17 (Grenoble) in collaboration with A. Bravin, C. Nemoz and P. Tafforeau, and we thank them for sharing the microtomographic records. For technical assistance, we are indebted to F. Bernardini, F. de Beer, B. Duployer, J.W. Hoffman, and C. Tuniz. For scientific collaboration and discussion, we sincerely thank Y.M. Hou, M. Kúndrát, R. Macchiarelli, and S. Xing. We thank Y.X. Hao for his insightful comments

which helped us to improve the manuscript. We also acknowledge the Centre de Microtomographie at the Université de Poitiers, the European Synchrotron Radiation Facility (ESRF) beamline ID17 at Grenoble, the Neanderthal Studies Professional Online Service (NESPOS) Society and the Senckenberg Research Institute. This study granted access to the HPC resources of CALMIP supercomputing center under the allocation 2016-(P1440] attributed to the AMIS Laboratory, Toulouse. This work was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDA19050102 and XDB26000000), the National Natural Science Foundation of China (Grant No. 41702026 and 41872030), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS; grant number 173119) and The French Centre National de la Recherche Scientifique (CNRS). We thank the Editor (David Alba), the Associate Editor, and three anonymous reviewers for their comments, which helped to improve the paper.

## References

- Bae, C.J., 2010. The late Middle Pleistocene hominin fossil record of eastern Asia: synthesis and review. *American Journal of Physical Anthropology* 143(S51), 75–93.
- Bailey, S.E., Liu, W., 2010. A comparative dental metrical and morphological analysis of a Middle Pleistocene hominin maxilla from Chaoxian (Chaohu), China. *Quaternary International* 211, 14–23.
- Beaudet, A., Dumoncel, J., Thackeray, F., Bruxelles, L., Duployer, B., Tenailleau, C., Bam, L., Hoffman, J., de Beer, F., Braga, J., 2016a. Upper third molar internal structural organization and semicircular canal morphology in Plio-Pleistocene South



483 African cercopithecoids. *Journal of Human Evolution* 95, 104–120.

484 Beaudet, A., Dumoncel, J., De Beer, F., Duployer, B., Durrleman, S., Gilissen, E.,  
 485 Hoffman, J., Tenailleau, C., Thackeray, J.F., Braga, J., 2016b. Morphoarchitectural  
 486 variation in South African fossil cercopithecoid endocasts. *Journal of Human*  
 487 *Evolution* 101, 65–78.

488 Beaudet, A., Dumoncel, J., Beer, F., Durrleman, S., Gilissen, E., Oettlé, A., Subsol, G.,  
 489 Thackeray, J.F., Braga, J., 2018. The endocranial shape of *Australopithecus*  
 490 *africanus*: surface analysis of the endocasts of Sts 5 and Sts 60. *Journal of Anatomy*  
 491 232, 296–303.

492 Bermúdez de Castro, J.M., Martínón-Torres, M., 2013. A new model for the evolution  
 493 of the human Pleistocene populations of Europe. *Quaternary International* 295, 102–  
 494 112.

495 Black, D., de Chardin, P.T., Young, C.C., Pei, W.C., Hao, W.W., 1933. Fossil Man in  
 496 China. The Choukoutien cave deposits with a synopsis of our present knowledge of  
 497 the late Cenozoic of China. *The Geological Survey of China Series A* 11, 1–158.

498 Bookstein, F., 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*.  
 499 Cambridge University Press, Cambridge.

500 Bookstein, F.L., 2019. Pathologies of between-groups principal components analysis in  
 501 geometric morphometrics. *Evolutionary Biology* 46, 271–302.

502 Braga, J., Thackeray, J.F., Subsol, G., Kahn, J.L., Maret, D., Treil, J., Beck, A., 2010.  
 503 The enamel-dentine junction in the postcanine dentition of *Australopithecus*

504 *africanus*: intra-individual metameric and antimeric variation. Journal of Anatomy  
505 216, 62–79.

506 Braga, J., Zimmer, V., Dumoncel, J., Samir, C., de Beer, F., Zanolli, C., Pinto, D., Rohlf,  
507 F.J., Grine, F.E., 2019. Efficacy of diffeomorphic surface matching and 3D  
508 geometric morphometrics for taxonomic discrimination of Early Pleistocene  
509 hominin mandibular molars. Journal of Human Evolution 130, 21–35.

510 Cardini, A., O’Higgins, P., Rohlf, F.J., 2019. Seeing distinct groups where there are  
511 none: spurious patterns from between-group PCA. Evolutionary Biology 46, 303–  
512 316.

513 Cardini, A., Polly, P.D., 2020. Cross-validated between group PCA scatterplots: A  
514 solution to spurious group separation? Evolutionary Biology 47, 85-95.

515 Chang, C.-H., Kaifu, Y., Takai, M., Kono, R.T., Grün, R., Matsu’ura, S., Kinsley, L.,  
516 Lin, L.-K., 2015. The first archaic *Homo* from Taiwan. Nature Communications 6,  
517 6037.

518 Chen, F., Welker, F., Shen, C.-C., Bailey, S.E., Bergmann, I., Davis, S., Xia, H., Wang,  
519 H., Fischer, R., Freidline, S.E., 2019. A late Middle Pleistocene Denisovan mandible  
520 from the Tibetan Plateau. Nature 569, 409-412.

521 Chen, T., Yuan, S., Gao, S., Hu, Y., 1987. Uranium series dating of fossil bones from  
522 Hexian and Chaoxian fossil human sites. Acta Anthropologica Sinica 6, 249–254.  
523 (In Chinese with English abstract)

524 Chia, L., 1957. Notes on the human and some other mammalian remains from

525 Changyang, Hupei. *Vertabrata PalAsiatica* 1, 179–190.

526 Coleman, M.N., Colbert, M.W., 2007. CT thresholding protocols for taking  
527 measurements on three-dimensional models. *American Journal of Physical*  
528 *Anthropology* 133, 723–725.

529 Cooper, A., Stringer, C., 2013. Did the Denisovans cross Wallace's line? *Science* 342,  
530 321–323.

531 Corruccini, R., 1987. The dentinoenamel junction in primates. *International Journal of*  
532 *Primatology* 8, 99–114.

533 Durrleman, S., Pennec, X., Trouvé, A., Ayache, N., Braga, J., 2012a. Comparison of  
534 the endocranial ontogenies between chimpanzees and bonobos via temporal  
535 regression and spatiotemporal registration. *Journal of Human Evolution* 62, 74–88.

536 Durrleman, S., Prastawa, M., Korenberg, J.R., Joshi, S., Trouvé, A., Gerig, G., 2012b.  
537 Topology preserving atlas construction from shape data without correspondence  
538 using sparse parameters. In: Ayache, N., Delingette, H., Golland, P., Mori, K. (Eds.),  
539 *Proceedings of Medical image Computing and Computer Assisted Intervention*.  
540 Nice, France, pp. 223–230

541 Durrleman, S., Prastawa, M., Charon, N., Korenberg, J.R., Joshi, S., Gerig, G., Trouvé,  
542 A., 2014. Morphometry of anatomical shape complexes with dense deformations  
543 and sparse parameters. *NeuroImage* 101, 35–49.

544 Fajardo, R.J., Ryan, T., Kappelman, J., 2002. Assessing the accuracy of high-resolution  
545 X-ray computed tomography of primate trabecular bone by comparisons with

546 histological sections. *American Journal of Physical Anthropology* 118, 1–10.

547 Glaunes, J.A., Joshi, S., 2006. Template estimation from unlabeled point set data and  
548 surfaces for computational anatomy. In: Pennec, X., Joshi, S. (Eds.), 1st MICCAI  
549 Workshop on Mathematical Foundations of Computational Anatomy: Geometrical,  
550 Statistical and Registration Methods for Modeling Biological Shape Variability.  
551 Copenhagen, pp. 29–39

552 Grine, F., 1994. Fossil hominid teeth from the Sangiran Dome (Java, Indonesia).  
553 *Courier Forschungsinstitut Senckenberg* 171, 75–103.

554 Grün, R., Huang, P.-H., Wu, X., Stringer, C.B., Thorne, A.G., McCulloch, M., 1997.  
555 ESR analysis of teeth from the palaeoanthropological site of Zhoukoudian, China.  
556 *Journal of Human Evolution* 32, 83–91.

557 Grün, R., Huang, P.-H., Huang, W., McDermott, F., Thorne, A., Stringer, C.B., Yan, G.,  
558 1998. ESR and U-series analyses of teeth from the palaeoanthropological site of  
559 Hexian, Anhui Province, China. *Journal of Human Evolution* 34, 555–564.

560 Han, F., Sun, C., Bahain, J.-J., Zhao, J., Lin, M., Xing, S., Yin, G., 2016. Coupled ESR  
561 and U-series dating of fossil teeth from Yiyuan hominin site, northern China.  
562 *Quaternary International* 400, 195–201.

563 Hershkovitz, I., Weber, G.W., Quam, R., Duval, M., Grün, R., Kinsley, L., Ayalon, A.,  
564 Bar-Matthews, M., Valladas, H., Mercier, N., 2018. The earliest modern humans  
565 outside Africa. *Science* 359, 456–459.

566 Jacobs, Z., Li, B., Shunkov, M.V., Kozlikin, M.B., Bolikhovskaya, N.S., Agadjanian,

567 A.K., Uliyanov, V.A., Vasiliev, S.K., O’Gorman, K., Derevianko, A.P., 2019. Timing  
 568 of archaic hominin occupation of Denisova Cave in southern Siberia. *Nature* 565,  
 569 594–599.

570 Huang, P.-H., Jin, S.-Z., Peng, Z.-C., Liang, R.-Y., Lu, Z.-J., Wang, Z.-R., Chen, J.-B.,  
 571 Yuan, Z.-X., 1993. ESR dating of tooth enamel: comparison with U-Series, FT and  
 572 TL dating at the Peking Man Site. *Applied Radiation and Isotopes* 44, 239–242.

573 Huffman, O.F., 2001. Geologic context and age of the Perring/Mojokerto *Homo erectus*,  
 574 East Java. *Journal of Human Evolution* 40, 353–362.

575 Kaifu, Y., Baba, H., Aziz, F., Indriati, E., Schrenk, F., Jacob, T., 2005. Taxonomic  
 576 affinities and evolutionary history of the Early Pleistocene hominids of Java:  
 577 Dentognathic evidence. *American Journal of Physical Anthropology* 128, 709–726.

578 Kaifu, Y., 2017. Archaic hominin populations in Asia before the arrival of modern  
 579 humans: their phylogeny and implications for the “Southern Denisovans”. *Current*  
 580 *Anthropology* 58, S418–S433.

581 Karkanas, P., Schepartz, L.A., Miller-Antonio, S., Wang, W., Huang, W., 2008. Late  
 582 Middle Pleistocene climate in southwestern China: inferences from the stratigraphic  
 583 record of Panxian Dadong Cave, Guizhou. *Quaternary Science Reviews* 27, 1555–  
 584 1570.

585 Liu, W., Schepartz, L.A., Xing, S., Miller-Antonio, S., Wu, X., Trinkaus, E., Martínón-  
 586 Torres, M., 2013. Late Middle Pleistocene hominin teeth from Panxian Dadong,  
 587 South China. *Journal of Human Evolution* 64, 337–355.

588 Liu, W., Martínón-Torres, M., Cai, Y.-j., Xing, S., Tong, H.-w., Pei, S.-w., Sier, M.J.,  
 589 Wu, X.-h., Edwards, R.L., Cheng, H., 2015. The earliest unequivocally modern  
 590 humans in southern China. *Nature* 526, 696–670.

591 Liu, W., Martínón-Torres, M., Kaifu, Y., Wu, X., Kono, R., Chang, C.-H., Wei, P., Xing,  
 592 S., Huang, W., Bermúdez de Castro, J.M., 2017. A mandible from the Middle  
 593 Pleistocene Hexian site and its significance in relation to the variability of Asian  
 594 *Homo erectus*. *American Journal of Physical Anthropology* 162, 715–731.

595 Macchiarelli, R., Bondioli, L., Debénath, A., Mazurier, A., Tournepiche, J.-F., Birch,  
 596 W., Dean, C., 2006. How Neanderthal molar teeth grew. *Nature* 444, 748–751.

597 Macchiarelli, R., Bayle, P., Bondioli, L., Mazurier, A., Zanolli, C., 2013. From outer to  
 598 inner structural morphology in dental anthropology: integration of the third  
 599 dimension in the visualization and quantitative analysis of fossil remains, In: Scott,  
 600 G.R., Irish, J. (Eds.), *Anthropological Perspectives on Tooth Morphology: Genetics,*  
 601 *Evolution, Variation*. Cambridge University Press, Cambridge, pp. 250–277.

602 Martínón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Arsuaga, J.L.,  
 603 Carbonell, E., Lordkipanidze, D., Manzi, G., Margvelashvili, A., 2007. Dental  
 604 evidence on the hominin dispersals during the Pleistocene. *Proceedings of the*  
 605 *National Academy of Sciences USA* 104, 13279–13282.

606 Martínón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Margvelashvili,  
 607 A., Prado, L., Lordkipanidze, D., Vekua, A., 2008. Dental remains from Dmanisi  
 608 (Republic of Georgia): morphological analysis and comparative study. *Journal of*

609 Human Evolution 55, 249–273.

610 Martínón-Torres, M., Xing, S., Liu, W., Bermúdez de Castro, J.M., 2018. A “source and  
611 sink” model for East Asia? Preliminary approach through the dental evidence.  
612 Comptes Rendus Palevol 17, 33–43.

613 Matsu’ura, S., Kondo, M., Danhara, T., Sakata, S., Iwano, H., Hirata, T., Kurniawan, I.,  
614 Setiyabudi, E., Takeshita, Y., Hyodo, M., 2020. Age control of the first appearance  
615 datum for Javanese *Homo erectus* in the Sangiran area. Science 367, 210–214.

616 Meyer, M., Kircher, M., Gansauge, M.-T., Li, H., Racimo, F., Mallick, S., Schraiber,  
617 J.G., Jay, F., Prüfer, K., De Filippo, C., 2012. A high-coverage genome sequence  
618 from an archaic Denisovan individual. Science 338, 222–226.

619 Meyer, M., Arsuaga, J.-L., de Filippo, C., Nagel, S., Aximu-Petri, A., Nickel, B.,  
620 Martínez, I., Gracia, A., Bermúdez de Castro, J.M., Carbonell, E., 2016. Nuclear  
621 DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. Nature  
622 531, 504.

623 Mondal, M., Bertranpetit, J., Lao, O., 2019. Approximate Bayesian computation with  
624 deep learning supports a third archaic introgression in Asia and Oceania. Nature  
625 Communications 10, 246.

626 NESPOS database, 2020, NEanderthal Studies Professional Online Service.  
627 <https://www.nespos.org>.

628 Pan, L., Dumoncel, J., de Beer, F., Hoffman, J., Thackeray, J.F., Duployer, B.,  
629 Tenailleau, C., Braga, J., 2016. Further morphological evidence on South African

630 earliest *Homo* lower postcanine dentition: enamel thickness and enamel dentine  
631 junction. *Journal of Human Evolution* 96, 82–96.

632 Pan, L., Thackeray, J.F., Dumoncel, J., Zanolli, C., Oettlé, A., De Beer, F., Hoffman, J.,  
633 Duployer, B., Tenailleau, C., Braga, J., 2017. Intra-individual metamerism variation  
634 expressed at the enamel-dentine junction of lower post-canine dentition of South  
635 African fossil hominins and modern humans. *American Journal of Physical*  
636 *Anthropology* 163, 806–815.

637 Pan, L., Zanolli, C., 2019. Comparative observations on the premolar root and pulp  
638 canal configurations of Middle Pleistocene *Homo* in China. *American Journal of*  
639 *Physical Anthropology* 168, 637–646.

640 Pan, L., Dumoncel, J., Mazurier, A., Zanolli, C., 2019. Structural analysis of premolar  
641 roots in Middle Pleistocene hominins from China. *Journal of Human Evolution* 136,  
642 102669.

643 R Development Core Team, 2012. R: A language and environment for statistical  
644 computing. R Foundation for Statistical Computing, Vienna.

645 Radovčić, J., Smith, F.H., Trinkaus, E., Wolpoff, M.H., 1988. The Krapina Hominids:  
646 An Illustrated Catalog of Skeletal Collection. Mladost and the Croatian Natural  
647 History Museum, Zagreb.

648 Reich, D., Patterson, N., Kircher, M., Delfin, F., Nandineni, M.R., Pugach, I., Ko, A.M.-  
649 S., Ko, Y.-C., Jinam, T.A., Phipps, M.E., 2011. Denisova admixture and the first  
650 modern human dispersals into Southeast Asia and Oceania. *The American Journal*



651 of Human Genetics 89, 516–528.

652 Rink, W.J., Schwarcz, H.P., Smith, F.H., Radovčić, J., 1995. ESR dates for Krapina  
653 hominids. *Nature* 378, 24.

654 Sahnouni, M., Van der Made, J., 2009. The Oldowan in North Africa within a  
655 biochronological framework. In: Schick, K., Toth, N. (Eds.), *The Cutting Edge: New  
656 Approaches to the Archaeology of Human Origins*. Stone Age Institute Press,  
657 Bloomington, pp. 179–210.

658 Schlager, S., Profico, A., Di Vincenzo, F., Manzi, G., 2018. Retrodeformation of fossil  
659 specimens based on 3D bilateral semi-landmarks: Implementation in the R package  
660 “Morpho”. *PLoS One* 13, e0194073.

661 Scott, G.R., Turner, C.G., 1997. *The Anthropology of Modern Human Teeth: Dental  
662 Morphology and its Variation in Recent Human Populations*. Cambridge University  
663 Press, Cambridge.

664 Shen, G., Jin, L., 1991. U-series age of Yanhui Cave, the site of Tongzi Man. *Acta  
665 Anthropologica Sinica* 10, 65–72.

666 Shen, G., Fang, Y., Bischoff, J.L., Feng, Y.-x., Zhao, J.-x., 2010. Mass spectrometric U-  
667 series dating of the Chaoxian hominin site at Yinshan, eastern China. *Quaternary  
668 International* 211, 24–28.

669 Skinner, M.M., Wood, B.A., Boesch, C., Olejniczak, A.J., Rosas, A., Smith, T.M.,  
670 Hublin, J.-J., 2008a. Dental trait expression at the enamel-dentine junction of lower  
671 molars in extant and fossil hominoids. *Journal of Human Evolution* 54, 173–186.

672 Skinner, M.M., Gunz, P., Wood, B.A., Hublin, J.-J., 2008b. Enamel-dentine junction  
 673 (EDJ) morphology distinguishes the lower molars of *Australopithecus africanus* and  
 674 *Paranthropus robustus*. *Journal of Human Evolution* 55, 979–988.

675 Skinner, M.M., 2008. Enamel-dentine junction morphology of extant hominoid and  
 676 fossil hominin lower molars. Ph.D. Dissertation, George Washington University.

677 Smith, B.H., 1984. Patterns of molar wear in hunter–gatherers and agriculturalists.  
 678 *American Journal of Physical Anthropology* 63, 39–56.

679 Turner, C.G., Nichol, C.R., Scott, G.R., 1991. Scoring procedures for key  
 680 morphological traits of the permanent dentition: the Arizona State University dental  
 681 anthropology system, In: Kelley, M.A., Larsen, C.S. (Eds.), *Advances in Dental*  
 682 *Anthropology*. Wiley-Liss, New York, pp. 31–31.

683 Urciuoli, A., Zanolli, C., Beaudet, A., Dumoncel, J., Santos, F., Moyà-Solà, S., Alba,  
 684 D.M., 2020. The evolution of the vestibular apparatus in apes and humans. *eLife* 9,  
 685 e51261.

686 Weber, W.G., 2001. Virtual anthropology (VA): A call for *Glasnost* in  
 687 paleoanthropology. *The Anatomical Record* 265, 193–201.

688 Weber, G.W., 2015. Virtual anthropology. *American Journal of Physical Anthropology*  
 689 156, 22–42.

690 Weidenreich, F., 1937. The dentition of *Sinanthropus pekinensis*: a comparative  
 691 odontography of the hominids. *Palaeontologia Sinica D* 1, 1–180.

692 Wu, M.-L., 1984. New discoveries of human fossil in Tongzi, Guizhou. *Acta*

693 Anthropologica Sinica 3, 195–202.

694 Wu, X., Wu, R., 1982. Human fossil teeth from Xichuan, Henan. *Vertebrata Palasiatica*

695 20, 1–10. (In Chinese with English abstract)

696 Wu, X., Poirier, F.E., 1995. Human evolution in China: a metric description of the

697 fossils and a review of the sites. Oxford University Press, New York.

698 Xing, S., 2012. Morphological variation of Zhoukoudian *H. erectus* teeth. Ph.D.

699 Dissertation, Graduate University of Chinese Academy of Sciences.

700 Xing, S., Martín-Torres, M., Bermúdez de Castro, J.M., Zhang, Y., Fan, X., Zheng,

701 L., Huang, W., Liu, W., 2014. Middle Pleistocene hominin teeth from Longtan Cave,

702 Hexian, China. *PLoS One* 9, e114265.

703 Xing, S., Martín-Torres, M., Bermúdez de Castro, J.M., Wu, X., Liu, W., 2015.

704 Hominin teeth from the early Late Pleistocene site of Xujiayao, Northern China.

705 *American Journal of Physical Anthropology* 156, 224–240.

706 Xing, S., Sun, C., Martín-Torres, M., Bermúdez de Castro, J.M., Han, F., Zhang, Y.,

707 Liu, W., 2016. Hominin teeth from the Middle Pleistocene site of Yiyuan, Eastern

708 China. *Journal of Human Evolution* 95, 33–54.

709 Xing, S., Martín-Torres, M., Bermúdez de Castro, J.M., 2018. The fossil teeth of the

710 Peking Man. *Scientific Reports* 8, 2066.

711 Xing, S., Martín-Torres, M., Bermúdez de Castro, J.M., 2019. Late Middle

712 Pleistocene hominin teeth from Tongzi, southern China. *Journal of Human*

713 *Evolution* 130, 96–108.

714 Yuan, S., Chen, T., Gao, S., 1986. Uranium series chronological sequence of some  
 715 palaeolithic sites in South China. *Acta Anthropologica Sinica* 2, 179–190. (In  
 716 Chinese with English abstract)  
 717 Zanolli, C., Bondioli, L., Mancini, L., Mazurier, A., Widiyanto, H., Macchiarelli, R.,  
 718 2012. Brief communication: Two human fossil deciduous molars from the Sangiran  
 719 Dome (Java, Indonesia): Outer and inner morphology. *American Journal of Physical*  
 720 *Anthropology* 147, 472–481.  
 721 Zanolli, C., Mazurier, A., 2013. Endostructural characterization of the *H.*  
 722 *heidelbergensis* dental remains from the early Middle Pleistocene site of Tighenif,  
 723 Algeria. *Comptes Rendus Palevol* 12, 293–304.  
 724 Zanolli, C., 2013. Additional evidence for morpho-dimensional tooth crown variation  
 725 in a New Indonesian *H. erectus* sample from the Sangiran Dome (Central Java).  
 726 *PLoS One* 8, e67233.  
 727 Zanolli, C., Pan, L., Dumoncel, J., Kullmer, O., Kúndrát, M., Liu, W., Macchiarelli, R.,  
 728 Mancini, L., Schrenk, F., Tuniz, C., 2018. Inner tooth morphology of *Homo erectus*  
 729 from Zhoukoudian. New evidence from an old collection housed at Uppsala  
 730 University, Sweden. *Journal of Human Evolution* 116, 1–13.  
 731 Zanolli, C., Kullmer, O., Kelley, J., Bacon, A.-M., Demeter, F., Dumoncel, J., Fiorenza,  
 732 L., Grine, F.E., Hublin, J.-J., Tuan, N., Nguyen Thi, M.H., Pan, L., Schillinger, B.,  
 733 Schrenk, F., Skinner, M.M., Xueping, J., Macchiarelli, R., 2019. Evidence for  
 734 increased hominid diversity in the Early-Middle Pleistocene of Java, Indonesia.

735 Nature Ecology and Evolution 3, 755–764.

**Table 1**

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

Chinese Pleistocene specimens	P <sup>3</sup>	P <sup>4</sup>	P <sub>3</sub>	P <sub>4</sub>	Provenance	Chronological range <sup>a</sup>	Citations <sup>b</sup>
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 <sup>c</sup>			1		Zhoukoudian Loc. 1 (Layer 3)	320–282 ka (C, D); 500 ka (E)	1–3
PA832 <sup>c</sup>	1				Hexian	437–387 ka (B)	5, 6
Shy071 <sup>c</sup>		1			Yiyuan	420–320 ka (F)	7–9
PA524 <sup>c</sup>	1				Xichuan	Unknown	10
PA525 <sup>c</sup>				1	Xichuan	Unknown	10
PA526 <sup>c</sup>			1		Xichuan	Unknown	10
PA527 <sup>c</sup>			1		Xichuan	Unknown	10
PA528				1	Xichuan	Unknown	10

Late Middle Pleistocene <i>Homo</i> sp. from China (HSPC)									
PA76 <sup>c</sup>	1				Changyang	196–194 ka (A)			11
PA81 <sup>c</sup>				1	Changyang	196–194 ka (A)			11
PA873 <sup>c</sup>	1				Tongzi	192–172 ka (A); 240 ka (G)			12
PA1577	1				Panxian Dadong	182–160 ka (H)			13
PA1578 <sup>c</sup>				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

---

<sup>a</sup> 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).

<sup>b</sup> 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).

<sup>c</sup> 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).

5

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

6

7

8

9

10

11

12

13

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

16

## 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 P<sup>3</sup> (A, B) and P<sup>4</sup> (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*.

39

40 **Figure 4.** Principal component analysis (PCA) and between-group principal component  
41 analysis (bgPCA) of the P<sub>3</sub> (A, B) and P<sub>4</sub> (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*.







