

BRIEF COMMUNICATION

Comparative observations on the premolar root and pulp canal configurations of Middle Pleistocene *Homo* in China

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Abstract

Objectives: The aim of this study is to explore the root and root canal morphology of *Homo* fossil occupying China during the Middle Pleistocene period. Human occupation and evolutionary dynamics in East Asia during the Middle Pleistocene period is one of the most intriguing issues in paleoanthropology, with the coexistence of multiple lineages and regional morphs suggesting a complex population interaction scenario. Although premolar root and canal morphology has certain phylogenetic, taxonomic, and functional implications, its morphological diversity, possible evolutionary trend and characteristics regarding Middle Pleistocene hominins inhabiting East Asia are still insufficiently understood; where these populations fits within the *Homo* lineage (with respect to root and pulp canal structure) needs to be explored.

Materials and methods: Using microtomography, we directly observed and assessed the non-metric variability of root and canal forms in maxillary and mandibular premolars of Chinese Middle Pleistocene *Homo* ($N = 19$), and compared our observed variations with Eurasian Early Pleistocene specimens from the Asia continent ($N = 1$) and Java ($N = 2$), as well as with Neanderthals ($N = 28$) and recent modern humans ($N = 67$).

Results: A total number of nine types of root-canal forms were recorded. As a whole, the Chinese Middle Pleistocene record shows an evolutionary trend toward a modern human-like condition (a reduction of root/canal number and a simplification of root surface structure). We documented primitive signals like high percentage of Tomes' root in lower premolars. A considerable occurrence of incompletely separated root branches and bifid root and canal apices, representing evolutionary transformation from multi-root to single-root condition was also noticed. The results were compared with previous publications on Early and Middle Pleistocene *Homo* in East Africa, North Africa, and Eurasia.

Conclusion: This work provides new original data, incorporates the latest human fossil discoveries and suggests that analyzing the variation of premolar root structural organization, notably integrating together root/canal form and number, could possibly contribute to taxonomic and phylogenetic assessments. The mid-Middle Pleistocene populations, or "classic" *Homo erectus*, in our study show closer affinity to Early and Middle Pleistocene hominins in Eurasia, than to East African early *Homo*, which supports the suggestion that at least some of the Early Pleistocene hominin groups in Eurasia contribute to the later population; on the other hand, it is still difficult to clearly trace the evolutionary fate of those late Middle Pleistocene populations (roughly assigned as archaic *Homo sapiens* through a craniodental perspective). More comparable materials from the Early to Middle Pleistocene period as well as precise chronological framework is needed to further explore the evolutionary trends of archaic hominins in the Asian continent before the arrival of modern humans.

KEYWORDS

Asian fossil *Homo*, canal morphology, micro-tomography, premolar, root morphology

1 | INTRODUCTION

Recent discoveries revealed different evolutionary lineages and a considerable degree of isolation among regional populations in Middle Pleistocene Asia (rev. in Kaifu, 2017). Marked differences were reported for the internal tooth crown morphology of Chinese and Indonesian Middle Pleistocene humans, possibly suggesting that distinct groups may have populated continental and (pen)insular Asia (Liu et al., 2017; Liu, Clarke, & Xing, 2010; Liu, Xing, & Wu, 2016; Xing, 2012; Xing et al., 2016). In particular, complex occlusal crown surface and enamel–dentine junction morphology (represented by additive traits like interconnected ridges, bifurcated essential crests, and accessory ridges and cusps) is found in the Chinese dental assemblages across the Middle Pleistocene, including the earliest specimens from Zhoukoudian (Xing, Martínón-Torres, & Bermúdez de Castro, 2018), the mid-Middle Pleistocene teeth from Chaoxian, Hexian, and Yiyuan (Bailey & Liu, 2010; Liu et al., 2017; Xing et al., 2014, 2016), and the late Middle to early Late Pleistocene material from Panxian Dadong and Xujiayao (Liu et al., 2013, 2016; Xing et al., 2015). These findings revealed characteristic patterns for the populations that inhabited East Asia during the Middle Pleistocene period, like highly crenulated enamel–dentine junction (EDJ) and its imprint on the roof of the pulp cavity (Xing et al., 2016, 2018), and highlighted a combination of primitive and derived features that cannot be organized along a temporal scale (Liu et al., 2017). Based on dental evidence, those early- and mid-Middle Pleistocene specimens are aligned to the “classic” *Homo erectus* hypodigm and it is proposed that Early Pleistocene hominins in Eurasia contributed to at least some of the later *H. erectus* lineages, and that these populations experienced relatively independent evolutionary courses compared with *H. erectus* in the African continent (Kaifu, 2017; Kaifu et al., 2005; Martínón-Torres et al., 2007, 2008). On the other hand, craniodental evidence is still insufficient to resolve the taxonomic and phylogenetic identity of late Middle Pleistocene hominins and how they relate to modern *Homo sapiens*. Except for a retention of primitive traits, like large and robust roots, and a trend toward root number reduction (Liu et al., 2013, 2017; Xing et al., 2014, 2018), the morphological diversity and phylogenetic implications of the root–canal structure of these hominin populations are still unclear; comparative study is needed to fully reveal the root and canal structure for the Chinese materials from this period.

The variability of form, number and position of fossil hominin and extant human premolar roots and/or pulp canals has been described in previous research as reflecting functional/biomechanical demand, developmental aspects, sexual dimorphism, and taxonomy (Abbott, 1984; Kottoor, Albuquerque, Velmurugan, & Kuruvilla, 2013; Kupczik & Dean, 2008; Kupczik, Spoor, Pommert, & Dean, 2005; Moore, Hublin, & Skinner, 2015; Moore, Skinner, & Hublin, 2013; Moore, Thackeray, Hublin, & Skinner, 2016; Spencer, 2003; Wood & Engleman, 1988). Root morphology and pulp canal form, number, and size are the result of variations in the development of Hertwig’s epithelial root sheath that determines the location, number and expression of inter-radicular processes (Kovacs, 1967, 1971; Shields, 2005; Moore et al., 2013). Hominid root complexity (single vs. multiple roots) and length are generally interpreted to play a role in the dispersion of occlusal loading during

mastication and paramasticatory activities, but root number alone does not reflect a functional adaptation related to area of root attachment (Kupczik et al., 2005). Root and canal configurations are also associated with complex genetic, and epigenetic mechanisms as well as environmental influences (Brook, 2009; Shields, 2005; Tobias, 1995). But tooth root structural organization also holds critical taxonomic information and represents a phylogenetic indicator for distinguishing closely related extinct hominid species (Moore et al., 2013, 2016).

Within the *Pan*-modern human lineage, while variations exist, the plesiomorphic great-ape pattern is represented by (a) three-rooted maxillary premolars with three canals, arranged as two buccal and one lingual root, and (b) double-rooted mandibular premolars with three (P_3) or four (P_4) canals (Abbott, 1984). In contrast, modern humans show a series of apomorphic condition: modern human upper premolars are usually single-rooted (Abbott, 1984; Peiris, 2008; Wood & Engleman, 1988), but in certain populations, predominant double-rooted P_3 s have been recorded (Shaw, 1931), and sub-Saharan populations even show a wider range of variability (Shields, 2005). Regarding lower premolars, the modern human condition is a single root, although variations such as Tomes’ root have been reported (see Loh, 1998; Peiris, 2008; Sert & Bayirli, 2004; Shields, 2005; Tomes, 1923). Among fossil taxa, elaborated or “molariform” lower premolar roots (each plate-like and contains two canals) are seen in *Australopithecus* and *Paranthropus* (Moggi-Cecchi, Menter, Boccone, & Keyser, 2010; Moore et al., 2016; White, Suwa, Simpson, & Asfaw, 2000; Wood, Abbott, & Uytterschaut, 1988). Regarding *Homo*, an apomorphic condition with respect to australopiths and a trend towards the reduction in root radicle and pulp canal number is expressed. Although double-rooted premolars exist, the East African *Homo* exhibits predominantly single or Tomes’ root conditions, whereas primitive double-rooted lower premolars can be observed in some other members of Early Pleistocene *H. erectus* s.l. from Dmanisi (D2600) and Sangiran (Sangiran 5, 8, and 9; Kaifu et al., 2005; Martínón-Torres et al., 2008), as well as in *H. antecessor* and *H. naledi* (Berger et al., 2015; Bermúdez de Castro, Martínón-Torres, Sier, & Martín-Francés, 2014; Bermúdez de Castro & Rosas, 1999). In addition, the mandibular premolars of *H. naledi* are somewhat molarized (Berger et al., 2015).

1.1 | Goals of this study

To date, root and pulp canal structure has been reported for a number of archaic *Homo* in East Asia (Chang et al., 2015; Liu et al., 2013, 2017; Xing et al., 2014, 2018; Zanolli et al., 2018); previous investigations (Liu et al., 2013; Xing et al., 2018) have revealed a general trend toward root number reduction, but a retention of primitive traits is still represented in particular cases like Hexian *H. erectus* (Liu et al., 2017; Xing et al., 2014) and Penghu 1 mandible (Chang et al., 2015). However, the root and pulp canal structure of Chinese Middle Pleistocene hominins has not been sufficiently recorded (especially late Middle Pleistocene specimens that are generally assigned to archaic *H. sapiens*). Moreover, comparative investigations focusing on the root and canal morphology are needed, to better understand where these populations fit along the *Homo* lineage. We incorporated the latest discoveries and characterized here the extent of root number and pulp canal variation in an extensive sample of Chinese Middle Pleistocene

premolars. More specifically, we used micro-CT scans of the majority of the Chinese Middle Pleistocene *Homo* specimens suitable for root-canal investigation to document and assess the variability of premolar root-canal system. We compared results on this Chinese fossil sample with Early Pleistocene *Homo* from the Asian continent and Java, as well as with Late Pleistocene Neanderthals and recent modern humans.

2 | MATERIALS AND METHOD

2.1 | Study sample

The samples comprise a total of 117 permanent maxillary and mandibular premolars from fossil and extant individuals from a variety of chronological and geographical origins (Table 1). The Chinese Middle Pleistocene *Homo* sample (CMPH) includes 19 teeth, with a chronological age ranging from mid-Middle to late Middle Pleistocene, distributed among 8 archeological localities. A number of these specimens were unambiguously identified as *H. erectus*; the rest of

them were considered archaic *H. sapiens*, or post-*erectus Homo* (Table 1). It should be noted that the specimens from Xichuan lack accurate stratigraphic context, but their morphological signature is comparable to Zhoukoudian *H. erectus* (Wu & Wu, 1982). For some of the CMPH specimens, the root and/or canal forms have been previously reported, but in this contribution, our observations (fossil as well as extant specimens) are directly based on original micro-CT data. We compared the results of Chinese Middle Pleistocene *Homo* with Neanderthals (NEA, $N = 28$), recent modern humans (RMH, $N = 67$) and two Early Pleistocene *H. erectus* individuals from East Asian and Indonesia. Our modern human reference material comes from clinical extractions and anatomical collections, sampling Asian ($N = 14$), European ($N = 5$), and South African ($N = 48$) individuals; our Neanderthal sample comes from Krapina, Croatia, and La Chaise, France ([dataset] NESPOS database, 2018; Supporting Information Table 1). We selected specimens with well-preserved roots, when antimeres exist, the better-preserved side was chosen; when both antimeres are well preserved, the left side was chosen (regarding our sample, well-preserved antimeres exhibit the same root pattern).

TABLE 1 Composition of the study sample

Specimen	P ³	P ⁴	P ₃	P ₄	Provenance	Age ^a	Citations ^b
Chinese Middle Pleistocene <i>Homo</i>							
PA 110			1		Layer 3 Zhoukoudian Loc. 1	282 ± 45 Ka (A); >300 Ka (B); 400–500 Ka (C)	1
PMU M3887				1	Layer 5	>600 Ka (C)	2
PA 67	1				Layer 11	585 ± 105 Ka (A)	1
PA 68		1					1
PA 831 ^c				1	Hexian	412 ± 25 Ka (D)	3, 4
PA 832	1						
Chaoxian	1	1			Chaoxian	335 ± 25 Ka (E)	5
PA 524 ^d	1				Xichuan	Unknown	6
PA 525				1			
PA 526				1			
PA 527				1			
PA 76	1				Changyang	195 Ka (F)	7
PA 81				1			
Sh. y. 003	1				Yiyuan	420–320 Ka (G)	8, 9
Sh. y. 007		1					
PA 102			1	1	Chenjiawo	650 Ka (H)	10
PA 1578			1		Panxian Dadong	300–130 Ka (I)	11
Early Pleistocene <i>H. erectus</i>							
PA105-4 ^d	1				Gongwangling	1.63 Ma (J)	12
Sangiran 4	1	1			Pucangan Fm. Sangiran	1.81 Ma (K)	13
Neanderthals	8	7	5	4	Level 8 Krapina	123 Ka (L)	14, 15
		1	2	1	Abri Bourgeois-Delaunay La Chaise ^d	123 Ka (M)	15, 16
Modern <i>H. sapiens</i>	15	13	19	20	Asian/European/South African		17

^a Age: (A) Huang et al. (1993); (B) Grün et al. (1997); (C) Shen et al. (2001); (D) Grün et al. (1998); (E) Shen, Fang, Bischoff, Y-X, and J-X (2010); (F) Yuan, Chen, and Gao (1986); (G) Han et al. (2016); (H) An and Kun (1989); (I) Schepartz and Miller-Antonio (2004); (J) Zhu et al. (2015); (K) Huffman (2001); (L) Rink, Schwarcz, Smith, and Radović (1995); (M) Macchiarelli et al. (2006).

^b Citations: (1) Xing (2012); (2) Black et al. (1973); (3) Xing et al. (2014); (4) Liu et al. (2017); (5) Bailey and Liu (2010) (6) Wu and Wu (1982); (7) Chia (1957); (8) Lü et al. (1989); (9) Xing et al. (2016); (10) Woo (1964); (11) Liu et al. (2013); (12) Woo (1966); (13) Zanolli et al. (2018); (14) Radović, Smith, Trinkaus, and Wolpoff (1988); (15) NESPOS database (2018); (16) Macchiarelli et al. (2006); (17) Pan et al. (2017).

^c Only the apical third is preserved within the corpus.

^d Damaged apex, but indications of two root branches.

Except for PMU M 3887 housed at Uppsala University (which was scanned using X-ray microtomography (μ CT) at the Multidisciplinary Laboratory of the ICTP, Trieste (Tuniz et al., 2013; Zanolli, Pan, et al., 2018)), all other Chinese specimens (fossil and recent humans) were scanned using a 225 kV- μ XCT scanner at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP, Chinese Academy of Sciences); micro-CT data or STL mesh of the Neanderthals were downloaded from the NESPOS Database ([dataset] NESPOS database 2018); data for South African modern human specimens were produced on an X-Tek (Metris) XT H225L industrial XCT system at the South African Nuclear Energy Corporation (Necsa; Hoffman & de Beer, 2012); European modern human specimens were acquired using a Phoenix Nanotom 180 scanner from the FERMAT Federation from the Inter-university Material Research and Engineering Centre (CIRIMAT, UMR 5085 CNRS). Isometric voxel size ranged from 40 to 70 μ m. Each specimen was segmented in Avizo 8.0 (Visualization Sciences Group, www.vsg3d.com). After the segmentation, the root and canal system was generated using the “unconstrained smoothing” parameter.

2.2 | Root and canal classification

Abbott (1984) and Wood et al. (1988) established categories to classify external root number and form: the first number refers to the number of roots, followed by letter(s) that indicate root form/configuration. Under such criteria, mandibular premolar roots could be characterized into four forms (Wood et al., 1988): 1R, 2T, 2R MB + D (mesiobuccal and distal) and 2R M + D (mesial and distal). 1R was defined as a single root with a single (main) canal (single-rooted Tomes' root with one apex is included in this category); 2T was defined as the Tomes' root or C-shaped root with bifid apex (Tomes, 1923), where each root has a separate pulp canal. This classification system was later extended by Moore et al. (2013, 2015, 2016) to combine both the external root traits and internal canal parameters.

The classification typology we used here was adapted from formula set by Moore et al. (2013, 2015, 2016), slight modifications were

made in order to highlight number of roots. The formula and description of each root/canal type is listed in Table 2. Multi-rooted premolars were defined on the basis of furcation exceeding more than 25% of the total root length, from cervix to root apex, and the classification of Tomes' root was done following ASUDAS (Turner, Nichol, & Scott, 1991). The evaluation of root and canal types were performed three times by the same observer (LP).

3 | RESULTS

Among the examined groups, we identified a total of nine types of root and pulp canal configurations (Table 2). Upper premolars show single, double, or triple roots with one, two, or three canals; lower premolars are single- or Tomes'-rooted and have one or two canals. Figures 1 and 2 show a representative cross-sectional image of each root-canal type, Table 3 shows the percentage of root-canal type in each group with reference to dental position. Corresponding to data shown in Table 3, Figure 3 is a bar-plot illustrating the percentage of premolar root/canal type. Root type of each fossil specimen was listed in Supporting Information Table 1.

3.1 | Variation of root and canal types among dental position and groups

3.1.1 | Maxillary premolars

Two-thirds of our CMPH P³s show double roots with two canals (Table 3 and Figure 3). *H. erectus* specimens have triple roots (PA 831, Supporting Information Table 1, also seen in Xing et al., 2014), incompletely separated B + L roots connected by cementum (PA 67) or fully independent B + L roots (sh.y.003); double roots and two B + L canals form is expressed for *H. erectus* specimen PA 524 (Supporting Information Table 1) and the buccal and lingual components are separated by a deep groove at the mesial side (n.b., this root is damaged, but a sign of two branches can be seen). Regarding archaic *H. sapiens*, one specimen (Chaoxian) expresses two independent, B + L roots—a primitive feature which is commonly observed in *H. erectus* and some Early

TABLE 2 List of premolar root and canal formulae identified in our sample

Formula ^a	Root number	Canal number	Description
1R ₁	1	1	No bifurcation; 1 root/1 canal
1R(Bf) _{1Bf}	1	1	1 bifid root/1 bifid canal
1R _{1Bf}	1	1	1 single root/1 bifid canal
1R _{2(1B + 1L)}	1	2	1 root (joined 1B + 1 L roots)/2 circular canals (1B + 1 L)
1T ₁	1	1	Tomes' root; 1 C-shaped root body (deep ML groove, round DB face)/1 C-shaped canal
1T _{2(1B + 1L)}	1	2	Tomes' root; 1 C-shaped root body/2 circular canals (1B + 1 L)
1T _{2(1MB + 1DL)}	1	2	Tomes' root; 1 C-shaped root body /2 circular canals (1 MB + 1DL)
2R: 1 ₁ B + 1 ₁ L	2	2	2 roots (1B + 1 L circular)/2 circular canals (1B + 1 L). Double roots but incompletely separated, fully-grown root branches are included
3R: 2 ₂ B + 1 ₁ L	3	3	3 roots (2B + 1 L)/3 circular canals (2B + 1 L)

Anatomical orientation legend: B = buccal; DB = disto-buccal; DL = disto-lingual; D = distal; L = lingual; M = mesial; MB = mesio-buccal; ML = mesio-lingual.

^a Standard numbers denote root number, standard letters denote root form; subscript numbers denote canal number, subscript letters denote canal form.

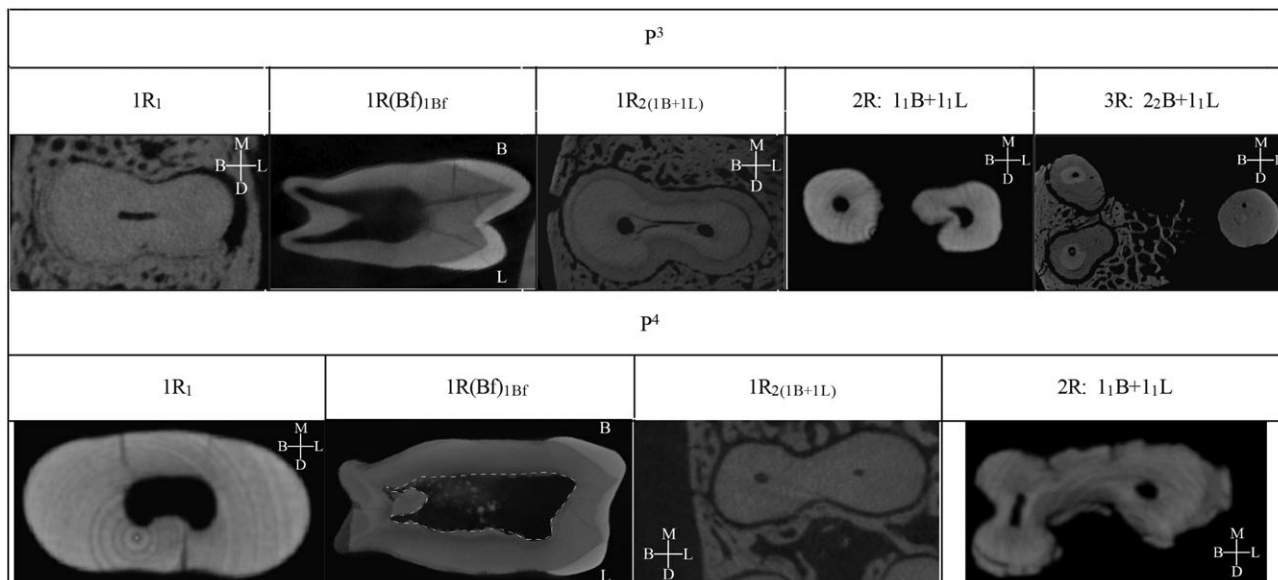


FIGURE 1 Root-canal types identified in upper premolar. Examples of each root type in cross-section image are shown. For 1R₁ premolars, cross-sectional images were captured at mid-root; for multi-rooted and/or multi-canaled premolars, cross-sectional images were captured at the furcation location; for bifurcated premolars, buccal-lingual sections were taken to show the furcation more clearly. All right-sided images were flipped to the left side

Pleistocene specimens; the other (PA 76) has single root with B + L canals (Supporting Information Table 1). The Early Pleistocene *H. erectus* representatives Sangiran 4 and PA 105-4 also show two separate roots with a pulp canal in each branch (Supporting Information

Table 1). Because of a small sample size, these older specimens were not included in the frequency counts or in Figures 1–3, but micro-CT sections are presented in Supporting Information. The frequency of double-rooted P³s is also high in recent modern humans and

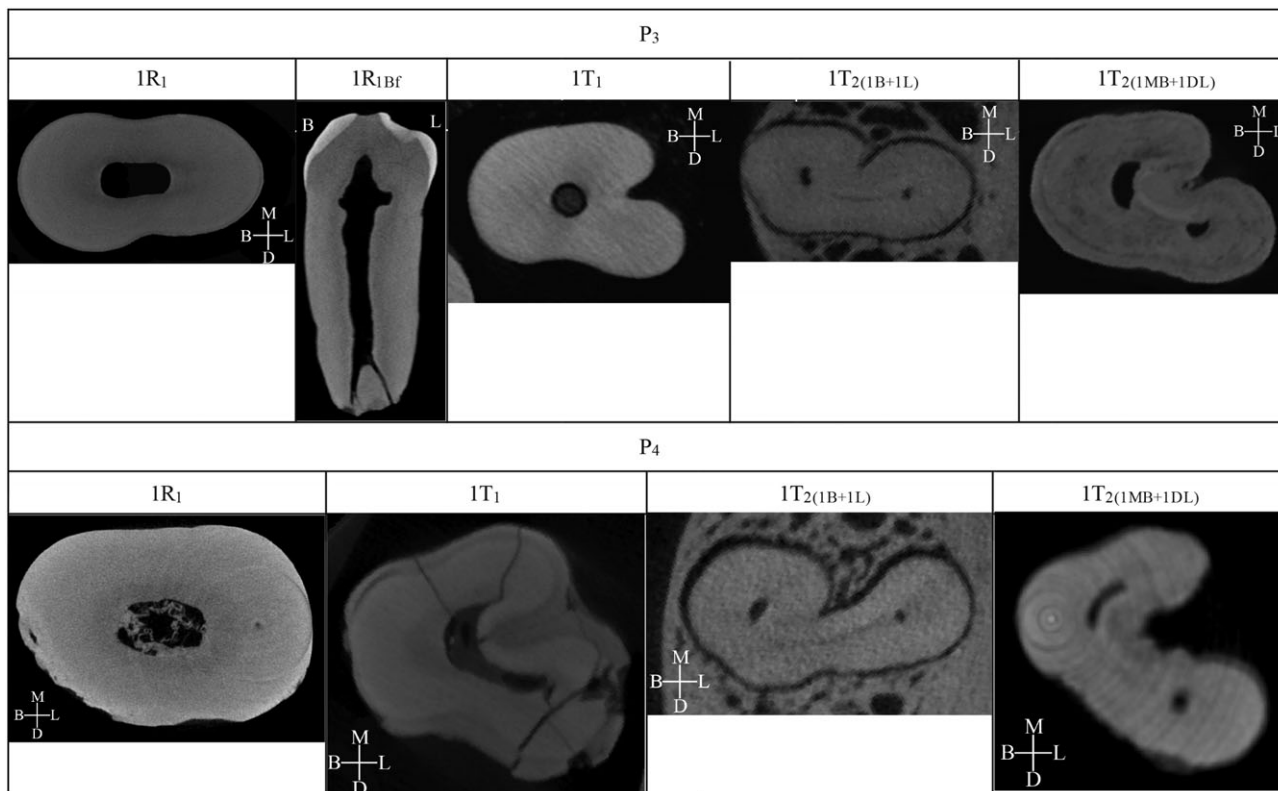


FIGURE 2 Root-canal types identified in lower premolar. Examples of each root type in cross-section image are shown. For 1R₁ and 1T₁ premolars, cross-sectional images were captured at mid-root; for multi-rooted and/or multi-canaled premolars, cross-sectional images were captured at the furcation location; for bifurcated premolars, buccal-lingual sections were taken to show the furcation more clearly. All right-sided images were flipped to the left side

TABLE 3 The frequency of root-canal types in each group with reference to dental position, see Table 2 for explanation for the formulae

P ³					
Root-canal type	1R ₁	1R(Bf) _{1Bf}	1R _{2(1B+1L)}	2R: 1 ₁ B + 1 ₁ L	3R: 2 ₂ B + 1 ₁ L
CMPH			16.7%	66.6%	16.7%
NEA				100%	
RMH	12.5%	6.2%	12.5%	68.8%	
P ⁴					
Root-canal type	1R ₁	1R(Bf) _{1Bf}	1R _{2(1B+1L)}	2R: 1 ₁ B + 1 ₁ L	
CMPH		33.3%	33.3%		33.3%
NEA	12.5%				87.5%
RMH	30.8%		30.8%		38.5%
P ₃					
Root-canal type	1R ₁	1R _{1Bf}	1T ₁	1T _{2(1B+1L)}	1T _{2(1MB+1DL)}
CMPH	40.0%				60.0%
NEA	62.5%	37.5%			
RMH	66.7%	5.6%	11.1%	16.7%	
P ₄					
Root-canal type	1R ₁	1T ₁	1T _{2(1B+1L)}	1T _{2(1MB+1DL)}	
CMPH	60.0%	20.0%		20.0%	
NEA	83.3%			16.7%	
RMH	85.0%	5.0%	5.0%	5.0%	

Groups: CMPH = Chinese Middle Pleistocene Hominins; NEA = Neanderthal; RMH = Recent modern human.

Neanderthals (68.8% and 100%, respectively; Table 3 and Figure 3), modern human P³ sample presents two cases of single joined root with two canals, and one specimen has apical bifurcation.

The P⁴s vary in root number between one and two. One third of Chinese Middle Pleistocene sample shows double roots and two canals (Figures 1 and 3; Table 3). Among the two *H. erectus* premolars, PA 68 has a bifid root apex with a bifid canal (Supporting Information

Table 1); sh.y.007 has single, plate-like root with two canals. The P⁴ of the Javanese specimen Sangiran 4 shows a deep furrow at the distal face of the root with two pulp canals almost linked together by thin buccolingual elongations, a similar configuration is shown in our late Middle Pleistocene specimen (Chaoxian P⁴, archaic *H. sapiens*). Double-rooted P⁴s are also observed in modern humans (38.5%), and more frequently, in Neanderthals (87.5%; Figures 1 and 3; Table 3).

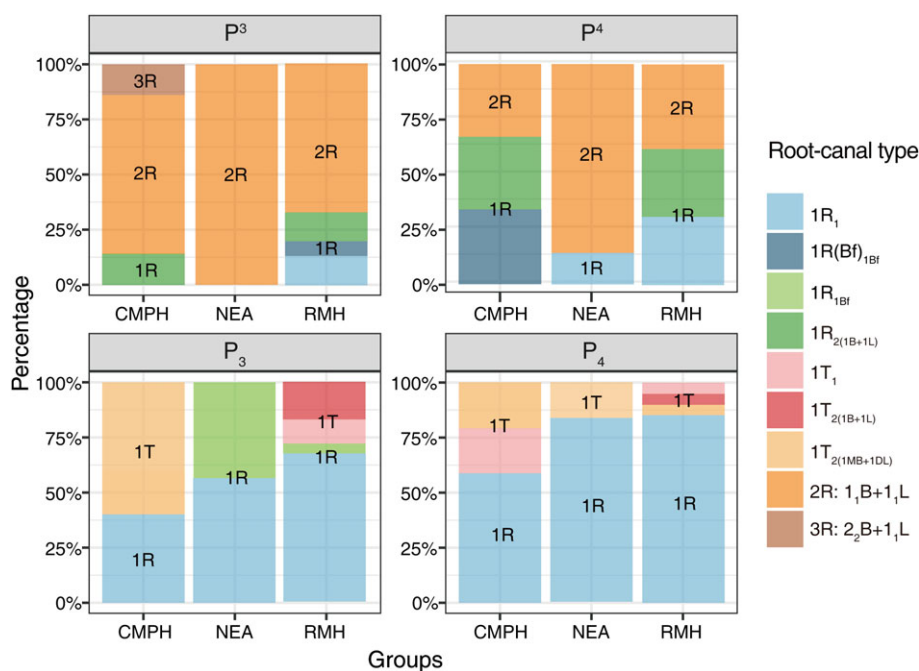


FIGURE 3 Frequency of root and canal type observed in Chinese Middle Pleistocene *Homo* (CMPH), Neanderthals (NEA), and recent modern humans (MH) [Color figure can be viewed at wileyonlinelibrary.com]

3.1.2 | Mandibular premolars

Across the sample, root type varies between single circular, bifid, and Tomes' root, canal number varies between one and two (Figure 2). A key difference between Chinese Middle Pleistocene fossils and the comparative sample is the relatively high prevalence of Tomes' root (Figure 3 and Table 3). In P_3 s, 3/5 of the Chinese fossils show a two-canaled Tomes' type with C-shaped buccal face and deep MB-DL groove; the other two specimens have single circular roots with one canal. In P_4 s, 2/4 fossil specimens were discovered with Tomes' root, whereas the other two specimens have single circular root with one canal. A two-canal, Tomes' rooted P_4 is reported in single case (PA 831, *H. erectus*): at the external surface of the root (Supporting Information Table 1), a mesiobuccal and a distolingual radical grooves are separated by a deep lingual invagination (Liu et al., 2017). Note that only the apical third of this P_4 is preserved, embedded in the mandibular corpus. Three moderate radicular grooves (M, D, and L) are seen at the root surface of one late Middle Pleistocene specimen (PA 81); together with a crescent-shaped canal in cross-section, these characteristics indicate a fused, three-rooted branch (a primitive feature), and we categorized it as a nontypical Tomes' root (Supporting Information Table 1). In modern human lower premolars, the prevalence of Tomes' root is 27.8% for P_3 and 15% for P_4 (Figure 3 and Table 3). It is also interesting to note that compared with the other two groups, Neanderthals P_3 s show a relatively high percentage of single root with bifurcation at the root and canal apex (37.5%; Figure 3 and Table 3).

3.2 | Additional morphological traits and variants within root/canal formula

As noticed by Moore et al. (2015, 2016), double-rooted upper premolars (referred as formula $1_1B + 1_1L$ or root type 2-A-2 by Moore and colleagues) have a number of variants within hominoids, and this is in accordance with our observations. In P^3 of Zhoukoudian *H. erectus*, two root branches are presented but not completely separated: cementum tissue connects root branches at the mesial face, and a deep and wide furrow is seen at the distal face, located at the middle third and extending to the apex of the root, with two, clearly separated B + L canals. This root configuration is also seen in the P^4 s of Javanese *H. erectus* Sangiran 4, Chaoxian P^4 , and also in some of the Neanderthal P^4 s (Supporting Information Table 1), but is absent in early *H. erectus* specimen PA 105-4, not frequently observed in our modern humans.

4 | DISCUSSION

4.1 | Inter-group comparisons of root and canal form

Recent studies on the dentition of Chinese hominin fossils from Middle Pleistocene period (including a number of fossils involved in this study) have reported a combination of derived and primitive traits expressed at premolar roots and/or root canals. Compared with early members of *H. erectus s.l.* (e.g., specimens from Dmanisi, East Africa, and Sangiran), upper premolars from Zhoukoudian and Yiyuan have

less complex root and canal structures, whereas the lower premolars are closer to the early *Homo* condition (Martinón-Torres et al., 2008; Xing et al., 2018; Zanolli, Pan, et al., 2018). On the other hand, Hexian *H. erectus* differs from northern Chinese *H. erectus* and European Middle Pleistocene hominins by showing primitive affinities (three-rooted upper premolar, robust mandible and premolar roots) with the Early Pleistocene specimens from Africa (*H. ergaster*) and Java (*H. erectus*; Liu et al., 2017; Xing et al., 2014). Another study states that P_3 from Panxian Dadong shows a slightly robust root compared with modern *H. sapiens*, but the archaic features are very weakly expressed (Liu et al., 2013); our observation on the root and canal form confirms that this late Middle Pleistocene hominin specimen has a simple root system (single root with one canal), a condition that is commonly found in recent humans.

Besides these above-mentioned, previous records, the root and canal system of Middle Pleistocene hominins from China is still insufficiently documented: little is known about their morphological variability, leaving inconclusive discussions about their taxonomical and phylogenetic places in relation to contemporary hominins from Africa and Eurasia. We extend the knowledge on fossil human tooth variability by providing the first detailed document of the root-pulp canal system variation of Asian hominins living in this particular time period.

The primitive hominin root morphology, as represented by the maxillary premolars of South African australopiths, are double- or triple-rooted (Moore et al., 2016). Triple-rooted P^3 s are also observed in Early Pleistocene *Homo* from Sangiran (older deposits; Kaifu et al., 2005; von Koenigswald, 1950). Contrasting this "molarized" primitive condition, our representatives of Asian Early Pleistocene *Homo* (Sangiran 4 and PA 105-4), as well as Chinese Middle Pleistocene sample, show a clear trend of root reduction (toward modern human condition). Chinese specimens in general exhibit a derived condition of predominantly double-rooted P^3 s and single-rooted P^4 s (see also Xing et al., 2018), close to the frequency seen in modern humans (Figure 1), although variations like triple- and single-rooted P^3 s do exist. It has to be noted that Xing et al. (2018) considered Zhoukoudian *H. erectus* specimen PA 67 as three-rooted because of the presence of a small and unattached pulp diverticulum between the two main canals (Xing et al., 2018: Figure 2). However, because of its position in the inter-radicular blade and flatten shape, we consider this to represent a side-effect of the partial fusing of the two radicles and not a third root canal (see Supporting Information Table 1).

If we enlarge our sample to other contemporaneous Zhoukoudian *H. erectus* materials (which were lost during WWII), Weidenreich (1937) described a few double-rooted premolars with incompletely separated root branches; in fact, 2/3 of P^3 s and 2/2 of P^4 s recorded by Weidenreich (1937) show this feature. Partly divided upper premolar roots are also frequently found in Neanderthals (this study) and is seen in one Middle Pleistocene *H. floresiensis*-like specimen (SOA-MM5) from Mata Menge, Flores (van den Bergh et al., 2016). While the premolar root morphology of the early modern human assemblage from Jebel Irhoud, in Morocco, is still unreported (Hublin et al., 2017), the recently published late Middle Pleistocene modern human maxilla from Misliya, in Israel, showed single-rooted upper premolars (Hershkovitz et al., 2018).

Double-rooted lower premolars are frequently reported for Early Pleistocene hominins found in Eurasian sites like Atapuerca TD6 (Bermúdez de Castro & Rosas, 1999) and Sangiran (Kaifu et al., 2005), but East African early *Homo* has predominantly single- or Tomes' rooted lower premolars (Wood et al., 1988), high percentage of Tomes' root is also observed in Early Pleistocene specimens from Atapuerca TD6 and Sima del Elefante (Prado-Simón et al. 2012, b), Dmanisi and Trinil (Martinón-Torres et al., 2008). As for the Middle Pleistocene period, Tomes' root has been described for the specimens found in Tighenif (accompanied with two or three canals; Zanolli & Mazurier, 2013), mid-Middle Pleistocene specimens like *H. erectus* P₄ from Hexian (Liu et al., 2017) and Zhoukoudian (3/5 P_{3s} and 1/2 P_{4s}; Weidenreich, 1937), P₃ from Chenjiawo (this study) and a late Middle Pleistocene P₃ of Penghu 1 (Chang et al., 2015). A three-grooved P₄ root (with one circular canal) is seen in late Middle Pleistocene specimen from Changyang (this study), representing a fusion of three root branches—a rather primitive feature. In all, our Middle Pleistocene record from China fits this evolutionary scenario, with a retention of primitive and derived features associated with root and canal simplification.

Single-rooted lower premolars are also frequently reported for the Middle Pleistocene hominins from Eurasia, including specimens from Zhoukoudian (Weidenreich, 1937; Xing et al., 2018; Zanolli, Pan, et al., 2018) and Chenjiawo (this study), the P₄ of Penghu 1 (Chang et al., 2015), Qesem Cave (Hershkovitz et al., 2011), Atapuerca Sima de los Huesos (Martinón-Torres et al., 2012), and Visogliano (Zanolli et al., 2018).

In the Late Pleistocene, Neanderthal premolars shows more homogeneity in their root-canal form. All the P_{3s} have double roots and all the P_{3s} have single root. Moreover, all the Neanderthal P_{4s} show single root (1R) with one or two canals except for one specimen (KRD 35) that exhibits Tomes' root with deep MB groove and two MB + DL canals (Supporting Information Table 1). These results based on a larger sample are comparable to those from Prado-Simón, Martinón-Torres, Baca, Olejniczak, et al. (2012). However, the majority of our Neanderthal sample comes from Krapina and further investigation is needed to test whether this low variability on the premolar root-canal form exists in other Neanderthal populations. The modern human lower premolars show derived root forms of predominantly, if not all, single root with one canal.

Despite the tendency towards a simplification of the root system across the Middle Pleistocene in Eurasian human groups, the ancestral pattern is found to be retained in multiple human groups through time and space, probably indicating the survival of primitive lineages, but more evidence is needed to make any phylogenetic interpretations. In all, premolar root and canal form of mid-Middle Pleistocene hominins inhabiting China (or "classic" *H. erectus*) show closer affinities with their contemporaneous or older counterparts in Eurasia, than with East African early *Homo*. This evidence is consistent with the hypothesis that at least some of the Early Pleistocene hominins occupying Eurasia contributed to the later "classic" *H. erectus* population (Kaifu et al., 2005; Martinón-Torres et al., 2007, 2008). As for the late Middle Pleistocene specimens, although they are often assigned to archaic *H. sapiens* and display a series of derived features, we record here a number of primitive features that cannot be strictly aligned across a

chronological sequence. Together with root-canal configurations reported here, current dental evidence cannot confidently link these Middle Pleistocene population to the *H. sapiens* lineage, although an evolutionary trend toward this condition is clearly observed (Bailey & Liu, 2010; Liu et al., 2013).

5 | CONCLUSIONS

Previous studies have reported a high degree of morphological complexity in tooth crown and enamel-dental junction (Liu et al., 2013, 2016, 2017; Xing et al., 2016; Xing, Zhou, & Liu, 2009), compatible with our results on the root and pulp canal. Together with a clear trend of root number reduction during the Middle and Late Pleistocene, our study revealed a previously undocumented level of diversity in root-canal configuration within the hominins that occupied East Asia in Middle Pleistocene period. In all, premolar root and canal form we observed in "classic" *H. erectus* population is comparable to Early and Middle Pleistocene hominins in Eurasia, but show distant morphological affinities to East African early hominins. This work shows that analyzing the variation of premolar root structural organization, and notably integrating together root/canal form and number, could possibly contribute to taxonomic and phylogenetic discussions. Future investigations is needed, for example, by characterizing the root-canal morphology of the Indonesian Early-Middle Pleistocene hypodigm in order to better understand the still obscure evolutionary relationships and population dynamics with the Asian continental groups.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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