A Newly Discovered Late Pleistocene Lower Third Premolar and the High Frequency Occurrence of Tomes' Root in the Human Fossil Record from China*

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Abstract

Dental remains provide crucial evidence for interpreting a populations' affinity as well as human evolution. Recent studies of fossil human teeth have enriched our current view of morphological variation during the Pleistocene in East Asia. In the present paper, we describe a newly discovered late Pleistocene human tooth, a lower third premolar from the Weijiadong cave in Bijie in south-western China, which is dated around 18-20Ka BP using AMS Carbon 14 dating. The tooth is identified as belonging to an early modern human based on its morphology and size. The Tomes' root is present in this lower third premolar, one of the non-metrical dental traits developed genetically. Moreover, we examine most of the fossil lower third premolars collected from China, as well as material from several Neolithic and historical human assemblages. We find that the Tomes' root is very common in Chinese human fossils and occurs in high frequency in Neolithic and historic human remains from China. We suggest the high frequency of Tomes' root may serve as a non-metric dental trait to support inferences regarding regional continuity of human evolution in East Asia.

Keywords: lower third premolar, non-metric trait, Tomes' root, late Pleistocene

** Author is responsible for language correctness and content.*

Introduction

New evidence of early modern humans fossils older than 100 ka BP have recently been found in China, from localities such as Huanglongdong in Hubei (1-3), Zhirendong (4-6) and Lunadong in Guangxi (7), Fuyandong in Hunan (8) and Mawokoudong in Guizhou (9). Together these discoveries shed light on the early emergence of modern human in East Asia and suggest the possibility that modern humans evolved from local archaic Homo. Recent studies also enrich our understanding of morphological variation and diversity in Late Pleistocene humans from East Asia (10,11). The hypothesis regarding the origin of modern humans in East Asia is an open question, which is hotly debated between the competing multiregional hypothesis and the out of Africa hypothesis. Therefore, additional fossil from East Asia has the potential to help us understand early human evolution and variation during the Late Pleistocene. Here we report on a newly discovered isolated human tooth, a lower third premolar uncovered from a cave site in south China. We compare the morphology and measurements of this new specimen to previously collected fossils including nearly all human fossil lower third premolars from China, including Neolithic and historical Chinese dental remains and information from modern human populations. We focus on the non-metrical morphological trait of the Tomes' root in this specimen and discuss the importance of this trait for understanding human evolution in East Asia.

1. Description

The isolated fossil tooth, specimen WJD-H1, was discovered in 2018 in the Weijiadong cave in Bijie City in Guizhou Province, south-western china. The cave formed in Triassic limestone, and has an altitude of approximately 1370m, E 105°30′35.5″, N 27°16′14.8″ (12). The deposit layers of human tooth fossil are dated around 18-20Ka, by AMS dating of Charcoal in the deposit conducted in Beta laboratory in USA.

The tooth is identified as a lower right third premolar of a human. The tooth crown is well preserved (Figure1), but the apical third of the root has been lost. A series of tiny parallel scratches are visible on the transected surface where the tooth is broken; these are interpreted as probable gnawing marks formed by small mammals such as rodents.

In occlusal view, the crown is oval with two main cusps. The buccal cusp is the larger of the two, and the lingual cusp is smaller. The buccal and lingual cusps are connected by a transverse ridge. No cingulum or accessory crest and cusps are present in the enamel surface. The mesial triangular fossa is clearly preserved, although the distal fossa is slightly worn. The wear degree falls in Smith stage 1 (13), and no dentine is exposed. The tooth most likely corresponds to a young adult individual.

Figure 1 Lower right third premolar WJD-H1 from Weijiadong cave: a occlusal view; b Buccal view; c Mesial view; d Lingual view; e Distal view.

In the root, a radicular groove is developed below the cervix on the mesial-lingual aspect of the root. Although the apical third of the root is missing, based on the trajectory of the preserved portion of this groove we assume that it developed vertically towards the root apex. This gives the root a C-shaped cross-section, a morphology that is referred to as Tomes' root. Two canals are visible through the fractured surface of the root.

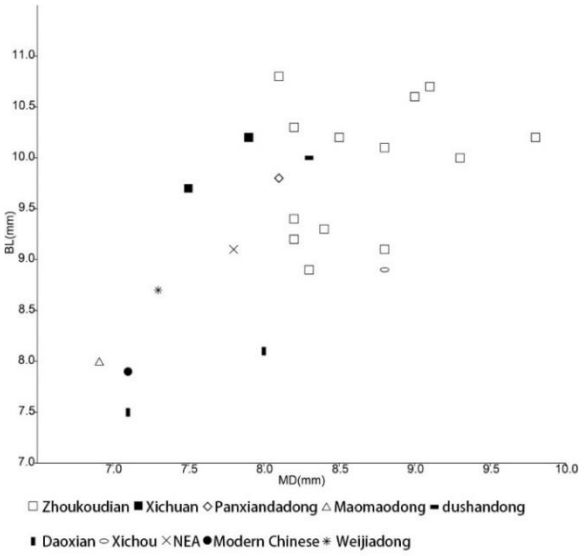

Figure 2 Dimension of lower third premolars of Chinese human fossils and Neanderthals (8,10, 15-18).

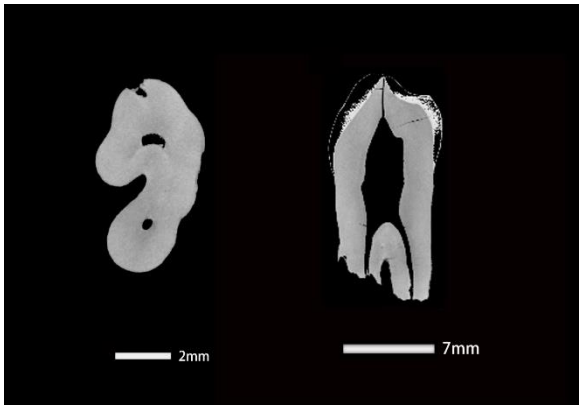

Figure 3 CT images of transversal and vertical sections of lower right third premolar from Weijiadong cave

2. Tooth measurement and comparison

We measured the tooth using the methods of Wolpoff (14) and Wang (15). The Buccal-Lingual length of the crown (BL) is 8.7mm and Mesial-Distal length (MD) is 7.3 mm.

Comparison of the MD and BL dimensions taken from the worldwide fossil record of Middle and Late Pleistocene specimens together with recent and modern human populations (Table 1 and Figure 2), indicate that WJD-H1 is smaller than the mean of East Asian Middle Pleistocene Homo and Neanderthals. MD and BL dimensions of the Weijiadong specimen are smaller and fall outside the range for archaic Homo from China. However, the MD and BL dimensions are within the range of Late Pleistocene early modern humans, Global and East Asian recent modern humans, and Modern Chinese samples.

Homo erectus from ZhouKoudian's lower P3s have very developed cingulum and robust roots (16). The Xichuan Homo erectus' lower P3s is similar to that from ZhouKoudian although its cingulum, which appears around the base of buccal side, is less prominent (19). In occlusal view the contour of the Xichuan Homo erectus is rhombic such that the maximum diameter runs mesiobuccal to distolingual, compared to the oval contour in the Weijiadong specimen and modern humans. In specimens of Early Modern Human fossils, such as those from Daoxian (8) in Hunan and Xichou in Yunnan (18), the lower P3 has a more symmetrical oval contour in occlusal view, and the crown size and morphology are more similar to that of the Weijiadong specimen. Based on this comparison, the lower third premolar WJD-H1 from Weijiadong cave in Bijie, South-western China most likely represents an Early Modern Human individual.

3. Tomes' root in Pleistocene human fossils in China

In modern humans, the mandibular first premolar is mostly single-rooted, however some variations are recorded. In one case, a radicular groove develops in the mesial aspect of the root, causing the root to have a "C" shaped cross-section. This partially or completely divided root of the lower first premolar is named as Tomes' root after C.S. Tomes (1889), who is credited as the first to define this trait in the human dentition (20).

In the Arizona State University Dental Anthropology System (ASUDAS) based on data from specimens with Turner II and Scott-Irish ancestry (21-23), 36 non-metric dental traits of modern humans are described, including the presence of Tomes' root. These have been widely accepted and adopted by numerous anthropologists. According to ASUDAS, the Tomes' root trait is divided into six grades 0-5,

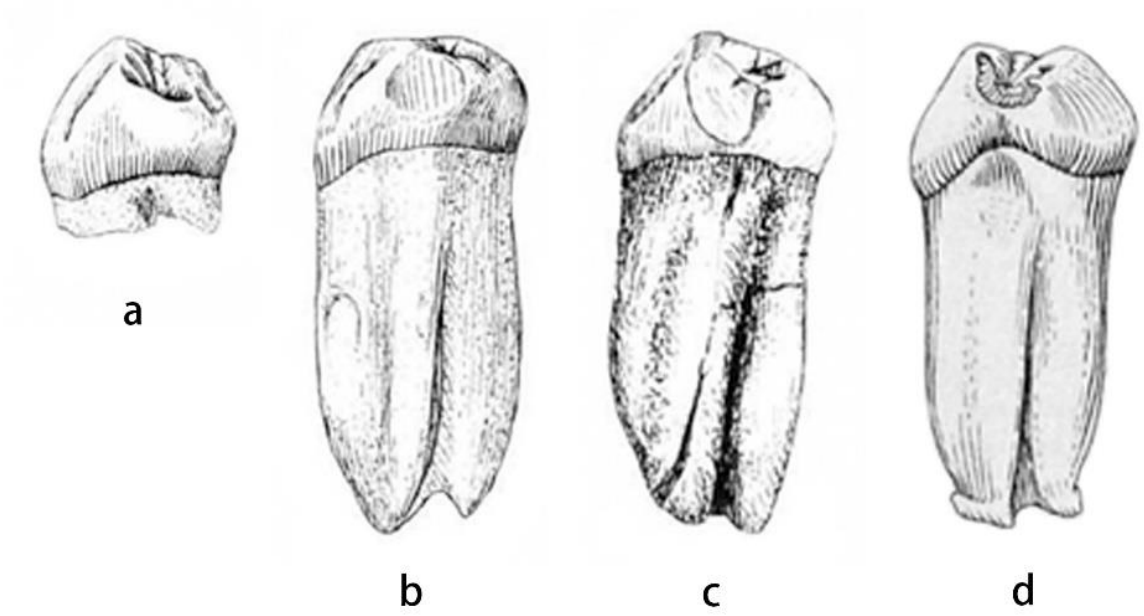

Figure 4 Mesial views of Tomes' root of lower P3 from Zhoukoudian Locality 1 (Modified from Weidenreich's plate 80,82,86,328 respectively (16) a No.20 b No.82 c No.85 d, No.130' No.85 of left P3 (16) has been flipped to make it easier to compare with right P3.

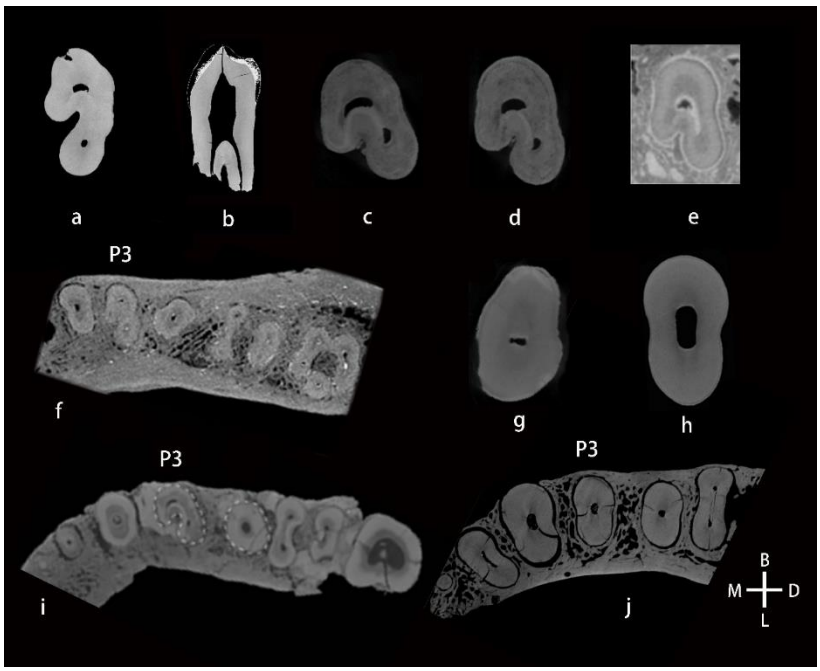

Figure 5 CT images of premolar P3 toot of fossil humans from China. a-b WJD-H1; c Henan Xichuan PA526 (25); d Xichuan of Henan PA527(25); e Xiahe (26); f Penghu1 of Taiwan (27); g PA110 from Zhoukoudian (25); h PA1578 Panxiandadong of Guizhou (25); i PA102 Chenjiawo of Lantian (25); j PA1281 Tianyuandong of Zhoukoudian. All the left P3 mirror flipped to make it easier to compare with the right P3.

based on the severity of the radicular groove. Grade 0-2 is essentially a non-Tomes' root; from Grade 3-5 the groove is present and extends at least 1/3 of total root length. The groove is deep

and forms a V-shape on the mesial-lingual aspect of root (24).

WJD-H1 lower P3 is missing the apical portion of the root, so the total length of the root is unknown. However, a clearly radicular groove is present a few millimeters below the cervical line. Using the modern Chinese teeth metric data provided by Wang (15), the average length of the root of the lower third premolar is 12.3mm (with total variation between 8.6-15.5mm). The preserved root of WJD-H1 P3 measures approximately 11.7 mm suggesting more than half of the length of the root is preserved. The radicular groove in the central of the root is v-shaped giving the root a "C"-shape cross-section (Fig.3). Using CT scans to investigate this morphology further, the bifurcation of the pulp is clearly visible in the buccal-lingual slices (Fig3). Therefore, the Weijiadong P3 can be defined as Tomes' root grade 3-4.

In order to investigate the frequency of Tomes' root in other human fossils, we collected data from all fossil lower P3 specimens discovered so far in China with a preserved root. We studied the original specimen first hand when possible, otherwise relying on data from the original publication. In total we obtained data from 18 specimens of fossil human P3S from 12 sites all from the Pleistocene of China (Table 2, Figure 3-6.).

A rich assemblage of Middle Pleistocene human fossils have been recovered from the Zhoukoudian Locality 1 in China. Despite the fact most specimens were lost during World War II, casts and original publications are available for reference. According to the description by Weidenreich (16), there are 15 lower P3S from the Zhoukoudian Locality 1; some of these show a root morphology comparable to chimpanzee and fossil orangutan, in which this structure is bipartite. The roots have two fused portions, a large buccal portion that projects mesially and a smaller lingual portion with a deep longitudinal furrow, each portion having a distinct and separate apex. The furrow on the lingual root is actually a radicular groove like the Tomes' root described by ASUDAS. In the present study, we examined seven lower P3S specimens from Locality 1 of the Zhoukoudian site (PA110, No.20, No.21, No.23, No.82, No.85, No.130'); four of these present Tomes' root (No.20, No.82, No.85, No.130') (Figure 4). Although No.20 is missing most of the root, a furrow is clearly present near the mesial aspect of the base of the root, which we infer corresponds to the Tomes' root.

We also collected data from fossil lower P3 of mandibles from other localities in China using Micro CT imaging. CT scans of the Tianyuandong mandible were generated by the present study, and compared to CT images from published reports (25-27) (Figure 5). Archaic Middle Pleistocene Homo from Xichuan in Henan and Chenjiawo in Lantian show similar contours in transverse section with two canals consistent with Tomes' root. The lower P3 fossil specimen PA110 from Zhoukoudian presents a single root without a groove (Figure 5 g). In late Middle Pleistocene and Late Pleistocene specimens, such as those from Xiahe in Gansu, Penghu1 in Taiwan, and also Weijiadong in Guizhou, the Tomes' root is present. However a few P3 specimens, such as Panxiandadong in Guizhou, Daoxian in Hunan and Tianyuandong in Zhoukoudian show single root (Figure 5 and Table 2).

4. Tomes' root in Neolithic, historic remains from China and modern human populations

The Tomes' root had been observed in three Neolithic sites including Xiawanggang, Miaozigou, Jiangjialiang, and one historical site Longxian in Shanxi (28-31) (Table 3). From the original report of the Xiawanggang site, the Tomes' roots range from grade 1 to 5. If we exclude the specimens of grade 1-2 (which are essentially Tomes' root absent), the occurrence of Tomes' root according to ASUDAS from grade 3 to 5 should be lower than 70.1%, occurring in approximately 28% of the population. The other three published reports do not display the score data of the Tomes' root, but we doubt that the occurrence of Tomes' root would be somehow lower. We also collected data from two historic human assemblages held in Northwestern University in China, dental remains from the Warring States Period from Zhaitouhe and Shijiahe in Huangling, dental remains of Qin Dynasty from Qujia and Wanli in Lintong and Fenggeling in Baoji. Both these assemblages have high frequency of Tomes' root, measuring 38.5% and 32% respectively (Table 3). However, in modern Chinese populations the frequency of Tomes' root is as low as 18.9% and 19.9% for modern humans globally (Table 3).

In modern populations worldwide (23), Tomes' root occurs in 20-25% of the population in Sub-Saharan Africa, Australia, and Southeast Asia, and has a relatively lower occurrence in Western Eurasia's populations (10-20%). Thus, Tomes' root is more common in the Sunda-Pacific groups compared to East Asians and Native Americans.

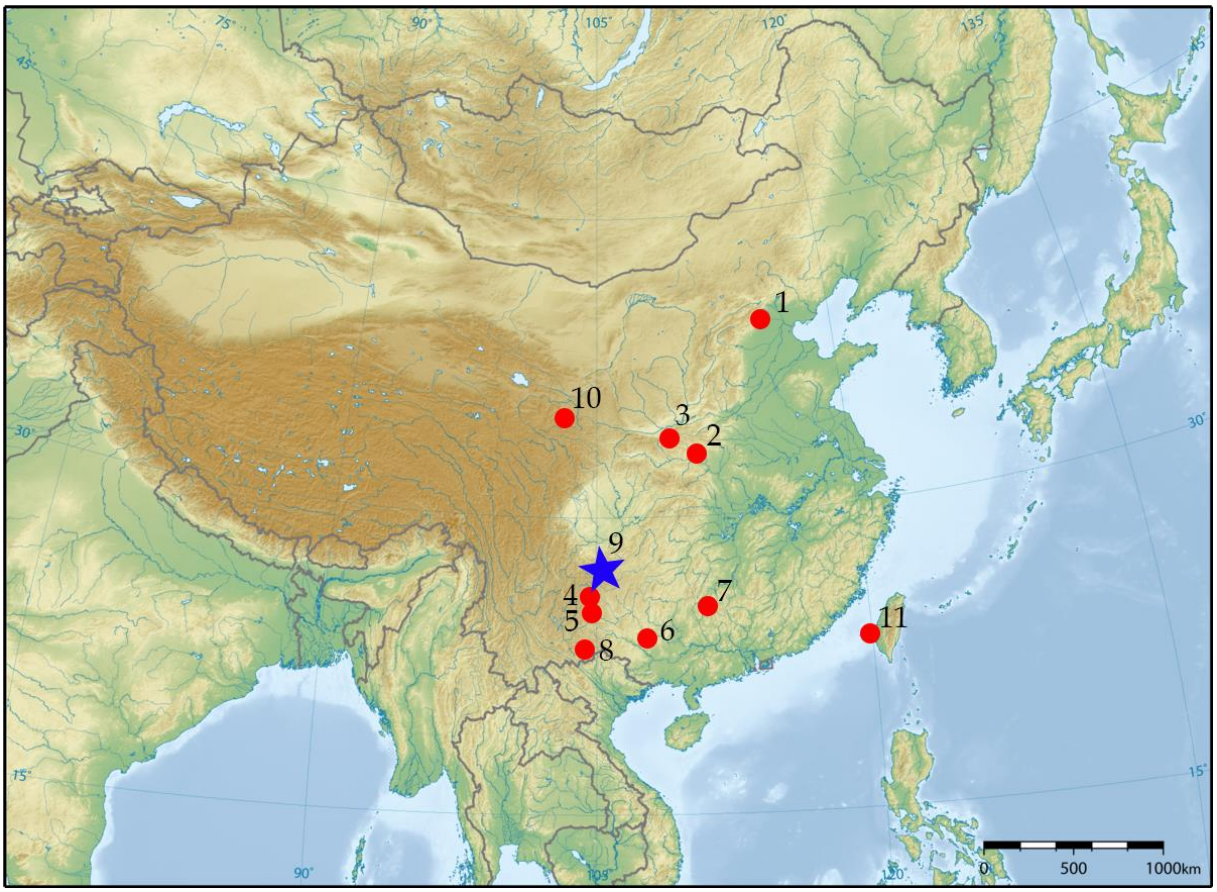

Figure 6 Human fossil sites of lower P3 in China. 1 Zhoukoudian Locality 1 and Tianyuandong 2 Xichuan in Henan 3 Chenjiawo in Lantian 4 Panxiandadong 5 Maomaodong 6 Dushandong cave 7 Daoxian 8 Xichou 9 Weijiadong 10 Xiahe 11 Penghu.

Melanesia is similar to the Sunda-Pacific groups. In New Guinea this trait is rare.

5. Discussion and conclusion

In this studies of mandibular postcanine root morphology in Early-Middle Pleistocene hominins Wood (36) suggested two evolutionary trends in premolar root formation. Australopithecus afarensis and great apes are primitive with two roots. One trend reduces this structure into a single root with a single canal as observed in modern humans and also in some specimens of archaic Homo. The C-shaped Tomes' root is a transitional form. The other trend is molarization towards to two separate roots as in Paranthropus boisei.

In Europe, the early Pleistocene Homo antecessor ATE9-1 from Sima del Elefante the p3 has two-roots with a Tomes' root (37). According to Castro's 1999 description, Homo antecessor ATD6-3 has a clear Tomes' root (38). However, the Middle Pleistocene European Homo and Neanderthals typically have a single-rooted lower P3 (37-39). According to our observations, 10 of 18 (55%) Pleistocene fossils from China have Tomes' root on the lower P3. The P3 collected from Dushandong cave is even more primitive with 3 roots (10). This pattern is very different from the contemporaneous fossil record from Europe. The frequency of Tomes' root is as high as 38.5%-28% in Neolithic and Historic remains from China. Therefore we suggest the high frequency of Tomes' root in Pleistocene human fossils of China might be indicative of regional continuity in East Asia. This trait is rooted in Homo erectus and maintains a relatively high rate of evolution from the Middle Pleistocene to late Pleistocene, succeeding in the Neolithic to the historical period. Tomes' root might be another regional-continuity trait that provides evidence of multiregional origins of modern human evolution in East Asia. However more comparative data from both Pleistocene fossil and Holocene

remains need to be collected and examined in the future to fully assess this hypothesis.

The presence of the Tomes' root in the Late Pleistocene new early modern human specimen from WeiJiaDong provides additional evidence of the high frequency occurrence of Tomes' root in Chinese Pleistocene human fossils. We suggest Tomes' root might be a non-metric dental trait of regional continuity in human evolution in East Asia.

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Table 1 Tooth measurement and comparison of the lower third molars (mm).

Specimens	MD (mm)	BL (mm)
WJD-H1	7.3	8.7
EAAH	8.5 (7.9-9.8)	9.6 (8.2-10.7)
EAEMH	7.1 (5.7-8.8)	8.3 (7.5-8.9)
GLEMH	7.2 (5.7-8.8)	8.6 (7.0-9.6)
NEA	7.8 (6.6-9.1)	9.1 (8.0-10.3)
EARMH	7.2 (6.4-8.0)	7.9 (6.7-9.0)
GLRMH	7.4 (5.7-9.2)	8.1 (6.5-10.2)
MC	7.1 (5.4-8.1)	7.9 (6.6-9.3)

WJD: Weijiadong Cave; EAAH: East Asian Middle Pleistocene archaic *Homo*; EAEMH: East Asian Early Modern Human; GLEMH: Global Early modern humans; NEA: Neanderthals; EARMH: East Asian recent modern humans; GLRMH: Global recent modern humans; MC: Modern Chinese. unit: mm. Source (10)

Table 2 Tomes' root in Pleistocene human fossils from China.

Fossil site	Specimen Number	Tomes' root	Geological Age	Source
Chenjiawo in Lantian	PA102	+ (Figure 5 i)	Early Middle Pleistocene	(25)
Zhoukoudian Locality 1	No.20	+ (Figure 4 a)	Middle Pleistocene	(16)
	No.21	–		(16)
	No.23	–		(16)
	No.82	+ (Figure 4 b)		(16)
	No.85	+ (Figure 4 c)		(16)
	No.130'	+ (Figure 4 d)		(16)
	PA110	– (Figure 5 g)		(25)
Xichuan in Henan	PA526	+ (Figure 5 c)	(Drug store)	(25)
	PA527	+ (Figure 5 d)		(25)
Panxiandadong in Guizhou	PA1578	– (Figure 5 h)	Late Middle Pleistocene	(25)
Xiahe in Gansu	Xiahe	+ (Figure 5 e)	Late Middle Pleistocene	(26)
Penghu in Taiwan	Penghu1	+ (Figure 5 f)	Late Middle Pleistocene	(27)
Daoxian in Hunan	PA1545	–	Early Late Pleistocene	(8)
	PA1585	–		
Tianyuandong in Zhoukoudian	PA1281	– (Figure 5 j)	Late Pleistocene	Present study
Weijiadong in Guizhou	WJD-H1	+ (Figure 5 a)	Late Pleistocene	Present study
Dushandong in Guangxi	Dushandong	3 roots	Late Pleistocene	(10)

(+ present, - absence)

Table 3 Frequency of Tomes' root in Neolithic and historic remains from China and modern populations.

Specimen site	Tomes' root frequency	Age	Source
Miaozigou	76.0% (N=25)	Neolithic 5000 BP	(28)
Xiawanggang	70.1% (N=137)?	Neolithic 4500-5000 BP	(29)
Jiangjialiang	80.65% (N=62)	Neolithic to 3000 BP	(30)
Shanxi longxian	47.4% (N=57)	Warring States Period, Han and Tang Dynasty 475-221B.C., 618-907A.D.	(31)
Zhaitouhe and Shijiahe	38.5% (N=13)	Warring States Period 475-221B.C. (32-33)	Present study
Lintong Qujia Lintong Wanli Baoji Fenggeling	32% (N=66)	Qin Dynasty 221-206 B.C. (34)	Present study
Modern Chinese	18.9% (N=249)	Modern population	(35)
Global Modern Human	19.9% (N=1371)	Modern population	(10)
Northeast Siberia, American Arctic, New Guinea.	0-10%	Modern population	(23)
Western Eurasia, Nubia, East Asia, North and South America, Polynesia, Melanesia, Micronesia.	10-20%	Modern population	(23)
Sub-Saharan Africa, Australia, Southeast Asia.	20-25%	Modern population	(23)