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The Xujiayao 14 Mandibular Ramus and Pleistocene *Homo* Mandibular Variation

*Branche mandibulaire de Xujiayao 14 et variation mandibulaire chez l'*Homo *pléistocène*

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ABSTRACT

The earlier Late Pleistocene mandibular ramus from Xujiayao (northern China) preserves traits that vary distributionally among western Old World Pleistocene *Homo* samples and between Early/Middle Pleistocene archaic humans and Late Pleistocene modern humans in eastern Eurasia. Xujiayao 14 presents a lateral mandibular notch crest, an open mandibular foramen, a wide ramus, an asymmetrical mandibular notch, an enlarged superior medial pterygoid tubercle, (probably) a retromolar space, and gonial eversion, as well as an unusual depression in the *planum triangulare*. The first two traits appear ancestral for Later Pleistocene and recent *Homo* and are dominant among modern humans. The second two traits largely separate Xujiayao 14 and archaic *Homo* from modern humans. The next two traits are found in the highest frequency among the Neandertals, although gonial eversion contrasts with Late Pleistocene Neandertals. Xujiayao 14, in the context of Pleistocene and recent *Homo* samples and the other Xujiayao human remains, therefore provides a morphological mosaic, highlighting regional variation through the Pleistocene.

RÉSUMÉ

Cet article décrit une branche mandibulaire humaine du Pléistocène supérieur ancien trouvée à Xujiayao (Chine du Nord). La pièce porte des caractères dont la distribution varie parmi les groupes attribués à *Homo* et issus de l'Ouest de l'ancien monde, mais aussi entre les hommes archaïques du Pléistocène ancien et moyen et les hommes modernes du Pléistocène supérieur d'Asie de l'Est. Dans le détail, Xujiayao 14 présente une incisure mandibulaire en position latérale par rapport au condyle, un foramen mandibulaire en forme de V, une branche large, une incisure mandibulaire asymétrique, un tubercule ptérygoïdien médial supérieur développé, un probable espace rétromolaire et une éversion goniaque, ainsi qu'une dépression peu commune dans le *planum triangulare*. Les deux premiers traits semblent être primitifs pour les représentants tardifs du genre *Homo* et sont

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prédominants chez les hommes modernes. Les deux caractères suivants séparent nettement Xujiayao 14 et les représentants primitifs du genre *Homo* des hommes modernes. Les cinquième et sixième caractères sont les plus fréquents chez les Néandertaliens, alors que l' éversion goniaque tranche avec les Néandertaliens du Pléistocène supérieur. Xujiayao 14, considéré dans le contexte à la fois des représentants récents et du Pléistocène du genre *Homo* et des autres restes humains de Xujiayao, présente une mosaïque morphologique qui met en évidence l'existence d'une variabilité régionale au cours du Pléistocène.

1. Introduction

There have been a number of assessments of mandibular variation among western Old World Pleistocene humans (from Europe, Africa and southwestern Asia), many of them focused on identifying the extent to which the mandibles of the western Eurasian Neandertals diverge from the ancestral *Homo* and modern human patterns (e.g., Carbonell et al., 2005; Howells, 1975; Lebel and Trinkaus, 2002; Rak et al., 1994; Rosas, 2001; Smith, 1978; Stefan and Trinkaus, 1998a). From these comparisons, despite documented variation within paleontologically defined samples (Rosas, 2001; Stefan and Trinkaus, 1998b), it has become apparent that certain aspects of the mandibular ramus achieved higher frequencies among the Neandertals than among other human groups.

In these assessments, there has been only occasional reference to Pleistocene human mandibular variation east of ~50° E longitude (Carbonell et al., 2005; Rosas, 2001); assessments of those eastern remains have been principally in the context of fossil descriptions (e.g., Kaifu et al., 2005; Shang and Trinkaus, 2010; Suzuki, 1982; Weidenreich, 1936; Woo, 1964; Wu, 1980), with pan-Old World reference principally to the Earlier Pleistocene remains. This situation has been driven in part by the dearth of Pleistocene *Homo* mandibles in eastern Eurasia, particularly of late archaic humans. Currently, one such specimen is known, the Xujiayao 14 mandibular ramus. It has received little more than inventorial mention (Wu, 1980; Wu and Poirier, 1995), but it provides information on several of the features that have figured prominently in western mandibular assessments. It can therefore be placed in the contexts of the Early and Middle Pleistocene specimens from Zhoukoudian, Sangiran and Chenjiawo (Lantian) and Late Pleistocene early modern humans from Tianyuandong, Moh Khiew, Upper Cave (Zhoukoudian) and Minatogawa, as well as samples of Pleistocene archaic and modern humans from the western Old World.

2. Materials and methods

2.1. Xujiayao 14

Xujiayao 14 is a right mandibular ramus with a largely complete lateral surface but a partial medial surface (Fig. 1). The condylar neck is complete, but the condyle is absent. The coronoid process is largely complete. The mandibular notch is intact, with minor damage to the anterior edge just below the coronoid tip but continuing to the original edge of the condyle. The tip of the coronoid process was reduced antemortem, such that the original height was probably a few millimeters higher and the highest point was more anterior. The posterior ramal margin is intact from the condylar neck around gonion and the medial pterygoid insertion. The inferior margin is present laterally but not medially. The anterior margin of the ramus is present to the level of the distal M_3 alveolus, but there is no trace of the M_3 socket or of the porous retromolar surface. The medial surface is missing bone along the inferior alveolar nerve canal, preserving the floor of the canal by the mandibular foramen; it lacks the anterosuperior canal margin and the lingula, but the superior 14.5 mm of the posteroinferior margin is intact.

The mandible (Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) PA 1497) was excavated in 1977 at the Xujiayao (Hsuchiayao) site, Locality 74093 in Houjiayao village, northwestern Nihewan Basin, Hebai Province, northern China (40° 06′ 02″ N, 113° 58′ 39″ E) (Wu, 1980). The deposits consist of open-air fluviatile and lacustrine deposits, with erosional surfaces present within stratigraphic layers of sandy or silty clay. The 1976, 1977 and 1979 excavations yielded thousands of lithic artifacts, abundant faunal remains, and 17 fragmentary human remains from a sloping layer of yellowish-green clay, that was between 8 and 12 m below the modern surface (Chia and Wei, 1976; Chia et al., 1979). The faunal assemblage is dominated by late Middle and earlier Late Pleistocene species (Chia et al., 1979) and includes both colder and more temperate species; a cooler climatic inference is supported by palynological remains (Yan et al., 1979).

A precise radiometric age for the archeological level has remained elusive. Uranium-series dating on *Equus* sp. and *Coelodonta antiquitatis* tooth enamel provided mean ages between ~104 ka BP and ~125 ka BP (Chen et al., 1982, 1984), within Marine Isotope Stage (MIS) 5. The deposits are above a paleomagnetically reversed sequence, below ~15 mm, which has been interpreted as the early MIS 5 Blake Excursion (Liu et al., 1992), 119–126 ka BP (Lund et al., 2006). Preliminary optically stimulated luminescence (OSL) dating of the archeological horizon provided late MIS 4 ages (60 ± 8 and 69 ± 8 ka BP) (Nagatomo et al., 2009). The Xujiayao human remains therefore derive from early Late Pleistocene (MIS 5 to 4) deposits. Morphologically, the full human fossil sample represents late archaic humans and are distinct from *H. erectus* and early modern humans (Chia et al., 1979; Wu, 1980, 1986; Wu and Poirier, 1995). In particular, the Xujiayao 6 and 12 occipital bones, the Xujiayao 15 temporal bone and the Xujiayao 1 dentition lack distinctive external morphological features of the Neandertals.

Fig. 1. Views of the Xujiayao 14 mandibular ramus. Above left: lateral; above right: superior; below left: medial; below right: posterior and slightly inferior. The condyle and the anterosuperior margin of the mandibular foramen (with the lingula) were lost postmortem. The coronoid tip was reduced antemortem, such that the original tip should have been higher and slightly more anterior.

Fig. 1. Vues de la branche mandibulaire de Xujiayao 14. En haut, à gauche : latérale ; en haut, à droite : supérieure ; en bas, à gauche : médiale ; en bas, à droite : postérieure et légèrement inférieure. Le condyle et le bord antéro-postérieur du foramen mandibulaire (avec la lingula) ont été perdus postmortem. L'extrémité coronoïde a été réduite antemortem, de sorte que l'extrémité d'origine devrait avoir été plus haute et légèrement plus antérieure.

The Xujiayao 14 mandible is assessed using the one standard linear measurement preserved (minimum ramal breadth) and a set of discrete traits. For internal visualization, the mandible was μCT scanned using an industrial CT scanner (225 KV μCT, made by the Institute of High Energy Physics CAS) in the IVPP (tube voltage 150 kV; tube current 110 μA; pixel size: 50.5 μm).

2.2. *Ramal Comparisons*

The Xujiayao 14 mandibular ramus is scored for the six discrete traits (Fig. 2). They include:

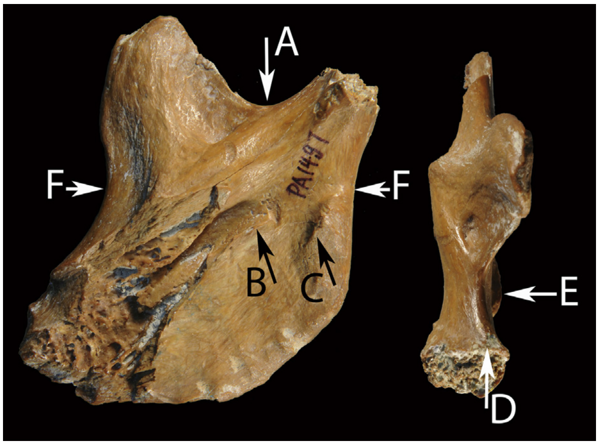

Fig. 2. Ramal discrete traits, indicated on the Xujiayao 14 mandible. A: mandibular notch (asymmetrical); B: mandibular foramen posterior margin (open); C: superior medial pterygoid tubercle (enlarged); D: notch crest to condyle (lateral); E: gonion (everted); F-F: minimum ramus breadth.

Fig. 2. Traits discrets de la branche, indiqués sur la mandibule de Xujiayao. A : incisure mandibulaire (asymétrique) ; B : bord postérieur du foramen mandibulaire (ouvert) ; C : tubercule ptérigoïdien supérieur médial (développé) ; D : crête d'encoche latérale par rapport au condyle ; E : éversion goniaque ; F : largeur minimum de la branche.

- mandibular notch asymmetry;
- mandibular foramen bridging;
- mandibular notch crest to condyle position;
- gonial eversion;
- superior medial pterygoid tubercle enlargement, as well as;
- retromolar space presence.

The first two features appear to be unrelated to craniofacial spatial or functional considerations, although the second has been associated with hypertrophy of the sphenomandibular ligament (Richards et al., 2003; Smith, 1978). The second pair of traits may be related to mediolateral proportions of the ramus relative to the cranial base and neurocranial vault, in that the crest to condyle position may reflect the mediolateral positioning of the crest and/or the condyle on the ramus, and gonial eversion may relate to masseteric hypertrophy and zygomatic positioning. An enlarged superior medial pterygoid tubercle, in the context of smaller more inferior ones, should reflect differential hypertrophy of those more superior fibers, which may relate to craniofacial proportions (Richards et al., 2003). And retromolar space presence is a product of the interrelationship of mandible length, ramal breadth and dental arcade length (Franciscus and Trinkaus, 1995) and appears to be allometrically scaled with superior mandibular length (Rosas and Bastir, 2004). In addition, as an indication of ramal size, the minimum ramus breadth [Martin #71a (Bräuer, 1988)] of Xujiayao 14 is compared across the Pleistocene *Homo* samples. The Xujiayao 14 ramus also has a distinct pit within the *planum triangulare*, an unusual feature briefly considered with respect to Pleistocene *Homo* rami. These features, most of which can be seen to be direct or indirect products of craniomandibular hypertrophy and/or proportions, can nonetheless serve to assess late archaic and early modern human mandibular ramal variation across the Old World.

The Xujiayao 14 mandible and Pleistocene *Homo* samples are compared to each other and to recent humans using alternative character state frequencies. Rami are bilateral, and right-left configurations are not necessarily independent; sample sizes therefore refer to individuals, and the frequencies employ bilateral averages, counting each side as 0.5 in cases of bilateral asymmetry and assuming symmetry when only one side is preserved for the trait. When character states divide a continuous morphology, intermediate forms are scored as 0.5 for each configuration.

2.3. Comparative samples

The first comparative sample consists of other East Asian Pleistocene human mandibular rami, listed individually in Table 1. The other such samples consist of Pleistocene *Homo* mandibles from the western Old World (Africa, Southwest Asia and Europe) (Table 2 and Appendix) and two recent (late Holocene) modern humans samples. These samples are composed so as to provide comparative distributions through the Pleistocene and take into account the Late Pleistocene differences between Neandertal and early modern human craniofacial morphology. In addition, given the emergence of "Neandertal" craniofacial and dental morphology in western Eurasia during the Middle Pleistocene (Arsuaga et al., 1997; Martinón-Torres et al., 2013; Stefan and Trinkaus, 1998a; Trinkaus, 1987), the Middle Pleistocene sample is separated into an African one and a western Eurasian one.

The first "western" sample therefore consists of Late Pleistocene western Eurasian late archaic humans (Neandertals), from MIS 6/5 to 3. They are joined by a sample of early modern humans from western Eurasia and north Africa, from MIS 5 to early MIS 2; there is little difference in ramal morphology between the MIS 5 and the MIS 3-2 early modern humans (Trinkaus and Rougier, 2013) and the samples are therefore pooled. The earlier samples consist of a Middle Pleistocene African one, a Middle Pleistocene "Neandertal lineage" one from western Eurasia, and a small Early Pleistocene sample from southwest Asia and Africa. Data for late Holocene recent humans derive from modern Chinese and Euroamericans.

The paleontological observations are from the original specimens (when possible), published descriptions, and/or high quality casts. The latter two sources apply particularly for the lost Předmostí and Zhoukoudian specimens. For traits that do not appear to change during development (mandibular notch asymmetry and mandibular foramen bridging), older juvenile and adolescent specimens are included in the samples; the other features are known to change with facial growth or may well do so (Coqueugniot, 1999; Rhoads and Franciscus, 1996; Richards et al., 2003), and they are only scored on late adolescent and adult mandibles.

Table 1
Configurations of mandibular ramal discrete traits for eastern Eurasian Pleistocene humans.
Tableau 1
Configurations des traits discrets de la branche mandibulaire pour les hommes pléistocènes de l'Eurasie orientale.

	Retromolar Space	Notch Asymmetry	Crest/Condyle	Mandibular Foramen	Medial Pterygoid	Gonial Eversion
Early/Middle Pleistocene						
Sangiran 8	Absent					
Sangiran 9	Absent					
Sangiran 21		Asym	Middle			
Chenjiawo 2	Absent					
ZKD G1	Absent			Open		
ZKD G2	Absent	Asym	Lateral	Open	Absent	Everted
ZKD H1	Absent		Lateral	Open	Absent	Everted
Late Pleistocene Archaic						
Xujiayao 14	**(Present)**	**Asym**	**Lateral**	**Open**	**Present**	**Everted**
Late Pleistocene Modern						
Minatogawa 1	Absent	Symm	Lateral	Open	Present	Straight
Minatogawa 5			Lateral	Open	Present	
Minatogawa 6						
Minatogawa 7	Present					
Moh Khiew 1	Absent	Symm	Lateral	Open		Everted
Tianyuan 1	Absent	Symm		Open	Absent	Inverted
ZKD UC 101	Pres/abs	Symm	Lateral	Open	Absent	Everted
ZKD UC 103	Absent					
ZKD UC 104	Absent	Symm	Lateral	Bridged	Absent	Everted
ZKD UC 108	Absent					
Early Holocene Modern						
Qi He 1	Absent	Symm	Lateral	Open	Absent	Inverted
Qi He 2	Absent	Symm	Lateral	Open	Absent	Everted

ZKD: Zhoukoudian Locality 1; ZKD UC: Zhoukoudian Upper Cave, or Upper Cave.

Table 2
Comparative frequencies of mandibular ramal discrete traits, for Pleistocene *Homo* and recent humans [% (N)], arranged in terms of the most common character state among recent humans.
Tableau 2
Fréquences comparées des traits discrets de la branche mandibulaire chez l'*Homo* pléistocène et les hommes récents (% (N)) arrangées en termes de l'état du plus commun caractère chez les hommes modernes.

	Retromolar Space % Absent	Mand. Notch % Symmetrical	Crest/Condyle % Lateral	Mandibular Foramen % Open	Sup. Medial Pterygoid % Absent
West Early Pleistocene	100% (3)	60.0% (5)	100% (3)	100% (4)	100% (3)[a]
Africa Middle Pleistocene	100% (6)	66.7% (3)	75.0% (4)	100% (5)	100% (2)
West Middle Pleistocene	35.0% (20)	55.0% (10)	26.7% (15)	91.7% (12)	40.0% (10)
West Late Archaic	25.0% (36)	27.8% (18)	50.0% (20)	61.5% (39)	19.0% (21)
West Early Modern	81.6% (38)	94.1% (34)	96.9% (32)	98.4% (34)	100% (19)[b]
All Early Modern	81.5% (46)	95.0% (40)	97.3% (37)	96.3% (40)	91.7% (24)
Recent East Asian (100)	100%	96.5%	91%[c]	100%	91.5%
Recent Euroamerican (40)	100%	95.0%	96.3%	97.5%	100%

[a] Carbonell et al. (2005) described the ATD6-96 mandible as having an enlarged superior medial pterygoid tubercle ("The medial pterygoid tubercle is well developed." p. 5675), but inspection of their photograph shows it to be far less prominent that those of Xujiayao 14 and most Neandertals. It is counted as absent here, but mentioned in the text.

[b] An enlarged superior medial pterygoid tubercle is also present on Dolní Věstonice 3 (Franciscus et al., 2006), but it is not included given the pathological condition of the mandible (Trinkaus et al., 2006).

[c] The percentages includes 10 East Asian and 3 Euroamerican mandibles with an intermediate position of the crest on the condyle, counted as 0.5 for each position.

3. Mandibular Ramus Variation

3.1. Ramal Breadth

The Xujiayao 14 has a minimum ramus breadth of 44.5 mm, which is the largest Pleistocene one known from East Asia (Fig. 3), falling above the two Middle Pleistocene values from Zhoukoudian and the early modern human values from Minatogawa, Moh Khiew, Tianyuan and Upper Cave; it is probably also modestly above that of the Early Pleistocene Sangiran 21 (Kaifu et al., 2005). It is at the top of the Late Pleistocene western samples, exceeded only by those of the Nazlet Khater 2 and Oase 1 early modern humans and the Shanidar 4 Neandertal. It falls in the middle of the pooled western Middle Pleistocene sample and below the two Early Pleistocene rami (Dmanisi D2600 and KNM-ER 992). It therefore has a ramal breadth most similar to those of western Middle Pleistocene mandibles. Nonetheless, although there is a general trend for rami to become narrower through Pleistocene *Homo* (ANOVA $P = 0.004$ across the comparative samples), there is substantial intergroup overlap.

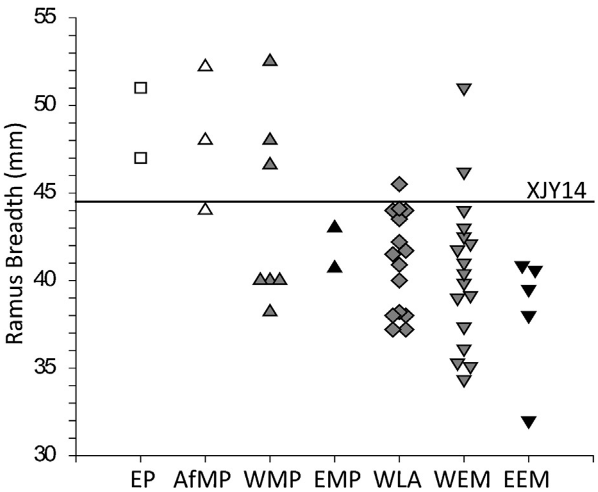

Fig. 3. Distributions of minimum ramus breadth in Pleistocene *Homo* samples. XJY14: Xujiayao 14; EP: Early Pleistocene; AfMP: African Middle Pleistocene; WMP: western Eurasian Middle Pleistocene; EMP: eastern Eurasian Middle Pleistocene; WLA: western Eurasian late archaic (Neandertals); WEM: western Eurasian early modern; EEM: eastern Eurasian early modern.

Fig. 3. Distributions de largeur minimum dans les échantillons d'*Homo* pléistocène. XJY14 : Xujiayao 14 ; EP : Pléistocène précoce ; AfMP : Pléistocène moyen africain ; WMP : Pléistocène moyen d'Eurasie occidentale ; EMP : Pléistocène moyen d'Eurasie orientale ; WLA : Archaïque récent d'Eurasie occidentale (Neandertals) ; WEM : Moderne précoce d'Eurasie occidentale ; EEM : Moderne précoce d'Eurasie orientale.

3.2. Mandibular Notch Asymmetry

It is possible to quantify the shape of the mandibular notch (Rak et al., 2002), but the taphonomic fragility of the region means that few Pleistocene *Homo* mandibles preserve the notch and coronoid process intact, thereby minimizing the number of individuals providing data (and hence the perceived variation). It is therefore scored as symmetrical (the lowest point in the middle third) versus asymmetrical (the lowest point in the posterior third) (Stefan and Trinkaus, 1998b), thereby permitting the inclusion of less complete rami. On this basis, the mandibular notch of the Xujiayao 14 is asymmetrical, in that the lowest point of the notch is posterior to the middle third of the distance from the condyle to the coronoid process. An asymmetrical notch is present in Sangiran 21 and Zhoukoudian G2 (as well as the juvenile Zhoukoudian C1), but it is absent from all East Asian early modern humans, all but two of the western early modern humans (Muierii 1 and Ohalo 2), and most recent humans (Table 2). Asymmetrical notches reach the highest frequency among the Neandertals (72.2%), but they are reasonably common among Early and Middle Pleistocene *Homo*. This feature of Xujiayao 14 contrasts principally with the early and recent modern humans, and it is generally similar to archaic *Homo* across the Old World.

3.3. Mandibular Foramen Bridging

The complete bridging of the mandibular foramen by the lingula, known as "lingular bridging" and the "horizontal-oval foramen" (Kallay, 1955; Yamano and Yamaguchi, 1976) (it is distinct from and independent of bridging of the mylohyoid groove), consists of lingular enlargement and its fusion to the posterior margin of the foramen (Jidoi et al., 2000; Kallay, 1955; Richards et al., 2003; Smith, 1978). It is rare among recent humans (Table 2; Jidoi et al., 2000; Smith, 1978; Yamano and Yamaguchi, 1976), but it has been frequently noted on Middle and Late Pleistocene Neandertal lineage mandibles since Gorjanović-Kramberger (1906) and McCown and Keith (1939). It is absent from Xujiayao 14, as is indicated by the intact posteroinferior margin of the mandibular foramen (Fig. 1). It occurs in one late Middle Pleistocene archaic specimen (Table 2), two early modern humans [Oase 1 (unilaterally) and Upper Cave 104 (bilaterally)], and 38.5% of the Neandertals.

3.4. Mandibular Notch Crest to Condyle Position

In most recent humans (all but one early modern human, Muierii 1), and most non-Neandertal Early to Middle Pleistocene humans (all but Sangiran 21 and Tighenif 2), the crest of the mandibular notch meets the condyle laterally, or within the lateral third of the condyle (Tables 1 and 2). Among the Middle and Late Pleistocene Neandertal lineage fossils, however, in a majority of them (60.0%; N = 35), the crest meets the middle third of the condyle. Although this variation is seen in terms of the position of the crest relative to the condyle, it probably relates principally to the positioning of the condyle on the condylar neck. Xujiayao 14 and all of the eastern Eurasian mandibles except Sangiran 21 conform to the majority pattern.

3.5. Gonial Eversion

In posterior view, the gonial region of Xujiayao 14 is distinctly everted, relative to the condylar neck and the lateral plane of the ramus (Fig. 1). In this feature, it is similar to the earlier Zhoukoudian remains. However, there is considerable variation within the fossil and recent samples (Tables 1 and 3). The Early to Middle Pleistocene samples are too small to be distributionally meaningful, the Neandertal mandibles are mostly inverted at gonion, the early modern humans ones are mostly straight, the recent human ones are mostly everted, and all of the forms occur in reasonable frequencies in each of the sufficiently large samples. Moreover, gonial profiles are asymmetrical in 7.1% of the pooled recent human sample (N = 140) and in two Pleistocene humans (Tighenif 3 and Dolní Věstonice 16). The Xujiayao 14 gonial eversion is therefore unexceptional in a fossil or recent human context, contrasting principally with the Neandertals.

Table 3
Comparative frequencies of gonial angle inversion, eversion and straight profiles, for Pleistocene *Homo* and recent humans.
Tableau 3
Fréquences comparées de l'inversion, éversion et des profils droits de l'angle goniaque chez l'*Homo* pléistocène et les hommes modernes.

	Inversion (%)	Straight (%)	Eversion (%)
West Early Pleistocene (3)	100	0.0	0.0
Africa Middle Pleistocene (3)	16.7	0.0	83.3
West Middle Pleistocene (7)	35.7	35.7	28.6
West Late Archaic (22)	68.2	27.3	4.5
West Early Modern (26)	15.4	71.2	13.5
All Early Modern (31)	16.1	62.9	21.0
Recent East Asian (100)	10.5	26.5	63.0
Recent Euroamerican (40)	6.3	26.3	67.5

3.6. Superior Medial Pterygoid Tubercle Enlargement

Neandertals have been noted (Rak et al., 1994) for the frequent differential enlargement of the superior medial pterygoid tubercle on the medial ramus, tubercle #6 or the "medial pterygoid tubercle" (MPT) of Richards et al. (2003); following them and Creed-Miles et al. (1996), it is considered equivalent to the *tuberculum pterygoideum inferius* of Weidenreich (1936). More specifically, it is scored as "present" if this tubercle is strongly developed *in contrast to* the smaller ones that occur more inferiorly on the gonial margin (cf. Rak et al., 1994). A general enlargement of all of the medial pterygoid tubercles around gonion, occasionally seen in recent human mandibles, does not qualify as "present" for this trait. Because the tubercle is frequently differentially enlarged on immature recent human mandibles (Creed-Miles et al., 1996; Richards et al., 2003), it is scored only on adolescent and adult mandibles.

On the Xujiayao 14 mandible, the superior tubercle is relatively and absolutely prominent (Figs. 1 and 4). There are five small ones inferiorly, each extending ~6 mm from the gonial margin and minimally raised from the medial surface. The superior tubercle, above these smaller ones, rises to a sharp point, extends 2 mm medially from adjacent surface bone and 8 mm anteriorly from posterior margin, and is ~12 mm high. Enlarged superior medial pterygoid tubercles, ones that are similarly enlarged both absolutely and relative to the more inferior ones, are occasionally present in other human mandibles (Table 2); they are evident in Minatogawa 1 and 5 and possibly ATD6-96 (Carbonell et al., 2005; Suzuki, 1982). They are found in elevated frequencies principally in the Neandertal lineage, occurring in 74.2% of the mandibles. This feature therefore aligns Xujiayao 14 predominantly, but not exclusively, with the roughly contemporaneous Neandertals.

3.7. Retromolar Space Presence

Xujiayao 14 retains all of the anterior ramal margin and a small portion of the superolateral corpus margin anterior of the ramus, but there is no trace of either the M_3 alveolus or of the retromolar alveolar bone (Fig. 1). There is a portion of the sulcus anterior of the *crista endocoronoidea* and *torus triangularis*. Internally, there is no evidence of trabecular bone or alveolar margin in the region in which an M_3

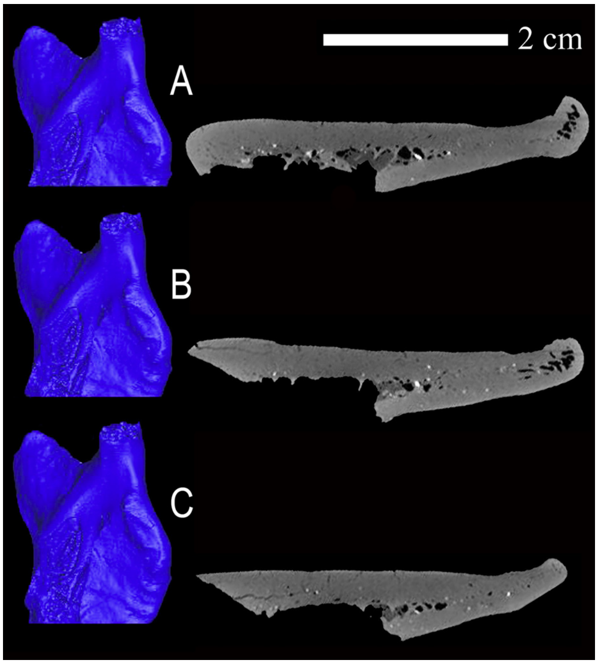

Fig. 4. Micro-computerized tomography (μCT) horizontal slices through the inferior Xujiayao 14 mandibular ramus, from the mid ramal height (A) to the inferior ramal portion (C). The CT slices are at the levels at which the ramus is truncated inferiorly in the posteromedial views of the mandible on the left.

Fig. 4. Coupes horizontales en tomographie informatisée (μm) au travers de la branche mandibulaire inférieure de Xujiayao 14, de la mi-hauteur (A) jusqu'à la portion inférieure(C). Les coupes CT, réalisées au niveau auquel la branche est tronquée dans sa partie inférieure, sont en vue postéro-médiale de la mandibule sur la gauche.

distal root socket should have occurred (Fig. 4). Comparisons with robust Late Pleistocene mandibles, with and without a retromolar space, indicate that evidence of the M_3 and/or retromolar alveolus should be on the preserved portion if a retromolar space was absent. In addition, the large dimensions of the Xujiayao 14 ramus, in a Pleistocene archaic human context, also suggest that a retromolar space should have been present (Rosas and Bastir, 2004). It therefore appears likely that the distal M_3 was mesial of the anterior ramal margin in *norma lateralis* [or that there was a retromolar space *sensu stricto* (Franciscus and Trinkaus, 1995)]. For these reasons, Xujiayao 14 is tentatively scored as having a retromolar space, bearing in mind the damage to the region.

As noted above, retromolar spaces are not features by themselves but are the results of the relative dimensions and positions of more primary aspects of the mandible (Franciscus and Trinkaus, 1995; Rosas and Bastir, 2004). They are absent in earlier *Homo* mandibles but are common among Neandertal lineage specimens and occasionally present among early modern humans (Table 2). If Xujiayao 14 possessed such a mandibular gap, it would suggest a relatively long mandible, given its wide ramus (Fig. 3) and the large dental dimensions of the Xujiayao 1 maxilla and the Xujiayao 2, 13 and 17 isolated molars (Chia et al., 1979; Wu, 1980). Among the ten Late Pleistocene mandibles with ramal breadths approaching or exceeding that of Xujiayao 14 (all ≥ 43 mm), half of them (all Middle Paleolithic in association) exhibit retromolar spaces.

3.8. *Planum Triangulare Depression*

On the medial aspect of the Xujiayao 14 superior ramus, between the *crista endocoronoidea* and the *crista endocondyloidea*, and hence within the *planum triangulare*, there is a distinct depression, with a small foramen in its anterior portion (Fig. 1). Among Pleistocene *Homo* (and recent human) mandibles, this region is generally flat or modestly concave, and it may be slightly convex. It rarely exhibits a distinct pit. In the pooled sample of Pleistocene *Homo* mandibles (N = 69), small depressions or pits are evident in only six mandibles, one of them unilaterally. They are distributed across most of the comparative samples [1 eastern early modern human (N = 6); 2 western early modern humans (N = 23); 1 Neandertal (N = 22); 1 western Middle Pleistocene human (N = 8); 1 Early Pleistocene mandible (N = 3)]. Moreover, in none of them does the size or depth of the depression approach that of Xujiayao 14. In eastern Eurasia, it is present only unilaterally on the Moh Khiew 1 mandible (Matsumura and Pookajorn, 2005) and on Xujiayao 14. Its significance is unclear, and it does not morphologically distinguish the comparative samples.

4. Discussion

From these comparisons, the Xujiayao 14 mandibular ramus provides a mixture of morphological affinities with respect to the Pleistocene *Homo* comparative samples. It is distinct from most early modern humans, across the Old World, in its wide ramus, asymmetrical mandibular notch and prominent superior medial pterygoid tubercle. It shows similarities to the Neandertals in its medial pterygoid insertion and probable retromolar space, as well as its asymmetrical mandibular notch, but it contrasts with most of them in having a distinctly everted gonion. Its open mandibular foramen appears ancestral, and it contrasts only with the one-third of the Late Pleistocene Neandertals who exhibit full lingular bridging.

It is nonetheless apparent that there is considerable variation within at least the larger paleontological samples. What largely emerges is a distinction between archaic *Homo* and modern humans, among both eastern and western Old World *Homo* mandibles and especially with respect to mandibular notch shape. The Neandertal lineage mandibles do exhibit higher frequencies of each of the configurations that contrast with the dominant recent human patterns (retromolar spaces, asymmetrical mandibular notches, middle condylar positions of the notch crest, bridged mandibular foramina, enlarged medial pterygoid tubercles and inverted gonions). Yet, all of the alternative character states are known among their mandibles. Moreover, each of the "Neandertal" patterns is documented in various of the comparative samples, albeit at lower frequencies.

Given these trait distributions, the Xujiayao 14 mandibular ramus principally contrasts with early and recent modern humans, from across the Old World. If it had derived from a western Eurasian early Late Pleistocene

(MIS 5-4) stratigraphic level, it could be easily subsumed within Neandertal ramal variation. Yet, several of its features (mandibular notch, crest/condyle, mandibular foramen and gonial forms) are easily subsumed within the variation of the presumed ancestral forms (including Early Pleistocene mandibles plus African and east Asian Middle Pleistocene specimens), and it is only its superior medial pterygoid tubercle enlargement (plus a probable retromolar space) that contrasts with earlier forms.

5. Conclusion

The early Late Pleistocene mandibular ramus from Xujiayao, Xujiayao 14, presents a wide ramus combined with several generalized archaic *Homo* discrete features of the ramus (asymmetrical mandibular notch, lateral notch crest on the condyle, open mandibular foramen and everted gonion). It exhibits a feature that is known principally among the western Eurasian Neandertals, an enlarged superior medial pterygoid tubercle in the context of small inferior ones, plus an inferred retromolar space. As the only available eastern Eurasian late archaic human mandible, and hence an N = 1, it cannot resolve the affinities among late archaic humans across Eurasia. However, rather than simply suggesting Neandertal affinities for this eastern contemporary of them, it raises questions regarding the distribution and significance of purported regional morphological variants among Pleistocene archaic humans.

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Appendix. Pleistocene mandibular ramal specimens included in the comparative samples. See text for sample parameters. Note that immature specimens (late juvenile and older) were only scored for traits that do not change during ontogeny (see text).

Spécimens de branches mandibulaires inclus dans des échantillons comparables. Voir le texte pour les paramètres des échantillons. À noter que les spécimens immatures (juvéniles tardifs et plus âgés) n'ont été répertoriés que pour les traits qui ne changent pas pendant l'ontogénie (voir texte).

Early Pleistocene: Africa, Europe & SW Asia	*Middle Pleistocene: Europe & SW Asia*
Atapuerca ATD6-96	Arago 2, 13
Dmanisi D2600, D2735	Atapuerca-SH 1, 75, 300, 303, 505, 604, 605, 607, 721, 792, 888, 950, 1157, 2193
KNM-ER 992	Aubesier 11
KNM-WT 15000	Azykh 1
	La Chaise-Suard 9
	Ehringsdorf 6
	Mauer 1
	Montmaurin 1
	Tabun 2
Middle Pleistocene: Africa	
Baringo KNM-BK 67, 8518	
Olduvai OH-23	
Tighenif 1, 2, 3	
Thomas 1	
Late Pleistocene: Modern Humans	***Late Pleistocene: Neandertals***
Brno 2, 3	Amud 1
Caviglione 1	Arcy-Hyène 9
Cro-Magnon 4253(1), 4256, 4258	Banyoles 1
Les Cottés 1	La Chaise-Bourgsois-Delaunay 1
La Crouzade 4	La Chapelle-aux-Saints 1
Dolní Věstonice 3, 13-16	Combe Grenal 3
Grotte-des-Enfants (Fanciulli) 4	La Ferrassie 1
Haua Fteah 1, 2	Guattari 2, 3
Kostenki 3, 4	Kebara 2
Mittlere Klause (Neuessing) 2	Krapina 53, 57, 59, 61, 63, 65-71, 73
Mladeč 52, 54	Malarnaud 1
Muierii 1	Le Moustier 1
Nazlet Khater 2	La Naulette 1
Oase 1	Palomas 1, 23, 59, 80
Ohalo 2	La Quina 5, 9
Paglicci 12, 20, 24, 25	Regourdou 1
Pataud 1	Saint-Césaire 1
Pavlov 1	Scladina 9, 4A-1
Předmostí 1-5, 9, 10, 14, 21,	Shanidar 1, 2, 4
Qafzeh 7, 9-11, 15, 27	Sidrón 1-3
Skhul 4-7	Spy 1, 2
Sunghir 1-3, 6	Subalyuk 1
	Švédův stůl (Ochoz) 1
	Tabun 1
	Vindija 206, 207, 226, 231, 250
	Zafarraya 2

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