Xujiayao *Homo*: A New Form of Large Brained Hominin in Eastern Asia

XIUJIE WU*
Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, CHINA; wuxiujie@ivpp.ac.cn

CHRISTOPHER J. BAE*
Department of Anthropology, University of Hawai'i at Manoa, Honolulu, HI, USA; cjbae@hawaii.edu

*corresponding authors: Xiujie Wu; *wuxiujie@ivpp.ac.cn*; and, Christopher J. Bae; *cjbae@hawaii.edu*

submitted: 7 April 2023; revised: 5 September 2023; revised: 26 February 2024; accepted: 10 March 2024

Guest Editors: Mirjana Roksandic (Department of Anthropology, The University of Winnipeg) and Christopher J. Bae (Department of Anthropology, University of Hawai'i at Manoa)

Handling Editor in Chief: Karen Rosenberg

ABSTRACT

Xujiayao, located in northern China, is an important paleoanthropological site because it dates to the late Middle Pleistocene (~200 ka – ~160 ka) and has a combination of hominin fossils, archaeology, and other vertebrate faunal traces. Unfortunately, since the Xujiayao hominin fossils were found in the mid-1970s, their taxonomic assignment has yet to be settled. Evaluations of the Xujiayao taxonomic position have ranged from being representative of Asian *Homo erectus*, Neanderthals, intermediate between *H. erectus* and modern *H. sapiens*, to being skeletal representatives of the Denisovans, to being related to Xuchang 1, Penghu 1, and/or Xiahe 1, or possibly even representing a previously unidentified hominin species. In fact, the Xujiayao hominin fossils are quite unusual in their morphology, primarily because of their: 1) very large cranial capacity combined with a low and wide cranial shape; 2) unusual Neanderthal-like bi-level nasal floor, temporal labyrinthine proportion, and thin occipital torus; 3) relatively large dentition that has a mosaic of primitive and derived features; 4) a slow rate of dental growth and development state that is more in line with modern humans than earlier hominins; and, 5) a mosaic of archaic and modern features of the mandible and temporal bone. The Xujiayao hominin fossils have several basal East Asian traits despite their young geological age, a few Neanderthal morphologies that are common but not exclusive to that lineage, and traits that are not seen in either archaic or recent humans including other late Middle Pleistocene hominins from the region, except Xuchang, Penghu 1, Xiahe 1, and the Denisovans. Collectively, these fossils represent a new form of large brained hominin (Juluren) that was widespread throughout much of eastern Asia during the late Quaternary.

INTRODUCTION

Pleistocene hominin fossils reported in China have been traditionally classified into *Homo erectus*, early modern humans, and something in the middle. This latter group of fossils generally date to the late Middle Pleistocene to early Late Pleistocene and cannot easily be assigned to *H. erectus*, but yet, cannot be called early *H. sapiens*. These intermediate hominins mainly include Dali, Jinniushan, Maba, and Xujiayao (Liu et al. 2014) and are traditionally referred to as archaic *H. sapiens* or mid-Pleistocene *Homo* (Bae 2010; Bae et al. 2017; Pope 1992; Wu and Athreya 2013; Wu and Poirier 1995). Fossils that have been more recently discovered like Xuchang (Li et al. 2017a), Penghu 1 (Chang et al. 2015), the Denisovans (Reich et al. 2010; Zubova et al. 2017), Hualongdong (Wu et al. 2019), Xiahe (Chen et al. 2019), Harbin (Ni et al. 2021), and the recently reported Tam Ngu Hao 2 mandibular molar (Demeter et al. 2022) are only adding further to this increasingly complex record (Harvati and Reyes-Centeno 2022).

Various hypotheses have been proposed to best explain this complex hominin fossil record, including the possibilities that these Chinese mid-Pleistocene *Homo* fossils represent: 1) regional continuity linking Asian *H. erectus* and modern Chinese (Wolpoff et al. 1984; Wu and Poirier 1995); 2) possibly an earlier hominin dispersal from western Eurasia (Groves and Lahr 1994); 3) or possibly even introgression between later dispersing western Eurasian hominins and indigenous groups (Martinón-Torres et al. 2007). Among these taxonomically unclear Chinese mid-Pleistocene *Homo* specimens, one of the most debated sets of fossils are the Xujiayao hominins. Since the discovery of the Xujiayao hominin fossils in the mid-1970s, they have been intensely analyzed, primarily because their unusual suite of traits does not conform to existing patterns of morphology either from the time period or the specific region. What particularly stands out about the Xujiayao hominin fossils is their very large cranial capacity, several primitive dental and cranial early East Asian traits despite their young geological age, Neanderthal traits that are common but not exclusive to that lineage, and traits that are not seen in either archaic or recent humans including other Middle Pleistocene hominins from the region (Wu et al. 2012, 2014, 2022; Wu and Trinkaus 2014; Xing et al. 2015).

Despite a plethora of studies (e.g., Chia et al. 1976, 1979; Wu 1980, 1986; Wu and Trinkaus 2014; Wu et al. 2012, 2014, 2022; Xing et al. 2015), the taxonomic assignment of the Xujiayao fossils has yet to be settled. Evaluations of the Xujiayao taxonomy have ranged from being representative of *H. erectus* (Chia et al. 1976, 1979), Neanderthals (Wu 1980), intermediate between *H. erectus* and modern *H. sapiens* (Wu 1986), to being the skeletal representatives of the Denisovans, a group that has previously been identified solely on their aDNA (Gokhman et al. 2019; Reich et al. 2010), to being related to Penghu 1 (Chang 2015), Xuchang 1 (Li et al. 2017a), and/or Xiahe 1 (Chen et al. 2019), or possibly even a previously unidentified hominin species (Xing et al. 2015). Here, we provide a new analysis, and delve deeper into this complex puzzle and provide some clarification regarding the taxonomic position of the Xujiayao hominin fossils (see also Bae 2024; Wu et al. 2022).

BACKGROUND AND GEOLOGICAL AGE

The Xujiayao hominin fossils were found in the 1970s *in situ* during excavations conducted at Locality 74093 (40° 06′ 02″ N, 113° 58′ 39″ E) of the Xujiayao (Houjiayao) site, north of the Yellow River in Hebei Province, northern China (Chia et al. 1976, 1979). The associated fauna is comprised of 19 taxa, including 10 that are extinct species (*Microtus brandtioides, Gazella* sp., *Coelodonta antiquitatis, Sus* sp., *Megaloceros ordosianus, Cervus nippon grayi, Bos primigenius, Spirocerus hsychayaocus, Spirocerus peii, Palaeoloxodon namadicus*), of which seven (36.8%) taxa (*Microtus brandtioides, Gazella* sp., *Canis lupus, Panthera* cf. *tigris, Coelodonta antiquitatis, Palaeoloxodon namadicus, Myospalax fontanieri*) are present at the older Middle Pleistocene Zhoukoudian Locality 1 site (Ji 1987).

The Xujiayao deposits are divided broadly into two main layers, with a total thickness over 20m deep. The base of the sedimentary deposits has yet to be reached. The cultural layers are located 4–12 m below the top soil, while the hominin fossils were found at a depth of 8–12 meters, in the middle and lower parts of the cultural layers (Chia et al. 1976, 1979). Based on the associated fauna and a set of optically stimulated luminescence (OSL) dates from samples drawn directly from the middle and lower cultural layers (Li et al. 2014, 2016; Tu et al. 2015), the Xujiayao hominins date to the late Middle Pleistocene, between 220 ka and 130 ka, or between 200 ka and 160 ka; largely placing the occupation in Marine Isotope Stage 6, a major glacial period. The average annual temperature in the Xujiayao area during occupation was estimated to have been 4°C lower than today (Hun et al. 2011). According to the analysis of the pollen grains found in the sediments, Xujiayao was once covered by a forest steppe vegetation (Yan et al. 1979). The thousands of stone balls unearthed from the site may have been a kind of projectile tool for the Xujiayao hominins to hunt *Equus przewalsky and E. hemionus* (Li et al. 2017b). Given the large number of faunal remains that have cutmarks and/or percussion marks, Xujiayao likely served as a butchering site and possibly a temporary home base for foraging groups (Norton and Gao 2008).

THE XUJIAYAO HOMININ FOSSILS

The Xujiayao hominin remains are comprised of twenty-one separate fossils, representing 16 individuals (Figure 1). These fossils include one partial left maxilla (XJY 1), three isolated teeth (XJY 2, 13, 16), two occipital bones (XJY 6a, 12), thirteen parietal fragments (XJY 3, 4a, 4b, 4c, 5a, 5b, 6b, 7, 8, 9, 10, 11, 15), one left temporal bone (XJY 6c), and one partial mandible (XJY 14). Although several of the Xujiayao hominin fossils have been studied in detail (e.g., Chia et al. 1976, 1979; Wu 1980, 1986; Wu and Trinkaus 2014; Wu et al. 2012, 2014, 2022; Xing et al. 2015), we present here, for the first time, a comprehensive description of the fossil collection. The Xujiayao fossils are curated at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences in Beijing.

XJY 1 MAXILLA

XJY 1 (PA 1480/No.1) is a left partial immature maxilla with six permanent teeth, one root, and one deciduous tooth all socketed (see Figure 1 A1–7). The dental row includes one tooth (the first molar M^1) *in situ* and in occlusion, the unerupted I^1 and C^1 originally in their crypts but currently separated, two unerupted premolars visible only radiographically ($P^3$and P^4), the second molar (M^2) in its crypt with partial occlusal exposure, and a deciduous second molar (dm2) fragment. Using x-ray multi-resolution synchrotron phase-contrast microtomography, the dental growth and development of XJY 1 were found to fall within modern human ranges, showing prolonged crown formation time and delayed first molar eruption. Based on the dental development standards of modern children, the age-at-death of XJY 1 is estimated to be ~6.5 years (Xing et al. 2019). The maxilla retains the alveoli from the intermaxillary suture to the distal M^2 crypt, with damage only to the labial I^2 alveolus and loss of thin bone over the incompletely erupted buccal M^2 crown. The intermaxillary

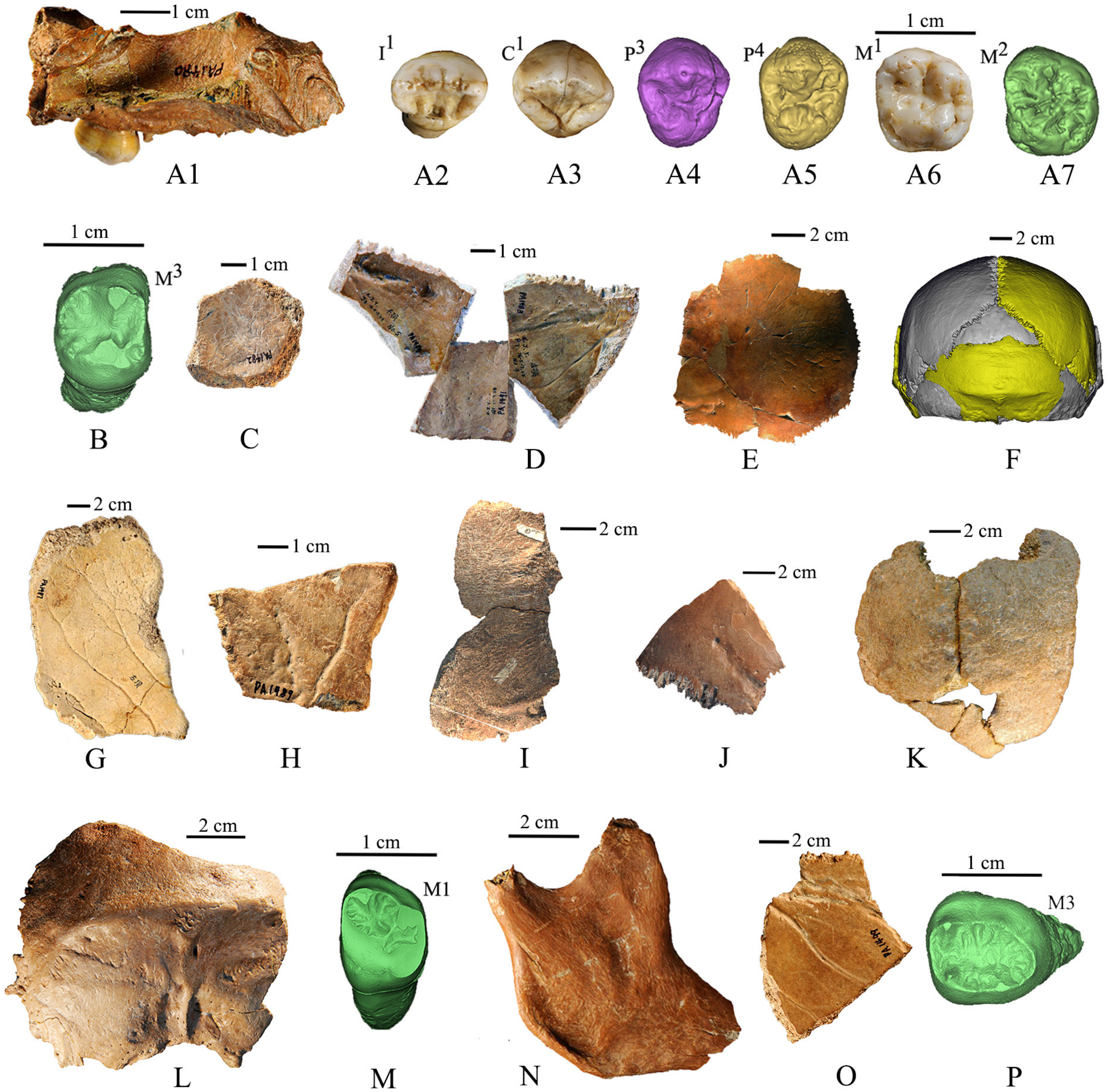

Figure 1. The Xujiayao human remains and individuals. **A1)** *XJY 1 maxilla in medial view;* **A2–7)** *The XJY 1 six permanent teeth in occlusal view,* I^1*,* C^1*, and* M^1 *are fossils;* p^3*,* p^4*, and* M^2 *are 3D virtual reconstructions;* **B)** *EDJ surface of XJY 2 upper right third molar;* **C)** *XJY 3 parietal bone in internal view;* **D)** *XJY 4 parietal bone in internal view;* **E)** *XJY 5 parietal bone in external view;* **F)** *3D virtual reconstruction of XJY 6 posterior cranium;* **G)** *XJY 7 parietal bone in internal view;* **H)** *XJY 8 parietal bone in internal view;* **I)** *XJY 9 parietal bone in external view;* **J)** *XJY 10 parietal bone in external view;* **K)** *XJY 11 parietal bone in external view;* **L)** *XJY 12 occipital bone in external view;* **M)** *EDJ surface of XJY 13 upper left first molar;* **N)** *XJY 14 mandibular ramus in lateral view;* **O)** *XJY 15 parietal bone in internal view;* **P)** *EDJ surface of XJY 16 upper left first molar.*

suture is intact from the nasoalveolar clivus from posterior to the incisive foramen, at which point the nasal floor/palate is broken obliquely from the posterior incisive foramen to the greater palatine foramen. The inferior margin of the nasal aperture and the adjacent nasal floor and nasoalveolar clivus are intact from where the vertical portion of the margin meets the sill to the midline. A distinct bi-level nasal floor of the maxilla is present, whose floor-palate line is 9.8mm below the anterior nasal spine. A bi-level nasal floor, although present in most Pleistocene hominins and recent humans, appears most frequently among western Eurasian Neanderthals. As such, this trait is considered a feature distinctive of Neanderthals (Wu et al. 2012).

The I^1 consists of a complete and unworn crown plus about one-third of the root. It displays a highly convex labial surface, a pronounced shovel shape, a well-developed tuberculum dentale, and two finger-like projections starting from the tubercle and ending at the middle of the deep lingual fossa.

The C^1 is unerupted and still sits in its crypt; it preserves the complete crown and part of the developing root. It displays a symmetrical pentagon crown profile, strongly developed marginal ridges, as well as several longitudinal projections on the lingual surface.

The P^3 and P^4 are unerupted and visible only radiographically. The crowns and developing roots are complete. The P^3 displays a relatively symmetric pentagon crown contour with one mesial and three distal accessory ridges, and a longitudinal depression along the mesial aspect of the root. The P^4 has a pentagon and slightly asymmetrical crown contour, a continuous transverse crest that connects the buccal cusp and the mesial marginal ridge, with strong distal accessory ridges on the buccal cusp, as well as a short and moderately pronounced distal groove on the buccal surface.

The M^1 is in its crypt and has a complete crown and nearly complete root. It is approximately square-shaped with a slight distobuccal constriction on the occlusal surface. The hypocone is large and can be divided into two portions by a groove that surrounds the lingual and distal aspects of the crown, with a distinct Carabelli's trait present. The occlusal surface is relatively complicated due to a developed accessory mesial marginal ridge, a deep Y-depression without a free apex (Carabelli's trait) in lingual aspect, and a three independent radicals root system, which bifurcate at about the cervical third of the root.

The M^2 has a complete crown, while the root has just begun its formation. It displays an asymmetrical trapezoid occlusal contour with an abbreviated distobuccal corner, a medium-sized hypocone, which is divided into two independent portions by a groove that appears continuous with the Carabelli's trait, a weakly developed but continuous crista obliqua, two mesial accessory ridges in the mesial aspect, and a small cuspule on the mesiolingual surface.

The XJY 1 dentition retains some primitive character traits classically found in East Asian Early and Middle Pleistocene hominins despite their young geological age. These include mass-additive features of the anterior dentition with well-developed tuberculum dentale, pronounced shovel shaped incisors, an asymmetrical crown outline of the premolar, a trapezoidal crown outline of the molar with a narrower distal half, and a robust and divergent root system of the molar, as well as a large crown size of all of the teeth, which generally fall outside or at the upper limit of variation of modern humans, European Middle Pleistocene hominins, and Neanderthals (Martinon-Torres et al. 2012; Xing et al. 2015). However, compared with other East Asian Middle Pleistocene hominins (e.g., Hexian, Chaoxian), the Xujiayao teeth are relatively more derived in some crown features. These more derived characters include less-pronounced finger-like projections in the incisor, a weaker canine essential ridge, simpler occlusal and buccal surfaces in P3 and P4, a more symmetrical P3 crown outline with a much smaller lingual cusp, a reduced M3 metacone, and an elliptical M3 crown outline (Xing et al. 2015). The Xujiayao teeth present some features that are common, but not exclusive to the Neanderthal lineage, such as a high degree of shovel shaping and labial convexity. However, they do not have classic Neanderthal-like dental characters, such as a continuous middle trigonid crest. The perikymata distribution of the unerupted I^1 and C^1 tends to be more similar to that of modern humans than to either early *Homo* or Neanderthals (Xing et al. 2015).

Pathologically, the Xujiayao juvenile maxillary teeth display a number of linear enamel hypoplasias. By matching the timing of linear enamel hyperplasia across multiple teeth, a minimum of five developmental disruptions were identified, indicating that the Xujiayao juvenile experienced several growth disturbances during its short lifespan. The large pit on the I^1 is an enamel hypoplasia due to its pre-eruptive enamel thinning instead of a post-eruptive fluorotic pit, and there is no evidence of chalkiness or opacity (Xing et al. 2015).

XJY 2, 13, AND 16 TEETH

Three isolated molars (see Figure 1 B, M, P), XJY 2, 13, and 16, are included in the assemblage. The three molars are all well-preserved, large, display moderate occlusal wear, and represent fully adult individuals.

XJY 2 is an upper right third molar with two coalesced buccal radicals plus one independent lingual root. It displays a semicircular crown outline, small metacone and hypocone, and a Carabelli's trait at the mesiolingual aspect of the crown.

XJY 13 is an upper left first molar with three independent robust roots. The molar shows an asymmetrical trapezoid crown outline, a continuous crista obliqua connecting the protocone with the metacone, projecting buccal and lingual walls of the mesial cusps, four different size accessory tubercles, and the Carabelli's trait in the mesiolingual aspect.

XJY 16 is a lower right third molar with two independent robust roots. The molar displays an oval crown outline, five main cusps with large hypoconulid, a continuous distal trigonid crest, highly crenulated dentine surface with a shelf-like structure on the buccal face of the hypoconid, and a conspicuous projection of the lateral surfaces of the mesial cusps from occlusal view.

XJY 3, 4, 5, 7, 8, 9, 10, 11, AND 15 PARIETAL FRAGMENTS

The Xujiayao isolated parietal bones belong to six adults (XJY 3, 4, 7, 8, 9, and 11) and three juveniles (XJY 5, 10, and 15). The Xujiayao parietal bones are thick with a mean of 10.9mm (range: 9.53–13.0mm) for adults, and 5.83mm (range: 4.52–7.74mm) for the juveniles. The measurements are taken in the center of the bones.

XJY 3 (see Figure 1 C) is a small portion of a left parietal bone which is 42.5mm in length and 34.1mm in width, with a thickness of 10.8mm in the center of the bone. The wide diploë (6.33mm) suggests an adult individual (Lynnerup et al. 2005).

XJY 4 (see Figure 1 D) includes three pieces of the anterior portions of the parietal bones—a fragment of left parietal bone with coronal suture; a fragment of the right parietal bone with coronal and sagittal sutures; and, part of a left parietal bone close to the sagittal suture. The preserved portion of all three when refit is 65.0mm in length and 119.0mm in width. Endocranially on the right side, there is a ~8mm diameter Pacchionian depression posterior to the bregma along the sagittal suture. The maximum thickness of the bone is 12.81mm with a wide diploë (8.1mm) in fine trabeculae. The coronal suture is bilaterally open with no indications of fusion. All characters suggest a young adult at death.

XJY 5 (see Figure 1 E) is a largely complete left parietal bone, 120.0mm in length and 107.0mm in width, with a thickness of 7.23mm in the center. The coronal, sagittal, squamous, and parietomastoid sutures all appear normal and open. The lambdoid suture has a largely straight section rising from asterion, and then a marked angle as it continues up to the posterior end of the sagittal suture. This probably represents the presence of a large lambda suture ossicle (or ossicles), such that anatomical lambda would have been posterior of the current extent of the sagittal suture. There is a slightly healed traumatic lesion in the posterosuperior area (Wu et al. 2015). Endocranially, there is a prominent sulcus along the coronal suture, and then a series of small and shallow sulci running superior and post-superior along the squamous suture, including a distinct posterior one. There is a broad Pacchionian depression along the mid-sagittal suture, 21mm long and 15mm wide. Given the completely open sutures on all sides and the relative thinness of the bone, XJY 5 probably represents an immature individual.

XJY 7 (see Figure 1 G) is the posterior portion of a left parietal bone that retains an eroded 40mm largely straight margin that was very close to the posterior sagittal suture that extends close to lambda. There is a largely complete parietomastoid suture that runs for 37mm, with the maximum dimension from anteroinferior to posterosuperior at 111mm. The intervening surfaces are present but show slight surface weathering. Endocranially, grooves for the posterior and posteroinferior meningeal vessels are clearly marked. Given the thickness of the bone (maximum: 9.53mm) and wide diploë (5.02mm), it is likely an adult.

XJY 8 (see Figure 1 H) is an anterior right parietal bone. It preserved 54mm in length, and retains 26mm of the coronal suture, but it is otherwise broken along its edges. The superior end of the anterior meningeal groove is present parallel to the coronal suture. The bone should therefore be close to bregma and the sagittal suture and well above the temporal line. There is a broad and shallow depressed area on the center of its exocranial surface that is suggestive of trauma (Wu et al. 2015). Given the thickness of the bone (10.71mm in the center) and the fine diploic trabeculae, XJY 8 is possibly an old adult (*sensu* Lynnerup et al. 2005).

XJY 9 (see Figure 1 I) is the inferior portion of a right parietal bone. It preserves the inferior coronal suture, all of the squamosal suture except the anteroinferior corner, the complete parietomastoid suture, and the inferior lambdoid suture. The temporal line is not evident anteriorly; posteriorly the superior and inferior temporal lines are separated, ending in a distinct linear angular torus whose anterior edge is along the temporal line and is accentuated by an irregular sulcus posteriorly. Endocranially, it exhibits the beginning of the anterior and posterior meningeal grooves, and the posteroinferior groove is evident above asterion. The bone is impressively thick (13.0mm in the center) and heavy, with a wide diploë (8.09mm). All of the sutures appear to have been completely open indicating a relatively young individual.

XJY 10 (see Figure 1 J) is the asterionic corner of the right parietal bone. It contains the posterior portion of the parietomastoid suture and the inferolateral end of the lambdoid suture. The endocranial surface preserves the end of the posteroinferior meningeal groove. Based on the thinness of the bone (4.53mm in the center) and the parietomastoid suture still being open, it belongs to a late juvenile to early adolescent.

XJY 11 (see Figure 1 K) is a pair of highly mineralized partial posteromedial parietal bones from an adult. The two larger pieces join tightly along the linear and partially obliterated sagittal suture, posteriorly extending to a congenital defect, that is an enlarged parietal foramen of unilateral (right) parietal lacuna with a posteriorly directed and enlarged endocranial vascular sulcus (Wu et al. 2013). The specimen extends 40–50mm to either side of the suture; the maximum preserved length is 91mm on one side and 74mm on the other side. Endocranially, there is a large Pacchionian depression along the suture on the largest of the pieces. Adjacent to the Pacchionian depression are two depressions, each identified as a granular foveola from Pacchionian granulations. The parietal bone is thick (10.62mm in the center) with a very thick diploë (5.64mm) and likely represents an adult individual.

XJY 15 (see Figure 1 O) is a small piece of the inferior anterior portion of a right parietal bone, with 20mm of the coronal suture, a portion of the deep groove for the anterior meningeal vessels, and the branches off of it. The preserved length is 63mm. The external surface has a series of parallel postmortem scratches, whose origin is probably sedimentary. Internally, a strong and double sulcus runs parallel to the coronal suture and then branches off of it, extending post-superiorly. Based on the thin bone (5.74mm in the center) and surface morphology, XJY 15 is a juvenile.

XJY 6 POSTERIOR CRANIUM

XJY 6 (see Figure 1 F) is comprised of an occipital bone (PA1486; XJY 6a), right parietal bone (PA1490; XJY 6b), and left temporal bone (PA 1498; XJY 6c). The three fossil fragments were found separately in 1976, 1977, and 1979, respectively. After virtual reconstruction (see also Wu et al. 2022), XJY 6 is represented by an almost complete posterior skull cap, consisting of largely complete parietal bones, almost complete temporal bones, an almost complete occipital planum and most of the nuchal planum. In general, the Xujiayao posterior cranium is large, low, and wide, with a round top in posterior view. The broadest region is situated in the posterior area of the temporal bone. No sagittal keel is present. Large sutural ossicles appear to have been present in the lambdoid area, with the original lambda present at the centrally converged point among the bilateral lambdoid and sagittal sutures.

The occipital torus is low, weak, and restricted to the middle 1/2 to 2/3 of the occipital bone, and becomes less thick laterally. The superior margin of the torus is not well delineated, but the inferior border seems coincident with the superior nuchal line. The torus surface is rounded laterally, with an oval rugose area in the middle. The external occipital protuberance is small and thin with a vertical crest on the midline torus, ~3.5mm superior to the tuberculum linearum with no evidence of a suprainiac fossa above the torus. The nuchal plane retains all of the right semispinalis capitis fossa and most of the left one, including the external occipital crest between the two fossae. The inferior nuchal line is present as a raised and wide rugosity at the inferior margins of each semispinalis capitis fossa. In lateral view, the transition between the nuchal planum and the occipital planum is an obtuse angle. Thickness in the midline sagittal section of the tuberculum linearum is 18.5mm with the outer table thick towards the middle. The parietal eminence area is smooth with no prominent parietal tubercle. The temporal lines are prominent, displaying separate superior and inferior temporal lines moving posteriorly to a gradually less projection of the line from stephanion to the parietomastoid suture, and ending in a distinct linear angular torus whose anterior edge is along the inferior temporal line and is accentuated by an irregular sulcus posteriorly. The vault is thick with a wide diploë and thin cortical bone. The temporal squama is quite high and probably with a rounded superior squamous border shape, which is similar to modern humans. The mastoid process is small and inwardly deflected, which is common in Asian *H. erectus*. The external auditory meatus is vertically ovoid with a superior zygomatic root. This pattern is different from Neanderthals whose auditory meatus is in a horizontal ovoid shape and the zygomatic root is through the middle of the porion. Yet, the internal temporal labyrinths are similar to Neanderthals.

XJY 12 OCCIPITAL BONE

XJY 12 (PA 1495; see Figure 1 L) is a large occipital bone with the left squamous portion present with 73mm of the lateral lambdoid suture and 35.5mm of the left mastooccipital suture, all of the left nuchal plane, and the medial half of the right nuchal plane extending ~38mm from the midline. The posterior edge of the foramen magnum with opisthion is present, but the most anterior extent (right) is broken off posterior to the occipital condyle and condylar fossa. Midline is preserved to ~18mm above inion. The remaining left asterion is intact with a prominent sutural projection between the mastooccipital and lambdoid sutures. The sinus confluence is preserved internally, with the midline ridge from opisthion to ~34mm above the confluence and the complete left sinus sulci. The right transverse sulcus is present for ~20mm from the midline. The bone is fully mature and clearly represents an adult.

The occipital torus of XJY 12 is weak with no posteriorly bulging occipital bun. The occipital protuberance is small and superior to the tuberculum linearum, with no depression above it. These features are different from Neanderthals who have a bulging occipital bun and a depression above the tuberculum linearum. The thickness crossing the midline sagittal section of the tuberculum linearum is 17.7mm, much thinner than Neanderthals and modern humans, and within the range of Early and Middle Pleistocene hominins, and Middle Paleolithic early modern humans.

XJY 14 MANDIBLE

XJY 14 (PA 1497; see Figure 1 N) is a right mandibular ramus with a largely complete lateral surface but a partial medial surface. The condylar neck, and coronoid process are complete and the posterior ramal margin and mandibular notch are intact. The inferior margin is present laterally but not medially. The anterior margin of the ramus is present to the area of the distal M_3 alveolus, but there is no remaining trace of the M_3 socket or the porous retromolar surface.

The XJY 14 mandible has an anteroposteriorly wide mandibular ramus and an enlarged superior medial pterygoid tubercle, which separate XJY 14 and more archaic *Homo* from modern humans. The asymmetrical mandibular notch and open mandibular foramen also largely separate XJY 14 and more archaic *Homo* from modern humans. Gonial eversion in posterior view and an unusual depression in the planum triangulare are found in the highest frequency among the Neanderthals, and are unexceptional in a fossil or recent human context. Thus, the XJY 14 mandible provides a morphological mosaic, highlighting regional variation during the Pleistocene (Wu and Trinkaus 2014).

COMPARATIVE MORPHOMETIC FEATURES

CRANIAL CAPACITY

The cranial capacity of XJY 6 is estimated to 1700mL (Wu et al. 2022), close to Xuchang 1 (1800mL), and is well outside the range of *H. erectus* (600–1251mL) and mid-Pleistocene *Homo* (1070–1450mL), and falls in the upper range of Neanderthals (1065–1740mL) and early modern humans (1090–1880mL).

MORPHOMETRIC ANALYSIS

In order to provide a comparative morphometric framework for the Xujiayao hominin fossils, we used a principal components analysis (PCA) to assess the morphological affinities for the XJY 6 neurocranium relative to comparative samples. SPSS v. 20.0 (IBM company, Beijing) was used for the PCAs. Based on the preservation and available anatomical information of the Xujiayao hominin fossils, the comparative samples (Table 1) used for PCA include: *H. erectus*/*Homo ergaster* (n=21); mid-Pleistocene *Homo* (n=13); Neanderthals (n=11); Middle Paleolithic modern humans (n=5); Upper Paleolithic modern humans (n=15); and Recent humans (RM; n=31).

Primarily following Bräuer and Knußmann (1988) and Howells (1973), linear measurements were taken on

TABLE 1. CRANIAL SAMPLES AND SPECIMENS USED IN THE PRINCIPAL COMPONENT ANALYSIS (PCA).

Geography/chronology	PCA-seven variables	PCA-five variables
Unassigned	XJY 6, XUC 1	XJY 6, XUC 1
H. erectus	KNM-ER 3733, 3833; Sale 1; Sangiran 2, 10, 17; Sambungmacun1, 3; Ngandong 6, 7, 12, 14; Narmada 1; Zhoukoudian (ZKD 3, 5, 10, 11, 12), Hexian (HEX) 1.	KNM-ER 3733, 3833, Sale 1, Sangiran 2, 17; Sambungmacun, 3; Ngandong 6, 7, 12, 13, 14; Zhoukoudian (ZKD 3, 5, 10, 11, 12), Nanjing (NAJ) 1, Hexian (HEX) 1.
mid-Pleistocene *Homo*	Broken Hill; Jebel Irhoud 1; Laetoli Hominid 18; Petralona 1; Steinheim; Atapuerca SH 4, 5; Dali 1, Jinniushan (JNS) 1, Harbin	Broken Hill; Jebel Irhoud 1; Petralona 1; Steinheim; Dali 1, Jinniushan (JNS) 1, Maba 1, Hualongdong (HLD) 6
Neanderthals	Saccopastore 1; Spy 2; La Chapelle aux Saints 1; La Ferrassie 1; La Quina 5; Le Moustier 1; Guattari 1; Gibraltar 1; Tashik Tash 1; Amud 1; Shanidar 1.	Saccopastore 1; Spy 1, 2; La Chapelle aux Saints 1; La Ferrassie 1; Le Moustier 1; Guattari 1; Gibraltar 1; Amud 1; Shanidar 1
Middle Paleolithic modern humans	Omo-Kibish 2, Qafzeh 9, Skhul 5; Tabun C2	Qafzeh 6, 9; Skhul 5
Upper Paleolithic modern humans	Liujiang 1; Upper Cave 101, 102, 103; Minatogawa 1; Brno 2; Mladeč 1, 5; Předmostí 3, 4	Liujiang 1; Upper cave 101, 102, 103; Minatogawa 1, 4; Brno 2, 3; Cro-Magnon 1; Mladeč 1, 5; Předmostí 3, 4; Oberkassel 1, 2.
Recent modern humans	N=31	N=31

the XJY 6 posterior cranium virtual 3D reconstruction and comparative samples. We collected measurements on seven variables [Maximum cranial width (XCB), Maximum frontal breadth (XFB), Auricular-vertex height (AVH), Parietal chord (PAC), Temporal squama height (TSQH), Lambda–asterion chord (LASC), Lambda-inion chord (LINC)] and five variables [Maximum cranial width (XCB), Maximum biparietal breadth (BPB), Maximum frontal breadth (XFB), Parietal chord (PAC), Parietal subtense (PAS)], respectively. The selected specimens and the Harbin fossil were included in the analysis of seven variables, and the Maba and Hualongdong fossils were included in the five variable analysis. These measurements capture the entire posterior cranium, but in order to avoid data redundancy and to reduce the effect of multicollinearity, certain arcs were excluded. PCA was computed on the covariance matrix to standardize the between-group variation. The comparative specimens are curated in the IVPP and the American Museum of Natural History in New York. All data were measured directly by Xiujie Wu.

The PCAs show a morphological space characterized by two dominant components with both the seven variables (Figure 2 A) and five variables (Figure 2 B) plots. In the seven-variable analysis (see Figure 2 A), the first two components account for 68.5% of the total variance. The first component (47.5%) has positive loadings on all variables and tends to have a big auricular-vertex height, Parietal chord, and Lambda–asterion chord. The second component (16.4%) tends to be related to wide Maximum cranial and frontal breadth measurements. The first PCA indicates that XJY 6 and XUC 1 are not typical of any of the comparative groups. When including Harbin, Dali, and Jinniushan in the analysis (see Figure 2 A), the biggest contrast across PC1 and PC2 is where *H. erectus* and Upper Paleolithic and Recent modern humans clearly fall on opposite sides, with substantial overlap among the Middle Pleistocene group, Neanderthals, Upper Paleolithic, and recent human samples. XJY 6 and XUC 1 fall largely outside the range of the other groups and are closest to Harbin compared with other specimens. Jinniushan and Dali overlap with *H. erectus*,

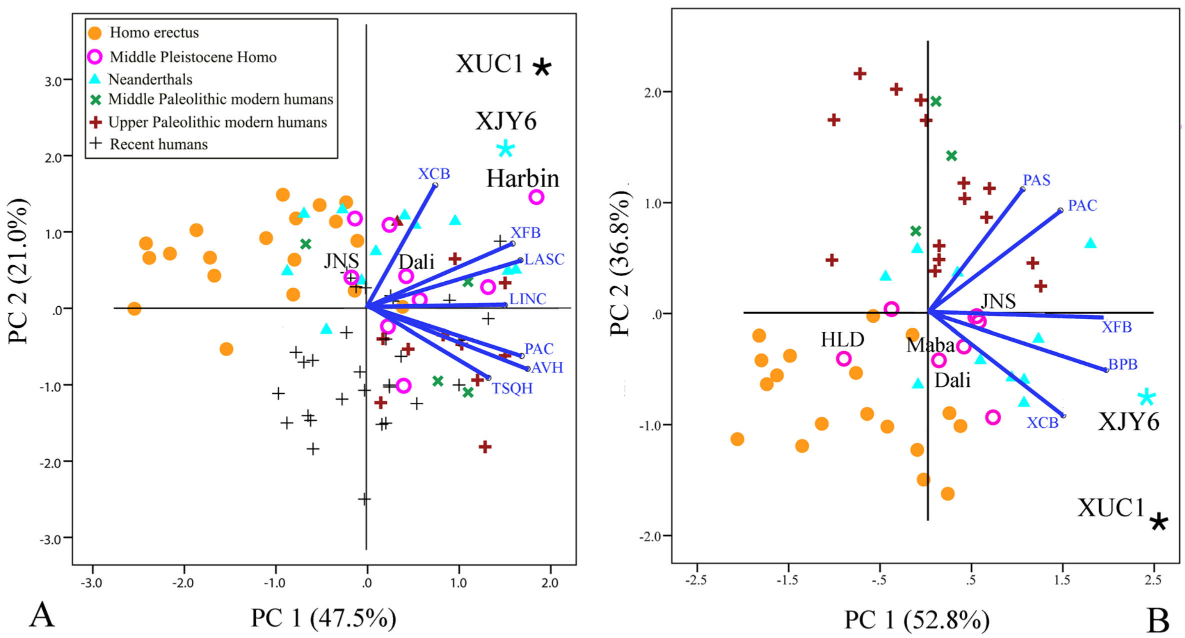

Figure 2. Principal components analysis of the XJY 6 neurocranium in relation to the comparative samples where comparable data were available. **A)** *using seven linear measurements (XCB, XFB, AVH, PAC, TSQH, LASC, LINC).* **B)** *using five linear measurements (XCB, XFB, PAC, BPB, PAS). XCB (maximum cranial width), XFB (maximum frontal breadth), AVH (auricular-vertex height), BPB (maximum biparietal breadth), PAC (parietal chord), PAS (parietal subtense), TSQH (temporal squama height), LASC (lambda–asterion chord), LINC (lambda-inion chord).*

Neanderthals, and Middle Pleistocene hominins.

When including Maba, Jinniushan, Dali, and Hualongdong in the five variable analysis (see Figure 2 B), the first and second principal components represent 52.8% and 36.8% of the total variance. The first component is related to the wide frontal and maximum biparietal breadth and the second component tends to the high parietal substense and long parietal chord. XJY 6 and XUC 1 are again outside the distribution of any taxon. Hualongdong falls within the range of *H. erectus*. Maba, Jinniushan, and Dali are between *H. erectus* and modern humans and overlap with Neanderthals and Middle Pleistocene hominins.

DISCUSSION

In general, the Xujiayao fossils display a mosaic of primitive and derived morphological features, and cannot easily be assigned to *H. erectus*, other mid-Pleistocene *Homo* (e.g., *H. bodoensis*, *H. longi*), Neanderthals, or modern humans (Tables 2 and 3).

The Xujiayao fossils retain some primitive characters classically found in East Asian Early and Middle Pleistocene hominins, such as the mass-additive features of the anterior dentition with well-developed tuberculum dentale, pronounced shovel shaped incisors, asymmetrical crown outline of the premolar, the trapezoidal crown outline molar with a narrower distal half, the robust and divergent root system of the molar, the large crown size of all of the teeth, the thick parietal and occipital bones, inferiorly maximum cranial width, a very low and very wide posterior cranial shape, a small and inwardly deflected mastoid process, and a parasagittal bilateral depression on the parietal bones. However, there are clear features that distinguish Xujiayao and Asian *H. erectus*. For instance, the Xujiayao teeth are relatively more derived in some crown features, such as less-pronounced finger-like projections in the incisor, a weaker canine essential ridge, simpler occlusal and buccal surfaces in P3 and P4, a more symmetrical P3 crown outline with a much smaller lingual cusp, a reduced M3 metacone, and an elliptical M3 crown outline (Xing et al. 2015). The XJY 6 posterior cranium is bigger, wider anteriorly and laterally enlarged, and the squamous portion is higher than in *H. erectus*. The transition between the nuchal plane and the occipital plane is at an obtuse angle, while in *H. erectus* this transition is close to a right angle. A further difference from *H. erectus* is the temporal line. In *H. erectus*, the temporal line is gradually weakening in the parietal bone with an angular torus that appears in a raised mound shape, while the end of the temporal line on XJY 6 is connected and accentuated toward the linear angular torus (see Table 2).

The Xujiayao fossils share a few features with Neanderthals, including a highly convex labial surface with a pronounced shovel shaped incisor in XJY 1, a rather large cranial capacity (XJY 6), enlarged parietal bones, the absence of a sagittal keel, a weak occipital torus, and an obtuse transition between the nuchal and occipital planes, a more inferiorly positioned lateral canal plane of the internal temporal labyrinth, a gonial eversion, and a depressed planum triangulare mandibular ramus. Different from Neanderthals, the Xujiayao molar (M^1) does not have clas-

TABLE 2. MORPHOLOGICAL COMPARISON AMONG XJY 6 AND COMPARATIVE GROUPS.

	XJY 6	***H. erectus***	**Middle Pleistocene hominins**	**Neanderthals**	**Modern humans**
Cranial capacity	1700	600-1225	1013-1450	1120-1740	1090-1880
Cranial shape	Low and wide	Most low and wide	Most low braincase	Long, round braincase	Round braincase
Broadest region	Very low on supramastoid area	Very low on supramastoid area	Low, most on temporal squama	Low on parietal or temporal squama	High on parietal, middle area
Sagittal keeling	Absent	Present in Asian *H. erectus*	Most absent	Absent	Absent
Parietal eminence	Less prominent	Less prominent	Varied	Prominent	Prominent
Parietal expansion	Yes	No	Most	Yes	Yes
Transition between nuchal and occipital planes	Rounded obtuse transition	Angular transition	Most rounded	Rounded obtuse	Rounded
Parietal temporal line	Prominent, superior and inferior temporal lines are separated	Prominent, superior and inferior temporal lines are not separated	Varied, most weak	Weak	Varied
Angular torus	Distinct but weak on its anterior edge along the temporal line, accentuated by a sulcus	Prominent, in a raised mound shape	Most present	Most absent	Most absent
Temporal squama	High, in a rounded superior border shape	Low, in a flat superior border shape	Varied, most in a flat superior border shape	Most low, in a flat superior border shape	High, in a rounded superior border shape
External auditory meatus	Vertically ovoid, zygomatic root at superior edge of the external auditory meatus	Vertically ovoid, zygomatic root at superior edge of the external auditory meatus	Vertically ovoid, zygomatic root at superior edge of meatus	Horizontal ovoid, zygomatic root in the middle of auditory meatus.	Vertically ovoid, zygomatic root at superior edge of the meatus

TABLE 2. MORPHOLOGICAL COMPARISON AMONG XJY 6 AND COMPARATIVE GROUPS (continued).

	XJY 6	*H. erectus*	Middle Pleistocene hominins	Neanderthals	Modern humans
Temporal sulcus	Wide, slope and deep				Narrow and shallow
Anterior tympanic	Thick	Thick	Varied	Thin	Thin
Supramastoid crest	Prominent	Prominent	Varied	Varied	Varied
Mastoid processes	Small and inward deflected	Small and inward deflected in Asian *H. erectus*	Varied	Most big and straight	Most big and straight
Postglenoid process	Small	Small	Most strongly developed	Strongly developed	Varied
Juxtamastoid eminence	Weak	Prominent	Varied	Large	Large
Occipital bun	Absent	Absent	Absent	Present	Absent
Occipital torus	Weak	Strong	Varied	Weak	Weak
Suprainiac fossa	Absent	Absent	Present	Present	Absent
Parasagittal depression	Present	Present in Asian	Present in Asian	Absent	Absent
Middle meningeal artery	Large anterior branch	Large posterior branch	Large anterior branch	Large anterior branch	Large anterior branch
Transverse sulcus	Cross the parietal	Cross the occipital	Most cross the occipital	Cross the parietal	

sic Neanderthal-like dental features, such as a continuous middle trigonid crest (Xing et al. 2015). The Xujiayao posterior cranium (XJY 6) is quite distinct from Neanderthals in having an overall low and wide cranial shape, a thicker cranial vault, a horizontal ovoid auditory meatus with a long zygomatic arch axis through the middle of the meatus, and a low height dimension (Wu et al. 2022). The perikymata distribution of the Xujiayao unerupted I^1 and C^1 tends to be more similar to that of modern humans than to either early *Homo* or Neanderthals (Xing et al. 2015a).

Compared with modern humans, the cranial capacity of XJY 6 is at the top of the range of Middle-Upper Paleolithic and recent modern humans (1090–1880mL). Different from XJY 6, modern humans have a round and high braincase with the broadest region on the parietal bone, a prominent parietal eminence, a narrow and shallow temporal fossa, a thin anterior tympanic, a large juxtamastoid eminence, the absence of a parasagittal depression, and thin cranial vault bones.

The mid-Pleistocene *Homo* crania from China generally date to between 300 ka and 100 ka and primarily include Dali, Maba, Jinniushan, Hualongdong, Harbin, and Xuchang. These important fossils can be compared with the Xujiayao remains presented here (see Table 3).

The Dali specimen was considered a "transitional" form between Chinese *H. erectus* and *H. sapiens* (Wu 1981). More recent studies suggest the facial skeleton of Dali aligns with Middle Paleolithic *H. sapiens* and is clearly more derived than African or Eurasian mid-Pleistocene *Homo* [or *H. bodoensis* (see Roksandic et al. 2022a, b)], while its neurocranium is most similar to African and Eastern Eurasian but not Western European mid-Pleistocene *Homo* (Wu and Athreya 2013). Compared to the XJY cranium, the Dali specimen has a smaller cranial capacity, with the widest area of the skull being rather high, with relatively short and arched parietal bones, a prominent parietal keel, an angled occipital bone, and a relatively long upper (lambda-inion) occipital plane. The common features between the XJY 6 and Dali neurocrania are a long and prominent temporal line, which connects to the weak parietal angular torus, a high temporal squama, small and inwardly deflected mastoid processes, a weak occipital torus, and a less prominent parietal boss.

The Jinniushan skull is long and robust with a relatively large cranial capacity of 1390mL (Wu 1988). The broadest region of Jinniushan is in the temporal squama, similar to Dali and higher than XJY 6. Compared with XJY 6, Jinniushan shows a weak sagittal keel, a thin cranial vault, a long upper occipital plane, a weakly bulged angular torus,

TABLE 3. MORPHOLOGICAL COMPARISON AMONG XJY 6 AND OTHER MAJOR MIDDLE PLEISTOCENE HOMININS FROM CHINA.

Trait	XJY 6	XUC 1	Dali	Jinniushan 1	Maba 1	HLD 6	Harbin
Cranial capacity	1700 mL	1800 mL	1120 mL	1390 mL	1300 mL	1150 mL	1420 mL
Cranial shape	Very low and wide	Very low and wide	Low and wide	Low and wide		Low	Low and wide
Broadest region	Supramastoid area	Supramastoid area	Temporal squama	Temporal squama			Supramastoid area
Transition between nuchal and occipital planes	Obtuse	Obtuse	Angled	Angular			Obtuse
Parietal keeling	Absent	Absent	Present	Present	Absent	Absent	Absent
Parietal enlarged	Expansion	Expansion	No	No	-	No	Expansion
Temporal line	Prominent	Weak			Prominent		Prominent
Angular torus	Distinct on its anterior edge along the temporal line, accentuated by a sulcus	Absent	present	Present			Distinct on its anterior edge along the temporal line, accentuated by a sulcus
Temporal squama	High, arched	Low	High, arched	High, arched		High, arched	High, arched
External auditory meatus	Ovoid, vertical long axis	Ovoid, vertical long axis	Ovoid, vertical long axis	Ovoid, vertical long axis		Ovoid, vertical long axis	Ovoid, vertical long axis
Temporal sulcus	Wide, sloped and deep	Wide, sloped and deep					Wide, sloped and deep
Supramastoid crest	Prominent						weak
Mastoid processes	Small, inward deflected	Small, inward deflected	Small, inward deflected	Small, inward deflected		Small, inward deflected	Small, inward deflected
Juxtamastoid eminence	Weak		Weak				
Occipital bun	Absent	Absent					Absent
Occipital torus	Weak	Weak	Strong	Weak			Weak
Parasagittal bilateral depression	Present	Present	Present	-	Present	Present	
Cranial thickness	Thick	Medium	Thick	Medium	Medium	Medium	

and an angular transition between nuchal and occipital planes. Morphologically, Jinniushan is more like Dali than XJY 6.

The Maba specimen displays a mosaic of archaic and derived features and has attracted extensive attention based on its Neanderthal-like thick, prominent and projecting supraorbital tori that arch over circular eye orbits, and a general archaic endocast morphology (Wu 1959). There are some common features between XJY 6 and the Maba partial posterior cranium, including a parasagittal bilateral depression in the endocast, an absent parietal keel, a long and prominent temporal line, and a high temporal squama. The cranial capacity of Maba is estimated to be 1300mL (Wu and Bruner 2016), which is within the normal range of modern humans and Neanderthals, but much smaller than XJY 6. Compared with XJY 6, Maba is small in all dimensions, thin in cranial vault, and has less enlargement in the parietal bones.

The recently reported Harbin skull presents a mosaic of primitive and derived characters (Ni et al. 2021). There are a number of common features between XJY 6 and Harbin—similar to XJY 6, the Harbin cranium is long and wide with enlarged parietal bones; the transition between the nuchal and occipital planes is obtuse; the parietal boss is less prominent; the temporal line is distinct with the end terminating at the linear angular torus; the temporal squama is high and arched; the temporal sulcus is wide, sloped, and deep; the mastoid processes are small and inwardly deflected; the glenoid fossa is deep; the occipital torus is weak; no suprainiac fossa is present; and, a sagittal keel is absent. The cranial capacity of Harbin is about 1420mL, which is close to Jinniushan (1360mL) but much smaller than XJY 6 (1700mL). The broadest region of Harbin is over the supramastoid area, higher than in XJY 6.

The Hualongdong 6 (HLD) neurocranium is a largely complete skull with a small cranial capacity of 1150mL (Wu et al. 2019). The HLD neurocranium is small and low, the parietal bones are not enlarged, the parietal temporal line is weak, and the vault is of a medium thickness. Neurocranium metric analysis places HLD 6 between *H. erectus* and modern humans, and close to Dali.

The Xuchang (XUC) 1 and 2 crania, dating to the early Late Pleistocene, are from the Lingjing site, about 650km south of Xujiayao. XUC 1 retains most of the neurocranial vault and portions of the cranial base. XUC 2 retains the posteroinferior neurocranium, with the majority of the occipital bone and the petrotympanic portions of the temporal bones (Li et al. 2017). Similar features between XJY 6 and XUC 1 include neocortical and parietal expansion, large cranial capacity, a low and posterior position of the broadest vault region, globular braincase in posterior view with no sagittal keel, small and inwardly deflected mastoid processes, an obtuse transition between nuchal and occipital planes, a weak occipital torus with no posteriorly bulging occipital bun, a high and arched temporal squama contour, an ovoid auditory meatus with a vertical long axis, Neanderthal-like temporal labyrinthine pattern, parasagittal bilateral depression, and anterior branches dominating the middle meningeal grooves. However, compared with XUC 1, XJY 6 shares more common features with Asian *H. erectus*, including a less prominent parietal boss, a more obvious temporal line, a very thin cranial vault, and a relatively closer posterior vault shape. Compared to other Pleistocene hominins, there are more similar features between XJY 6 and XUC 1. Although there are also a few features, for instance, the wide diploë and distinct linear angular torus that are not present in the XUC fossils, XUC and XJY can be comfortably considered closely related to each other.

In addition to the above crania, other hominins that have often been mentioned in comparisons with Xujiayao include the dentognathic remains of the Denisovans, Penghu 1, and Xiahe 1 (Chang et al. 2015; Chen et al. 2019; Zubova et al. 2017). The Xujiayao dentognathic remains share several notable characters, including extremely large and complex teeth and a low and wide mandibular ramus.

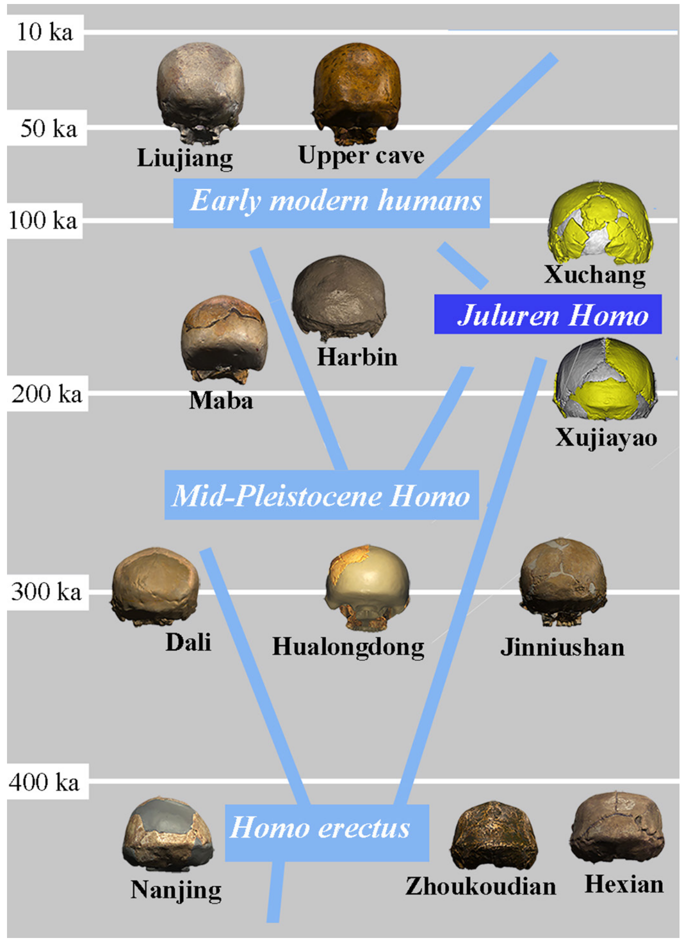

Figure 3. Posterior views of select Chinese Pleistocene hominin crania. Hypothetical evolutionary position of the Xujiayao hominin and more broadly, the Julurens. The blue connecting lines means a likely source or close relationship.

THE TAXONOMY OF THE XUJIAYAO HOMININS

Although the dental-cranial morphological features of the late Middle-early Late Pleistocene hominins display a good amount of variation, there are some commonalities between Xujiayao and most of the Middle Pleistocene *Homo* fossils, including enlarged parietal bones, brain expansion, the absence of a sagittal keel, a rounded transition between nuchal and occipital planes, a vertically oriented external auditory meatus, the absence of an occipital bun and suprainiac fossa, and generally large teeth. Compared with the specimens from Europe and Africa, Xujiayao expresses more shared features with Asian mid-Pleistocene *Homo,* especially the very low and wide cranial shape, and very enlarged cranial capacities. Xujiayao, as well as Xuchang, demonstrates a previously unknown degree of morphological variability in China. Xujiayao and Xuchang clearly differ from many other Middle and early Late Pleistocene hominins based on the degree and patterning of brain expansion, a very wide and big sized cranial shape, and related cranial changes, particularly given their temporal position. These late Middle and early Late Pleistocene hominin fossils from China and southern Siberia represent a greater degree of morphological variation than originally anticipated.

Because the Xujiayao and Xuchang crania group closely together in multiple analyses and are quite different from all other comparative Pleistocene hominin crania, we suggest that they represent a new hominin population for the region, namely Juluren (Figure 3), meaning "large head people." Given the dentognathic similarities between Xujiayao, Xiahe, Penghu, and the Denisovans, in all likelihood these latter fossils can be assigned to the Julurens as well (see Bae et al. 2023, Wu et al. 2022; but particularly Bae 2024 for taxonomic clarification). It is quite possible that this population represents gene flow between Asian *H. erectus*, and possibly *H. antecessor*, *H. bodoensis*, and/or early Neanderthals, supporting the idea of continuity with hybridization as a major force shaping human evolution in eastern Asia during the late Middle and early Late Pleistocene.

ACKNOWLEDGEMENTS

This paper was prepared for the workshop organized in Novi Sad, Serbia (May 2023) entitled "What's in a Name? Late Middle and Early Late Pleistocene Hominin Systematics." This study has been supported by the National Natural Science Foundation of China (42372001). Funding to participate in the workshop was generously provided by the Wenner-Gren Foundation and the Social Science and Humanities Research Council. We greatly appreciate the comments from three anonymous reviewers and Karen Rosenberg, the handling editor. We are responsible for any errors that may be present.

DATA AVAILABILITY STATEMENT

All data are available in this article.

REFERENCES

Bae, C.J., 2010. The late Middle Pleistocene hominin fossil record of eastern Asia: synthesis and review. Yearb. Phys. Anthropol. 53, 75–93.

Bae, C.J., 2024. The Paleoanthropology of Eastern Asia. University of Hawaii Press, Honolulu.

Bae, C.J., Liu, W., Wu, X.J., Zhang, Y.M., Ni, X.J., 2023. 'Dragon Man' prompts rethinking of the Middle Pleistocene hominin systematics in Asia. The Innovation 4(6), 100527. https://www.doi.org/10.1016/j.xinn.2023.100527

Bae, C.J., Douka, K., Petraglia, M.D., 2017. Multidisciplinary perspectives on the human evolution in Late Pleistocene Asia: introduction to Supplement 17. Curr. Anthropol. 58(S17), S373–S382.

Bräuer G., Knußmann R., 1988. Grundlagen der Osteometrie. In: Anthropologie I, R. Knussman (Ed.). Fischer Verlag, Stuttgart, pp. 129–159.

Chang, C.H., Kaifu, Y., Takai, Kono, R.T., Gru¨n, R., Matsu'ura, S.M., 2015. The first archaic *Homo* from Taiwan. Nat. Commun. 6(1), 6037.

Chen, F.H., Welker, F., Shen, C.C., Bailey, S.E., Bergmann, I., Davis, S., Xia, H., Wang, H., Fischer, R., Freidline, S.E., Yu, T.L., Skinner, M.M., Dong, S.S.G., Fu, Q.M., Dong, G.H., Wang, J., Zhang, D.J., Hublin, J.J., 2019. A late Middle Pleistocene Denisovan mandible from the Tibetan Plateau. Nature 569, 409–412.

Chia, L.P., Wei, C. 1976. A Palaeolithic site at Hsü-Chia-Yao in Yangkao County, Shansi Province. Acta Archaeol. Sin. 2, 97–114.

Chia, L.P., Wei, Q., Li, C.R. 1979. Report on the excavation of Hsuchiayao man site in 1976. Vertebrata PalAsiatica 17, 277–293.

Demeter, F., Zanolli, C., Westaway, K.E., Joannes-Boyau, R., Duringer, P., Morley, M.W., Welker, F., Rüther, P.L., Skinner, M.M., McColl, H., Gaunitz, C., Vinner, L., Dunn, T.E., Olsen, J.V., Sikora, M., Ponche, J.L., Suzzoni, E., Frangeul, S., Boesch, Q., Antoine, P.O., Pan, L., Xing, S., Zhao, J., Bailey, R.M., Boualaphane, S., Sichanthongtip, P., Sihanam, D., Patole-Edoumba, E., Aubaile, F., Crozier, F., Bourgon, N., Zachwieja, A., Luangkhoth, T., Souksavatdy, V., Sayavongkhamdy, T., Cappellini, E., Bacon, A.M., Hublin, J.J., Willerslev, E., Shackelford, L., 2022. A Middle Pleistocene Denisovan molar from the Annamite Chain of northern Laos. Nat. Commun. 13, 2557.

Gokhman, D., Mishol, N., de Manuel, M., de Juan, D., Shuqrun, J., Meshorer, E., Marques-Bonet, T., Rak, Y., Carmel, L., 2019. Reconstructing Denisovan anatomy using DNA methylation maps. Cell 179, 180e192 e110.

Groves, C.P., Lahr, M.M., 1994. A bush not a ladder: speciation and replacement in
human evolution. Perspect. Hum. Biol. 4, 1–11.

Harvati, K., Reyes-Centeno, H., 2022. Evolution of *Homo* in the Middle and Late Pleistocene. J. Hum. Evol. 173, 103279.

Howells, W.W., 1973. Cranial variation in man. Pap. Peabody Mus. 67, 1–259.

Hun, L.Y., Xu, Q.H., Zhang, S.R., Wang, F.G., Liu, L.Q., Li, J.Y., Li, M.Y., 2011. Paleoenvironment and paleoclimate changes of Houjiayao site in Yangyuan county, Hebei province based on pollen analysis. Quatern. Sci. 31(6), 951–961.

Ji, H.X., 1987. The distribution and partition of Chinese quaternary mammal fauna (in Chinese). J. Stratigraphy 4, 91–109.

Li, J.S., Zhang, S.Q., Bunn, H.T., Sarathi, A., Gao, X., 2017b. A preliminary application of dental cementum incremental analysis to determine the season-of death of equids from the Xujiayao site, China. Sci. China Earth Sci. 60, 1183–1188.

Li, M.Y., Zhang, S.R., Xu, Q.H., Xie, F., Wang, F.G., 2016. New recognition of Houjiayao relic site: stratum age and environment (in Chinese with English abstract). Acta Palaeontol. Sinica 55, 122–135.

Li, Z.T., Xu, Q.H., Zhang, S.R., Hun, L., Li, M.Y., Xie, F., Liu, L.Q., 2014. Study on stratigraphic age, climate changes and environment background of Houjiayao Site in Nihewan Basin. Quatern. Intl. 349, 42–48.

Li, Z.Y., Wu, X.J., Zhou, L.P., Liu, W., Gao, X., Trrinkaus, E., 2017a. Late Pleistocene archaic human crania from Xuchang, China. Science 355, 969–972.

Liu, W., Wu, X.J., Xing, S., Zhang, Y.Y., 2014. Human Fossils in China. Science Press, Beijing.

Lynnerup, Ni., Astrup, J., Sejrsen, B., 2005. Thickness of the human cranial diploe in relation to age, sex and general body build. Head Face Med. 1, 13. https://head-face-med.biomedcentral.com/articles/10.1186/1746-160X-1-13

Martinón-Torres, M., Bermúdez, de Castro J.M., Gómez-Robles, A., Arsuaga, J.J., Carbonell, E., Lordkipanidze, D., Manzi, G., Margvelashvili, A., 2007. Dental evidence on the hominin dispersals during the Pleistocene. Proc. Natl. Acad. Sci. U.S.A. 104(33), 13279–13282.

Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Prado-Simón, L., Arsuaga, J.L., 2012. Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). J. Hum. Evol. 62, 7–58.

Ni, X.J., Ji, Q., Wu, W.S., Shao, Q.F., Ji, Y.N., Zhang, C., Liang, L., Ge, J.Y., Guo, Z., Li, J.H., Li, Q., Grun, R., Stringer, C., 2021. Massive cranium from Harbin establishes a new Middle Pleistocene human lineage in China. The Innovation 2, 100130.

Norton, C.J., Gao, X., 2008. Hominin-carnivore interactions during the Chinese Early Paleolithic: taphonomic perspectives from Xujiayao. J. Hum. Evol. 55, 164–178. https://doi.org/10.1016/j.jhevol.2008.02.006

Pope, G.G., 1992. Craniofacial evidence for the origin of modern humans in China. Yrbk. Phys. Anthropol. 35, 243–298.

Reich, D., Green, R.E., Kircher, M., Krause, J., Patterson, N., Durand, E.Y., Viola, B., Briggs, A.W., Philip, U.S., Johnson, L.F. Maricic, T., Good, J.M., Marques-Bonet, T., Alkan, C., Fu, Q., Mallick, S., Li, H., Meyer, M., Eichler, E.E., Stoneking, M., Richards, M., Talamo, S., Shunkov, M.V., Derevianko, A.P., Hublin, J.J., Kelso, J., Slatkin, M., Pääbo, S., 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468, 1053–1060.

Roksandic, M., Radovic, P., Wu, X.J., Bae, C.J.**,** 2022a. Resolving the "Muddle in the Middle": the case for *Homo bodoensis* sp. nov. Evol. Anthropol. 31, 20–29.

Roksandic, M., Radovic, P., Wu, X.J., Bae, C.J., 2022b. *Homo bodoensis* and why it matters. Evol. Anthropol. 31, 240–244.

Tu, H., Shen, G.J., Li, H., Xie, F., Granger, D.E., 2015. ^{26}Al/^{10}Be Burial Dating of Xujiayao-Houjiayao Site in Nihewan Basin, Northern China. PLoS One 10, e0118315.

Wu, M., 1980. Human fossils discovered at Xujiayao site in 1977 (in Chinese with English abstract). Vertebrata PalAsiatica 18, 227–238.

Wu, M., 1986. Study of temporal bone of Xujiayao man (in Chinese with English abstract). Acta Anthropol. Sinica 5, 220–226.

Woo, R.K., Peng, R.C., 1959. Fossil human skull of early Paleoanthropic stage found at Mapa, Shaoquan, Kwantung Province. Vertebrata PalAsiatica 3, 176–182.

Wolpoff, M.H., Wu, X.Z., Thorne, A.G., 1984. Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from East Asia. In: Smith, F.H., Spencer, F. (Eds.), The Origins of Modern Humans. A World Survey of the Fossil Evidence. Alan R. Liss, New York, pp. 411–483.

Wu, R.K., 1988. The reconstruction of the fossil human skull from Jinniushan, Yingkou, Liaoning Province and its main features (in Chinese with English abstract). Acta Anthropol. Sinica **7**, 97–101.

Wu, X.Z., 1981. The well preserved cranium of an early *Homo sapiens* from Dali, Shaanxi. Scientica Sinica 24, 530–543.

Wu, X.Z., Poirier, F.E., 1995. Human Evolution in China. A Metric Description of the Fossils and a Review of the Sites. Oxford University Press, New York.

Wu, X.Z., Athreya, S.A., 2013. Description of the geological context, discrete traits, and linear morphometrics of the Middle Pleistocene hominin from Dali, Shaanxi Province, China. Am. J. Phy. Anthropol. 150, 41–157.

Wu, X.J., Bae, J.C., Martin, F., Xing, S., Athreya, S., Liu, W., 2022. Evolution of cranial capacity revisited: a view from the late Middle Pleistocene cranium from Xujiayao, China. J. Hum. Evol. 163, 103119.

Wu, X.J, Crevecoeur, I., Liu, W., Trinkaus, E., 2014. The temporal labyrinths of eastern Eurasian Pleistocene humans. Proc. Natl. Acad. Sci. U.S.A. 111(29), 10509–10513.

Wu, X.J., Bruner E., 2016. The endocranial anatomy of Maba 1. Am. J. Phy. Anthropol. 160, 633–643.

Wu, X.J, Trinkaus E., 2014. The Xujiayao 14 mandibular ramus and Pleistocene *Homo* mandibular variation. C. R. Palevol 13, 333–341.

Wu, X.J, Maddux, S.D., Pan L., Trinkaus, E., 2012. Nasal floor variation among eastern Eurasian Pleistocene *Homo*. Anthropol. Sci. 120(3), 217–226.

Wu, X.J., Pei, S.W., Cai, Y.J., Tong, H.W., Li, Q., Dong, Z., Sheng, J.C., Jin, Z.T., Ma, D.D., Xing, S., Li, X.L., Cheng, X., Cheng, H., De la Torre, R.I, Edwards, L., Gong, X.C., An, Z.S., Trinkaus, E., Liu, W., 2019. Archaic human remains from Hualongdong, China, and Middle Pleistocene human continuity and variation. Proc. Natl. Acad. Sci. U.S.A. 116, 9820–9824.

Wu, X.J., Xing S., Trinkaus, E., 2013. An enlarged parietal foramen in the Late Archaic XJY 11 neurocranium from northern China. PLoS One 8, e59587.

Xing, S., Martinón-Torres, M., Bermúdez de Castro, J.M., Wu, X.J., Liu, W., 2015. Hominin teeth from the early Late Pleistocene site of Xujiayao, northern China. Am. J. Phy. Anthropol. 156, 224–240.

Xing, S., Tafforeau, P., O'Hara, M., Modesto-Mata, M., Martín-Francés, L., Martinón-Torres, M., Zhang, L., Schepartz, L.A., Bermúdez de Castro, J.M., Guatelli-Steinberg, D. 2019. First systematic assessment of dental growth and development in an archaic hominin (genus, *Homo*) from East Asia. Sci. Adv. 5, eaau0930.

Yan, F.H., Ye, Y.Y., Mai, X.S., 1979. On the environment and geological age of Xujiayao site from pollen analysis data. Seismol. Geol. 1(4), 72–78.

Zubova, A.V., Chikisheva, T.A., Shunkov, M.V., 2017. The morphology of permanent molars from the Paleolithic layers of Denisova Cave. Archaeol. Ethnol. Anthropol. Eurasia 45, 121–134.