Archaic Human Remains from Hualongdong, China: Middle Pleistocene Continuity and Variation

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Abstract:

Middle to Late Pleistocene human evolution in East Asia has remained controversial regarding the extent of morphological continuity through archaic humans and to modern humans. Newly found ~300,000 year old human remains from Hualongdong (HLD), China, including a largely complete skull (HLD 6), share East Asian Middle Pleistocene human traits of a low vault, low and wide nasal aperture, pronounced supraorbital torus, sloping nasal floor and small/absent third molars. HLD 6 also exhibits a flat face, more vertical mandibular symphysis, pronounced mental trigone, and simple occlusal morphology, close to modern humans. The HLD human fossils augment later Middle Pleistocene variation in East Asia and support Middle and Late Pleistocene regional continuity with a transition from archaic to modern morphology in East Asia.

One Sentence Summary:

The new Middle Pleistocene Hualongdong human fossils provide evidence augmenting later archaic human diversity and supporting continuity through archaic to modern human morphology in East Asia.

Main Text:

The human remains from Zhoukoudian have dominated perceptions of Middle Pleistocene human morphology and variation in East Asia (*1-3*). Subsequent discoveries of human fossils from East Asia have augment later archaic human variability and trends (*4, 5*), with insights into the background and patterns of modern human emergence in the region (*6, 7*). Some researchers have proposed that human evolution in East Asia followed a regionally continuous pattern from the Early Pleistocene, through later archaic humans, and into Late Pleistocene early modern humans (*e.g. 8*), an inference which remains challenged *(e.g. 9)*. Therefore, additional human fossils with better preservation and more reliable dating will help shed further light on these problems. In this context, we describe a newly discovered human skull from the Middle Pleistocene site of Hualongdong (HLD), China.

Hualongdong contains two major depositional units, of carbonate cemented cavern breccia and unconsolidated clay mixed with granules (Fig. 1, Figs. S1-S4). Excavations (2006; 2014-17) yielded fifteen human fossils in association with abundant mammalian remains and a small Mode 1 core and flake lithic assemblage (SI-1). Forty-seven speleothem fragments from the cavern breccia yielded a maximum depositional age of 330.5 ± 14.5 kyr BP. The U-Th age of 274.8± 9.2 kyr BP for a calcitic crust that formed around a void inside the cavern breccia provides a minimum age for the cavern breccia accumulation. An additional U-Th age of 272.8± 7.0 kyr BP from a dripstone, likely grown on the cavern breccia, provides a similar minimum age constraint, and both are consistent with the best fit age using the iDAD model for the U-series measurements of fossil teeth (SI-2). These radiometric dates are supported by the faunal assemblage, in which the principal elements of the *Ailuropoda-Stegodon* fauna are dominant; it lacks archaic Early Pleistocene species and the later appearing Asian elephant (*10*). Therefore, Hualongdong human fossils can be confidently dated between 275-331 kyr BP (Fig. 1C), spanning Marine Isotope Stages (MIS)

9e to 8c.

The HLD 6 cranium (SI-3, Fig. 2) preserves 18 pieces, including most of the frontal and left parietal bones, the maxillae and left zygomatic bone, a posterior temporal portion, palatine bones and the lateral left sphenoid. The mandible retains the right corpus and posterior left corpus to the ramus (Fig. 3). The elements are undistorted, and the midline is preserved for the frontal and parietal bones, maxillae and mandibular symphysis, permitting mirror imaging of absent portions.

The dentition retains eight molars in occlusion (Fig. 3), a P_4, a P^3 root, developing left M3 crowns, and all alveoli on at least one side. The apically open distal M2 roots and the M3 crown stages (C_c and $C_{3/4}$) provide an age-at-death of 13-15 years based on modern samples (*e.g. 11*, SI-3).

The estimated endocranial capacity (~1150 cc) is unexceptional for its age and context (Middle Pleistocene (MPl) global: 1179±146 cc, n=49; east Asia MPl (eAMPl): 1109±131 cc, n = 18) (SI-5). It occurs in a low neurocranial vault with an even curve from the supratoral sulcus to lambda. HLD 6 has a modest and rounded frontal keel from the supratoral sulcus to anterior of bregma, as in 88.9% eAMPl crania (SI-6). The parietal bone lacks a sagittal keel, as do later but not earlier eAMPl. Its supramastoid crest ends at entomion, and hence there is no angular torus, unlike 75.0% of eAMPl. The biparietal arc is even with no angulation at the eminences and little at the sagittal suture.

The supraorbital torus is continuous across midline with an inferiorly placed glabella and even arches over the orbits, as with most eAMPl (88.9%). The torus is thickest medially, similar to Dali 1 but with a more pronounced lateral constriction. Nasion is recessed, as with 66.7% of eAMPl, and it projects minimally relative to frontomalare orbitale. The frontal keel and the lateral supraorbital torus might have become thicker with maturity, but their forms are unlikely to have changed. Multiple variable analysis with seven cranial vault metrics shows HLD 6 far from Chinese *H. erectus* but in a position overlapping between Indonesian late *H. erectus*, Neandertals and Middle Pleistocene humans in PCA (SI-5).

HLD 6 presents a low and wide nasal aperture (30.0 mm) similar in breadth to other eAMPl (western MPl: 33.0±4.4 mm, n=13). The lateral nasal crest is simple (category 1) (*12*), and the anterior nasal spine is minimally developed (category 0/1) (*12*). The nasal floor is sloping rather than bilevel (Fig. 3-B4) as in other eAMPl (*13*). The infraorbital foramina are double, with open CN-V2 orbital paths. The infraorbital surfaces are largely flat, lack canine fossae, and continue to a rounded zygomatic profile with its root above M^1 (the last aspect likely to have changed with facial growth). The inferior zygomaxillary profile lacks an infraorbital notch, similar to Jinniushan and unlike other eAMPl. The subnasal height is low, reflecting modest incisor root lengths (SI-6, 7).

The mandibular symphysis presents a modest anterior retreat (79º), a planum alveolare, and a clearly delimited mental trigone (category 3 (*14*)) (Fig. 3, Fig. S23). The last feature is between the 1 and 2 categories of earlier eAMPl (and other MPl symphyses) and that of 4 for Zhiren 3 (SI-8), and similar to 25.8% (n=31) of Late Pleistocene archaic humans. The lateral corpus size scaled to mandibular length is similar to other eAMPl (Fig. S24), but possibly affected by immaturity.

The ramus breadth (39.4 mm) is modest but unexceptional when scaled to mandible length (Fig. S24). The medial ramus has an open mandibular foramen, and the gonial angle is mildly everted. However, it presents a large superior medial pterygoid tubercle, similar to Xujiayao 14 and unlike Zhoukoudian mandibles (*2, 15*).

The HLD dental remains present simple occlusal morphologies, especially vis-à-vis those from Zhoukoudian, Hexian and Xujiayao (*3, 16, 17*). HLD 6 has four cusp maxillary molars and five cusp mandibular ones; its M^2s present two additional small distal cusps, and its P_4 has a large distal fossa. The HLD 1 M_2 has a cusp-6, and the shovel-shaped HLD 13 I^2 lacks a lingual tubercle. The HLD M1s, M2s, P_4 and C_1s crown dimensions are unexceptional in an eAMPl context, although HLD 6 M_2s are narrow for their mesiodistal lengths (Table S13). The HLD 7 and 9 P^3s are relatively small, and the HLD 3 M_3 is quite small ("area": 93.1 mm^2), slightly smaller than Zhoukoudian A2 and H1. HLD 6 exhibits right M^3 agenesis, as does the M_3 of Chenjiawo, and its left M^3 crown is very small; its "area" of 69.2 mm^2 is 2.44 SDs from an eAMPl mean. It is approached only by the Jinniushan 1 and Atapuerca 274 M^3s ("areas": 81.5 and 80.8 mm^2) among MPl humans (Table S13). The HLD teeth are therefore notable for their simple occlusal morphology and the reduction/agenesis of M3s.

There is accumulating evidence for Middle Pleistocene (variably into Late Pleistocene) morphological continuity among regional archaic human groups in Europe, Northwest Africa and insular Southeast Asia, as well as into early modern humans in East Africa (*e.g. 18-21*). In this context, the growing human fossil sample from mainland East Asia, enhanced by the Hualongdong remains, provides an additional example of continuity among later archaic humans.

The human remains from East Asia can be grouped into four chronological groups, from the earlier Lantian (including Gongwangling and Chenjiawo) and Zhoukoudian, to Hexian and Nanjing, then Chaoxian, Dali, Hualongdong and Jinniushan, and ending with Xuchang, Xujiayao and Zhiren. Along with these remains, HLD human fossils exhibit consistent patterns of neurocranial form (wide, low and rounded in posterior view), frontal keeling, nasal aperture form (low and wide), rounded supraorbital tori with an inferior glabella and a recessed nasion (except Nanjing 1), sloping to bilevel nasal floors, consistent mandibular hypertrophy, and M3 reduction (Chenjiawo, Zhoukoudian A2 and H1, Jinniushan, and HLD 3 and 6). There are also trends in endocranial capacity (from the smaller Zhoukoudian and Nanjing 1 to the very large Xuchang 1), neurocranial superstructures (reductions in sagittal keels and supraorbital tori, especially into the Late Pleistocene), mandibular symphyses (becoming more vertical with more pronounced mental trigones), infraorbital notches (lost in HLD 6 and Jinniushan), and mandibular rami (medial pterygoid tubercles in HLD 6 and Xujiayao 14). Other aspects are variable, as in dental occlusal complexity (low at HLD) and medial supraorbital thickening (strong in Dali and HLD 6). In addition, several cranial, mandibular and dental features in the HLD human fossils link them to early modern humans, supporting regional consistency from archaic to modern morphology.

These East Asian considerations, with the East and Northwest African, peninsular Southeast Asian and European Middle into Late Pleistocene human remains, document that the dominant trend through archaic humans, and variably into early modern humans, was one of regional consistency. Several divergent peripheral samples (Denisova, Dinaledi, Liang Bua (*18*)) are interesting evolutionary experiments, but it is the core continental regions that provide the overall pattern of Middle to Late Pleistocene human evolution and the background for the emergence of modern humans.

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Supplementary Materials:

Supplementary Text

Figures S1-S23

Tables S1-S13

References

Fig. 1. The Hualongdong site. (**A**) Location of the Hualongdong site in Dongzhi county, Anhui Province, China; (**B**) Aerial photography showing the plane figure of the Hualongdong site; (**C**) Overview of U-series dating results; all ages are given with 2$\boldsymbol{\sigma}$ error bars. The dashed lines indicate the maximum (≈331 kyr) and minimum (≈275 kyr) age estimations of the Hualongdong breccia [SI-2, Figs. S9 and S10]; (**D**) The longitudinal section of the deposits with the *in situ* location of the human cranium. kyr, thousand years before present.

Fig. 2. The virtually reconstructed HLD 6 skull. **A:** anterior view; **B:** left lateral view; **C:** posterior; **D:** isometric (right lateral) view; **E:** superior view; **F:** inferior view. Gray: filled-in mirror-imaged portions.

Fig. 3. The HLD 6 frontal bone, maxilla and mandible. **A:** frontal bone. **A1:** anterior view; **A2:** left lateral view; **A3:** superior view. **B:** right maxilla. **B1:** anterior view; **B2:** lateral view; **B3:** superior view; **B4:** basal view; **C-E:** mandible. **C1-C2:** anterior and medial views of right symphyseal region from I_1 to P_3; **D1-D2:** external and internal views of left corpus and ramus; **E:** cross-section at symphyseal region and medial view of right corpus showing the mental angle between infradentale-pogonion and alveolar plane.

Fig. 4. Occlusal views of HLD 6 teeth. **A**: right M^1 and M^2; **B**: left M^1 and M^2; **C:** left M_1 and M_2; **D:** right P_4, M_1 and M_2.