REPORT

PALEOANTHROPOLOGY

Late Pleistocene archaic human crania from Xuchang, China

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Two early Late Pleistocene (~105,000- to 125,000-year-old) crania from Lingjing, Xuchang, China, exhibit a morphological mosaic with differences from and similarities to their western contemporaries. They share pan–Old World trends in encephalization and in supraorbital, neurocranial vault, and nuchal gracilization. They reflect eastern Eurasian ancestry in having low, sagittally flat, and inferiorly broad neurocrania. They share occipital (suprainiac and nuchal torus) and temporal labyrinthine (semicircular canal) morphology with the Neandertals. This morphological combination reflects Pleistocene human evolutionary patterns in general biology, as well as both regional continuity and interregional population dynamics.

The period between ~200,000 and ~50,000 years ago saw the amplification across the Old World of regional diversity in human biology, which provided both the background for the pan–Old World spread (after 40,000 years ago) of modern human biology and the evolutionary background for recent human diversity (*1*, *2*). Eastern and northeastern Africa saw the emergence of the earliest modern humans, spreading briefly into southwest Asia and then across southern Asia. Western Eurasia saw the continuing emergence of the Neandertals. Other forms of late archaic humans emerged elsewhere in Africa. Until recently, the nature of these late Middle and early Late Pleistocene humans in the more northern portions of eastern Eurasia has been unclear, given the fragmentary nature of that human fossil record (*3*).

From their fossil record, eastern Asian late archaic humans have been interpreted to resemble their Neandertal contemporaries to some degree (*4*–*6*), with considerations of whether the fragmentary remains of the former exhibit features characteristic of the latter. Yet it is only with the discovery of two human crania (plus additional elements) from the Lingjing site in Xuchang County, Henan Province, China, that the nature of these eastern Eurasian early Late Pleistocene archaic humans is becoming clear.

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Excavated in situ between 2007 and 2014, the Xuchang 1 and 2 crania exhibit a distinctive morphological pattern combined with paleobiological trends that appear to have been pan–Old World.

The open-air Lingjing site consists of a series of horizontal strata around a spring, extending from the earliest Late Pleistocene to the early Holocene (Fig. 1 and supplementary materials, section I). The Xuchang 1 and 2 crania were found broken, each cranium dispersed within a circumscribed horizontal area within layer 11. They were associated with a diverse macromammalian faunal assemblage, rich in *Equus*, *Bos*, *Megaloceros*, *Procapra*, *Cervus*, and *Coelodonta*. The layer contains a Middle Paleolithic lithic industry, mostly on quartz, along with bone tools on diaphyseal splinters (*7*). Layer 11 has produced a consistent series of optically stimulated luminescence (OSL) ages (supplementary materials, section II), placing the human remains between about 105,000 and 125,000 years, and the overlying layers 10 and 9 have provided ages of about 100,000 and 90,000 years (Fig. 1). The human crania are therefore securely dated to marine isotope stage (MIS) 5, within MIS 5e or 5d (table S8).

The more complete Xuchang 1 cranium (Fig. 2) retains most of the neurocranial vault and portions of the cranial base, including especially the parietal, occipital, and temporal bones, plus sufficient portions of the left frontal bone to position the lateral supraorbital region. The less complete Xuchang 2 cranium (Fig. 3) retains the posteroinferior neurocranium, with the majority of the occipital bone and the petrotympanic portions of the temporal bones. The individual pieces are fossilized without distortion, and it was possible to restore the crania manually and virtually (figs. S11 and S12). Three additional pieces, Xuchang 3 to 5, were also found (table S1).

The Xuchang crania, from a broader Middle and Late Pleistocene perspective, exhibit a mosaic morphological pattern. In common with other early Late Pleistocene humans (whether morphologically archaic or modern), they share neurocranial expansion and gracilization. The endocranial volume (ECV) of Xuchang 1, ~1800 cm^3, is at the high end of Neandertal and early modern human variation (fig. S14). It indicates marked encephalization, even if the body mass of Xuchang 1 had been among the largest known for Late Pleistocene humans (*8*) (supplementary materials, section VI). This ECV is associated with lateral expansion of the parietal bones across the eminences (figs. S17 and S23), even though the midsagittal parietal profile is among the flattest for a Late Pleistocene human (Fig. 2 and fig. S23). Xuchang 2 has a smaller ECV, but one likely to have been at least average for a Late Pleistocene human, based on cranial base breadths (Fig. 3 and fig. S16).

Although Xuchang 1 and 4 exhibit prominent supraorbital tori, their tori are modest in thickness, similar in that respect to those of Neandertals and some early modern humans (fig. S20). Moreover, they share with Late Pleistocene humans a consistent toral thickness with minimal lateral expansion (fig. S21). Their cranial gracility is evident in their modest parietal thicknesses, the small nuchal torus of Xuchang 1 being restricted to the middle two-thirds of the occipital bone, and the absence of a nuchal torus on Xuchang 2 (figs. S17 and S26). Neither exhibits an angular torus (fig. S27). In reduced hypertrophy, as well as overall ECV, the Xuchang crania contrast with early Middle Pleistocene humans, particularly those from eastern Eurasia.

The large Xuchang 1 neurocranium closely approximates the shapes of those of Middle Pleistocene humans, especially eastern Eurasians (Fig. 2 and fig. S17). The vault height is low, similar to those of the Neandertals and the higher Middle Pleistocene vaults, and the low vault height is reflected in a low temporal squamous portion (figs. S27 and S28). It is also produced by the very flat midsagittal parietal arc. In contrast, the maximum cranial breadth is the largest known in the later Pleistocene (fig. S15), and it is securely based on an undistorted posterior cranium. Moreover, the widest point is low, on the temporal bones (fig. S17), as in most earlier crania, rather than on the parietal bones, as among Neandertals and most modern humans. In addition, the one complete mastoid process is short and slopes inward (fig. S17), rather than being longer and more vertical, as in modern humans and some Neandertals. These features combine to provide the cranium with an occipital profile similar to those of earlier human crania, contrasting with the rounded profiles of Neandertals and the laterally vertical ones of modern humans.

In combination with these derived and ancestral features, the Xuchang crania display two complexes that primarily align them with the Neandertals (*9*, *10*): their midoccipital areas and temporal labyrinths. The occipital bones exhibit a modest or minimal nuchal torus limited to the middle two-thirds of the superior nuchal line, an absence of an external occipital protuberance, a

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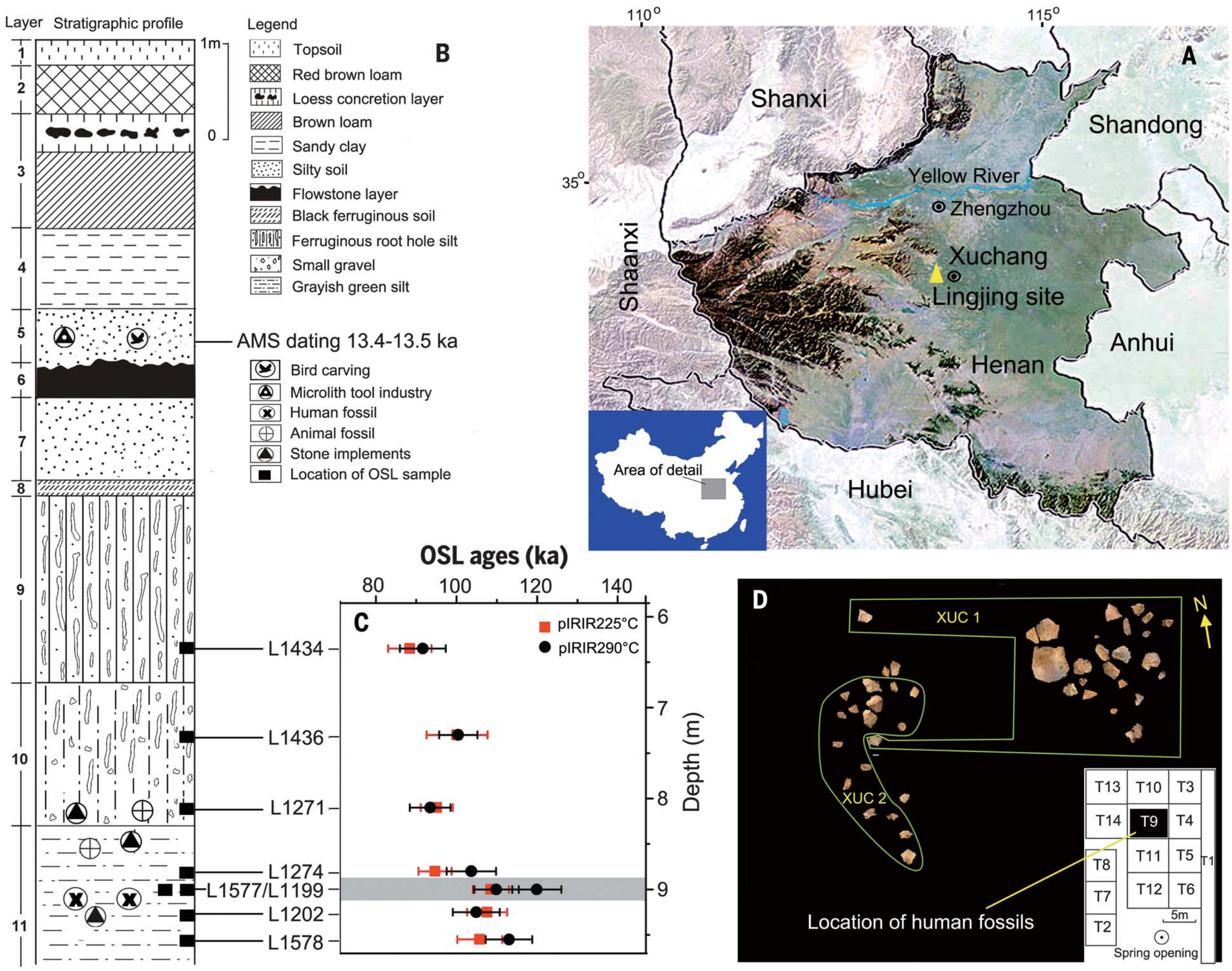

Fig. 1. The Lingjing site. (**A**) Location of the Lingjing site in Xuchang county, Henan Province, China. (**B**) Schematic stratigraphy of the Lingjing site, with the locations of the OSL samples indicated. (**C**) The OSL ages of the samples, obtained with two protocols (supplementary materials, section II) and plotted with a 1σ error range. (**D**) The scatters of the Xuchang (XUC) 1 and 2 cranial remains in excavation area T9. AMS, accelerator mass spectrometry; ka, thousand years.

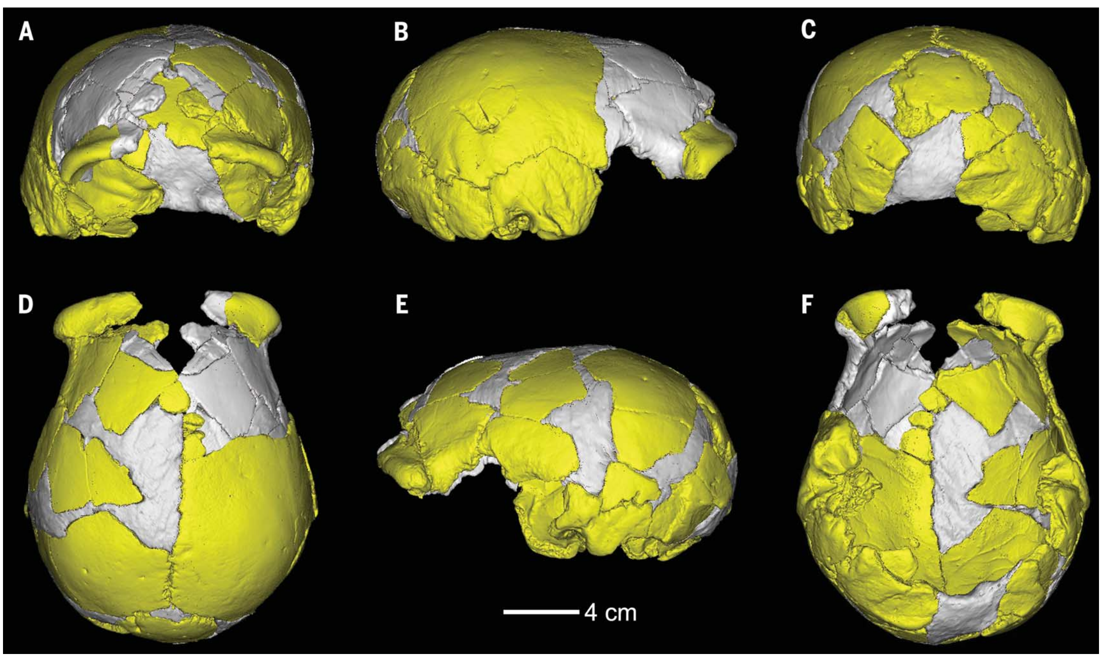

Fig. 2. Virtual reassembly of the Xuchang 1 cranium. (**A**) Anterior, (**B**) right lateral, (**C**) posterior, (**D**) superior, (**E**) left lateral, and (**F**) inferior views. Gray, filled-in absent portions and mirror-imaged right frontal squamous portion.

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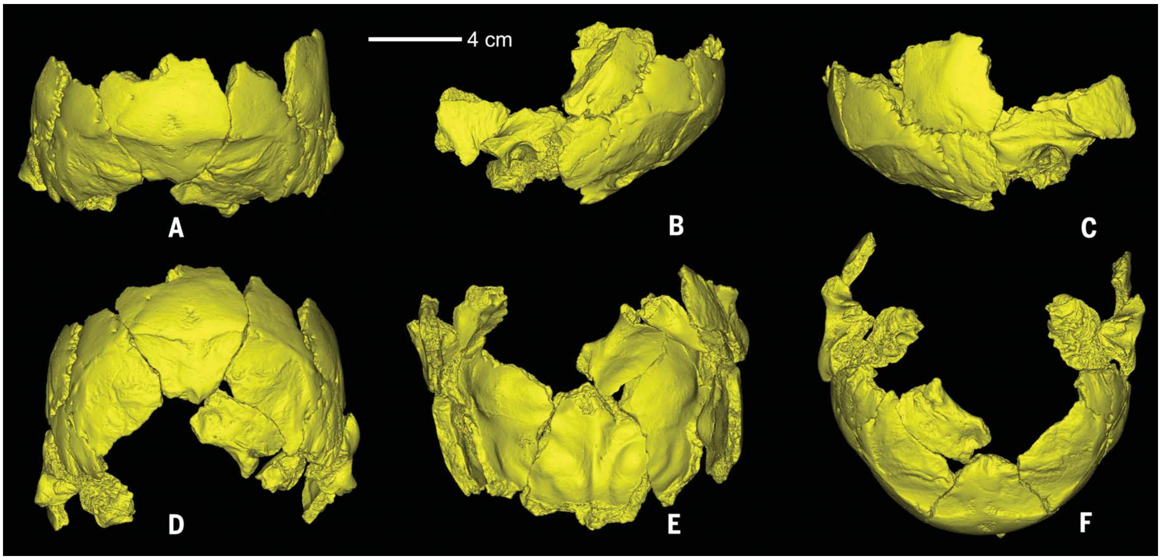

Fig. 3. Virtual reassembly of the Xuchang 2 cranium. (**A**) Posterior, (**B**) left lateral, (**C**) right lateral, (**D**) posteroinferior, (**E**) superior, and (**F**) inferior views.

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distinct suprainiac fossa, and a continuous external table thickness through the inion region (Fig. 4 and fig. S26). Although aspects of this complex are evident in non-Neandertals (*11*), the full set is known only in Neandertals and the Xuchang crania (*9*). The temporal semicircular canals in both crania exhibit relatively small anterior canal radii and more superior lateral versus posterior canals (Fig. 4 and figs. S29 and S30), a pattern evident in most Neandertals (*10*) and known elsewhere only in the early Late Pleistocene eastern Asian Xujiayao 15 temporal bone (*6*).

The Xuchang early Late Pleistocene archaic human crania therefore exhibit features that are (i) ancestral and reminiscent particularly of early Middle Pleistocene eastern Eurasian humans; (ii) derived and shared by earlier Late Pleistocene humans elsewhere, whether morphologically archaic or modern; and (iii) distinctive of the Neandertals. This morphological combination, and particularly the presence of a mosaic not known among early Late Pleistocene humans in the western Old World, suggests a complex interaction of directional paleobiological changes and intra- and interregional population dynamics.

With respect to directional changes, the presence of marked encephalization, at least in Xuchang 1, conforms to the trend of major increases in brain size (and encephalization) through the Middle Pleistocene, culminating in recent human brain sizes by the earlier Late Pleistocene (*12*). Given the costs, as well as benefits, of larger brains (*13*, *14*), the Xuchang ECVs reinforce the uniform levels of behavioral elaboration evident through this time period across the Old World (*15*, *16*). Although its broader implications are unclear, the gracilization of the Xuchang crania relative to Middle Pleistocene fossils follows similar patterns to those evident further west.

At the same time, the overall cranial shape, and especially the combination of the wide cranial base and low neurocranial vault, indicates a pattern of continuity with the earlier, Middle

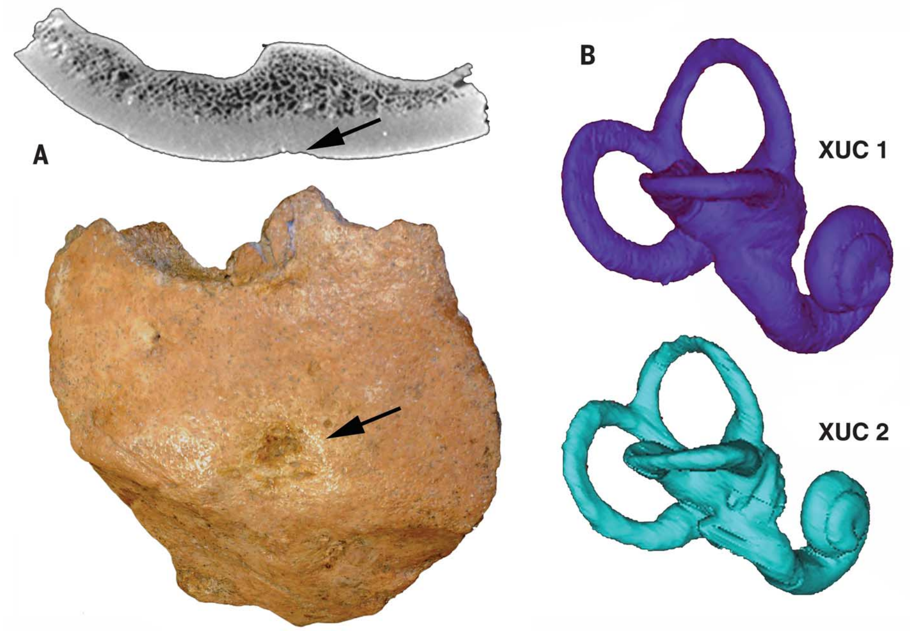

Fig. 4. Neandertal features of the Xuchang cranial remains. (**A**) External view of the Xuchang 2 suprainiac fossa with the superior nuchal line (bottom) and micro–computed tomography (μCT) section through the Xuchang 2 suprainiac fossa (top), showing the continuous external table thickness. (**B**) μCT-extracted temporal labyrinths of the Xuchang 1 and 2 right petrous bones, in lateral view, showing the relatively small anterior canals and the more superior lateral versus posterior canals. [Not to scale]

Pleistocene eastern Eurasian humans. Yet the presence of two distinctive Neandertal features—one (iniac and nuchal morphology) unknown among earlier eastern crania, and the other (labyrinthine proportions) evident in only one similarly aged eastern Eurasian fossil—argues for populational interactions across Eurasia during the late Middle and early Late Pleistocene. Similar interactions can be inferred from the presence of Neandertal ancient DNA in western Siberia (*17*) and in the Tianyuan 1 early modern human from northern China (*18*). These data therefore argue both for substantial regional continuity in eastern Eurasia into the early Late Pleistocene and for some level of east-west population interaction across Eurasia.

The Xuchang crania therefore provide an important window into the biology and population history of early Late Pleistocene eastern Eurasian people. As such, they are a critical piece in our understanding of the human evolutionary background to the subsequent establishment of modern human biology across the Old World, a process that was already under way in eastern Africa and (apparently) further south in eastern Asia (*19–22*).

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SUPPLEMENTARY MATERIALS

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Supplementary Text
Figs. S1 to S30
Tables S1 to S14
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Morphological mosaics in early Asian humans

Excavations in eastern Asia are yielding information on human evolution and migration. Li *et al.* analyzed two fossil human skulls from central China, dated to 100,000 to 130,000 years ago. The crania elucidate the pattern of human morphological evolution in eastern Eurasia. Some features are ancestral and similar to those of earlier eastern Eurasian humans, some are derived and shared with contemporaneous or later humans elsewhere, and some are closer to those of Neandertals. The analysis illuminates shared long-term trends in human adaptive biology and suggests the existence of interconnections between populations across Eurasia during the later Pleistocene.

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