Morphological description and evolutionary significance of 300 ka hominin facial bones from Hualongdong, China

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1. Introduction

The late Middle Pleistocene to early Late Pleistocene (ca. 300–126 ka) is a crucial period for clarifying hominin evolutionary relationships, especially the transition to modern humans in both Africa and Eurasia. Over the past several decades, a series of fossil discoveries and subsequent debates have reshaped our understanding of hominin evolution, morphological variation, phylogeny, and systematics around the world (Rightmire, 1998a, 2008; Stringer, 2016). In Africa and the Levant, morphologies and dates of several critical fossils from Herto, Omo, Jebel Irhoud, and Misliya established the emergence of early modern humans in Africa between 160 and 315 ka (White et al., 2003; McDougall et al., 2005; Hublin et al., 2017; Hershkovitz et al., 2018). Morphology expressed in the Bodo cranium suggests that speciation of Homo heidelbergensis or archaic H. sapiens may have occurred even earlier in Africa (Rightmire, 1996). Contemporaneous with the emergence of...
modern *H. sapiens* in Africa, hominins characterized by more archaic features still inhabited much of Eurasia, further complicating evolutionary relationships between these groups. It appears increasingly likely based on new fossil evidence that more hominin taxa (e.g., Denisovans and possibly additional unknown or ‘ghost’ hominin lineages) besides *H. heidelbergensis* and Neanderthals occupied Eurasia in the late Middle and early Late Pleistocene (Reich et al., 2010; Xing et al., 2015; Li et al., 2017; Chen et al., 2019). Some researchers have alternatively suggested that specimens such as Dali and Jinniushan should be classified as *H. heidelbergensis* (Rightmire, 1996, 1998a, 2008; Stringer, 2002).

In present-day China, late Middle Pleistocene hominin craniodental fossils have been found at more than ten sites (Wu and Poirier, 1995; Liu et al., 2014). Among these are some well-preserved crania such as Dali, Jinniushan, and Maba. For many years, these Chinese late Middle Pleistocene fossils have been similarly regarded as archaic *H. sapiens* and positioned phylogenetically as an intermediate between *H. erectus* and anatomically modern humans (Wu and Poirier, 1995; Wu, 2009, 2014; Wu and Athreya, 2013).

During the last decade, substantial progress has been made in expanding the hominin fossil record in China. Several notable late Middle and early Late Pleistocene hominin fossils have been discovered including Huanglongdong, Zhirendong, Lunadong, Daoxian (Fuyandong), Xuchang, and Hualongdong (Liu et al., 2010a, b, 2015; Bae et al., 2014; Li et al., 2017; Wu et al., 2019). Studies of these recent finds have confirmed the notion that hominin evolution in the region was more complicated during the late Middle and early Late Pleistocene than previously hypothesized (Wu et al., 2011, 2014; Xing et al., 2015; Li et al., 2017). Specifically, Zhirendong and Daoxian mandibular and dental fossils provide evidence for the emergence of modern human morphology in eastern Asia as early as 120 ka (Liu et al., 2010a, b, 2015; Cai et al., 2017; but also see Kaifu and Fujita, 2012; Michel et al., 2016). Studies of late Middle Pleistocene hominin fossils from Xuchang, Xujiauyo, and other sites have documented a high degree of morphological variation in the region due to gene flow with Neanderthals and possibly the presence of a ‘ghost’ lineage (Wu et al., 2014; Chang et al., 2015; Xing et al., 2015; Li et al., 2017). Lastly, reappraised dates, morphological analyses, ancient protein analysis, and mitochondrial DNA from sediments have linked the Middle Pleistocene Xaibe specimen with Denisovans (Chen et al., 2019; Zhang et al., 2020).

Even with these recent advances in documenting late Middle Pleistocene human evolution in China, some key issues pertaining to the origin of late Middle Pleistocene morphology in East Asia and evolutionary relationships between taxa in the region have remained unclear (Liu et al., 2016, 2019). Recent studies of some late Middle Pleistocene hominins (e.g., Dali, Panxian Dadong, and Hualongdong) emphasized their mosaic combination of derived characteristics, resembling those of modern humans, and primitive (or archaic) features (e.g., low vault, robust supraorbital structure, and a strong maxillary incisor lingual tubercle; Wu, 2014; Liu et al., 2013; Wu et al., 2019), resembling those of Early and Middle Pleistocene hominins such as Zhokoudian, Nanjing, and Hexian. Comparative studies of the Dali cranium indicated its cranial morphological pattern is a mosaic combination of East Asian *H. erectus* and early modern human features (Wu, 2014, 2020). Specifically, the Dali cranium combines characteristic features of Early and Middle Pleistocene *H. erectus* (i.e., a pronounced supraorbital torus, low cranial vault, thickened cranial wall, and an angular-shaped occipital region) with modern human-like features including the broadest cranial position occurring at the posterior temporal region, a flattened face, vertical infraorbital plate, and weak prognathism (Wu and Athreya, 2013). Hominin teeth from the 130–300 ka site of Panxian Dadong in South China also exhibit a mosaic of archaic and derived features that align with Middle and Late Pleistocene fossils from East and West Asia and Europe (Liu et al., 2013). Notably, the Panxian Dadong P3 displays derived traits falling within the range of variation exhibited by Chinese Late Pleistocene hominins, and particularly West Asian early modern humans. The preponderance of these modern human-like features suggests that the Panxian Dadong hominins are evidence of a transition in the region to modern human morphology (Liu et al., 2013). Thus, evolutionary timing and the dynamics of the transition from archaic to modern morphology in the late Middle and early Late Pleistocene of China are not fully elucidated by the existing fossil record.

The Hualongdong (Hualong Cave) site is located in Dongzhi County, Anhui Province, China. Initial excavations at the Hualongdong site in 2006 yielded a hominin frontal fragment and a lower second molar (Gong et al., 2014). Renewed excavations taking place annually between 2014 and 2019 resulted in the discovery of numerous additional hominin fossils (e.g., a partial cranium, mandible, teeth and three partial femora; Wu et al., 2019). Cumulatively, 27 human fossils have been recovered at Hualongdong representing a minimum of 16 individuals (Wu et al., 2019). The site is also characterized by an abundance of lithic artifacts and fossil mammal fauna (Tong et al., 2018). Evidence of cut marks on faunal remains in the same brecciated deposits also demonstrates human activity at the site (Wu et al., 2019). Biorstratigraphic study of faunal remains, as well as Uranium-Thorium dating of speleothems and animal teeth in the deposits, provides secure dates in the late Middle Pleistocene, ca. 300 ka (~270–330 ka; Tong et al., 2018; Wu et al., 2019).

Among the hominin fossils from Hualongdong, a juvenile partial cranium and mandible (numbered as HLD 6) were recovered and described (Wu et al., 2019). Initial comparisons of HLD 6 emphasized similarities in the combination of its pronounced supraorbital torus and low and wide neurocranial vault with those in Early and Middle Pleistocene hominins (Wu et al., 2019). The same analysis, however, also noted other characteristically modern human features in HLD 6 including a flat face and a nearly vertical mandibular symphysis with a pronounced mental trigone. The dentition of HLD 6 is gracile with right M3 agenesis, but the developing left M3 crown is still in its crypt. In the combination of these craniodental features, the HLD 6 hominin expanded the range of morphological variation exhibited by late Middle Pleistocene hominins in East Asia. Moreover, the HLD 6 hominin also was suggested to have corroborated regional continuity in East Asia by retaining archaic features and foreshadowing changes evident in emergent modern humans in the region (Wu and Athreya, 2013; Chang et al., 2015; Li et al., 2017; Wu et al., 2019; Chen et al., 2019).

Previous studies of the Pleistocene hominin face have demonstrated pronounced morphological variability (Weidenreich, 1943; Rightmire, 1998b; Arsuaga et al., 1999). Although the exact selective pressures driving human facial morphological variation in the Middle to Late Pleistocene are not fully understood, with some characters (e.g., supraorbital torus and nasal aperture) probably influenced disproportionately by environment, developmental constraints or function (Franciscus and Trinkaus, 1988; Dean, 1988), other anatomical complexes of the face (e.g., infraorbital morphology, nasal profile and floor, and malar morphology) are reasonably more informative for understanding evolutionary process and taxonomy (Rightmire, 1998b; Bermúdez de Castro and Martínón-Torres, 2014). For example, some aspects of facial structure can distinguish regional human populations, such as the morphological features that have been used to support regional continuity in East Asia (Wolpoff et al., 1984; Wu, 1990, 2004). The HLD 6 partial cranium includes a nearly complete frontal bone, both left and right maxillary bones and a left zygomatic bone (Fig. 1), and
thus, it retains some of these informative regions for potentially advancing current understanding of late Middle Pleistocene human evolution in East Asia.

It is believed that facial features that develop early in ontogeny may be good phylogenetic indicators because they likely have a low level of phenotypic plasticity (Rak, 1983, 1986; Lieberman et al., 2002). Because the HLD 6 individual is a juvenile with an estimated age of 13–15 years (Wu et al., 2019), the degree to which its facial features may change during ontogenetic growth before adulthood warrants consideration. In this matter, it is instructive to classify the age of ATD6-69 (i.e., comparatively less change due to remaining ontogenetic growth in facial morphology may have further accentuated the course of its remaining ontogenetic growth (Freidline et al., 2013). Given the apparent insulation of these modern human-like characters to ontogenetic change (Lacruz et al., 2013, 2015, 2019) and given the older estimated age of HLD 6 relative to the estimated age of ATD6-69 (i.e., comparatively less change due to remaining growth would be expected in HLD 6), it is reasonable to propose that any remaining ontogenetic growth experienced by HLD 6 would have had minimal effects on any resemblances of its features to those of modern humans or archaic H. sapiens. Thus, the observed facial morphological pattern in the juvenile HLD 6 cranium would likely not have changed substantially in adulthood, although some slight changes with growth cannot be entirely ruled out.

Here, we provide a detailed anatomical description and comparative analysis of the HLD 6 cranium. Specific anatomical features of the HLD 6 face along with its overall morphological configuration are used as the basis of qualitative and quantitative assessments. HLD 6 facial morphology is compared with facial morphology of Pleistocene hominins and modern humans from East Asia to evaluate regional variation during the Middle Pleistocene. Comparisons of HLD 6 and Pleistocene hominins from other regions are made to assess the nature of the transition from archaic to modern morphologies in East Asia. Ultimately, we evaluate the implications of HLD 6 for the emergence of modern humans in East Asia.

2. Materials and methods

2.1. Preservation and reconstruction of HLD 6

Four facial fragments from the HLD 6 partial cranium have been recovered (Fig. 1). Fragment 1 (Fig. 1A) preserves a complete frontal bone including its supraorbital region and most of the frontal process of the left maxilla. Fragment 2 (Fig. 1B) preserves a nearly complete right maxilla with only its frontal process missing. The entire alveolar process and most of its palatine process are well preserved with M1 and M2 retained in situ. Micro-CT scanning confirms right M3 agenesis. Fragment 3 (Fig. 1C) preserves a majority of the left maxilla and the articulating partial left zygomatic bone. The maxilla preserves most of the infraorbital region, nearly all of the alveolar process (with I1 missing), and a portion of the palatine process with M1 and M2 retained in situ. A crown of the left M3 is still in its crypt. Fragment 4 (Fig. 1D) preserves a small piece of the left maxilla consisting of the lower inferior orbital rim and its adjacent infraorbital region and most of the left rim of the nasal aperture. This fragment refits with fragment 3 in the vicinity of the infraorbital foramen and also refits with the frontal process of the left maxilla in fragment 1.

By assembling the frontal process of the left maxilla in fragment 1, the left maxillary portion in fragment 4, and the left maxillary portion in fragment 3, the left maxilla can be nearly fully reconstructed. The restored left maxilla can be articulated with the frontal bone at the left portion of the frontomaxillary suture. Although there is a small area of the left alveolar process missing near I3 in fragment 2, the complete right alveolar process was sufficiently well preserved from the anterior border at its midline of

![Figure 1. The HLD 6 partial cranium. A) Frontal bone and a small articulating portion of the frontal process of the left maxillary bone; B) right maxillary bone; C) left maxillary bone and an articulating portion of the left zygomatic bone; D) a small portion of the left maxilla.](image-url)
1\(^1\) (infradentale superior) to its posterior end, permitting confident restoration of the location of the intermaxillary articulation. This enabled reliable reconstruction of the whole maxilla and its dental arcade. To evaluate the general facial profile and mid-facial prognathism of HLD 6 and to conduct comparative analyses, we undertook both a physical reconstruction and a virtual reconstruction based on high-resolution microcomputed tomography (\(\mu\)CT) scanning (Wu et al., 2019) of individual facial fragments comprising the HLD 6 partial cranium (Fig. 2).

Figure 2. Virtual reconstruction of the HLD 6 cranium based on \(\mu\)CT imaging. A) Anterior view; B) left lateral view; C) latero-right view; D) superior view. (Darker green represents mirrored portions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2. CT scanning

The HLD 6 isolated fragments were \(\mu\)CT scanned using an industrial high precision \(\mu\)CT scanner (Institute of High Energy Physics, Chinese Academy of Sciences; tube voltage: 150 kV; tube current: 110 \(\mu\)A; voxel size: 30–65 \(\mu\)m) housed at the Institute of Vertebrate Paleontology and Paleoanthropology. Virtual reconstruction of HLD 6 from renderings of isolated cranial fragments was performed using Mimics v. 20.0 (Materialise NV, Leuven). Each rendered fragment in the virtual reconstruction was repositioned and reoriented using sutures, postmortem fractures, and morphological surface features to re-establish anatomical continuity in the reconstructed partial cranium (Fig. 2).

2.3. Comparative samples

In accordance with the date of the HLD 6 individual (ca. 300 ka), appropriate comparative samples were gathered consisting of Middle and Late Pleistocene hominins from different geographic regions. To explore temporal change and regional variation in facial features, additional comparative specimens from both Early Pleistocene hominins and samples of modern humans from different geographic regions were also included.

Although a taxonomic framework has been proposed for Pleistocene hominins (Wood and Richmond, 2000), there have been debates on the evolutionary and taxonomic status for many African and Eurasian hominin fossils throughout the Pleistocene. Hominins from the Early Pleistocene and early Middle Pleistocene are usually attributed to \(H. erectus/\)H. ergaster or \(H. antecessor\) (Bermúdez de Castro et al., 1997; Gabunia et al., 2000). By comparison, taxonomic assignments of late Middle and Late Pleistocene hominins are often more widely debated (Wood and Richmond, 2000; Stringer, 2016). Late Middle Pleistocene hominins are usually attributed to archaic \(H. sapiens\) or \(H. heidelbergensis\) (Rightmire, 1998a, 2008); some are unclassified or even referred to as early \(H. sapiens\) (Arsuaga et al., 2014; Li et al., 2017; Hublin et al., 2017). Various additional taxonomic nomenclatures have been attributed to late Middle and Late Pleistocene hominins around the world (i.e., \(H. neanderthalensis\), \(H. sapiens idaltu\), \(H. floresiensis\), \(H. luzonensis\), and Denisovans; Wood and Richmond, 2000; White et al., 2003; Brown et al., 2004; Détroit et al., 2019; Reich et al., 2010).

Cognizant of the debates over these Pleistocene hominin fossils, in this study, we organize comparative samples by geographic regions and chronological periods (Table 1). Specifically, we divide comparative samples into regional locations including East Asia, Africa, West Asia, and Europe. We further partition comparative samples into Early, Middle, and Late Pleistocene periods. In some studies, Neanderthals have been treated as a separate group in analyses (Bailey, 2000, 2002; Rosas, 2001; Martínón-Torres et al., 2007, 2012). However, because most Neanderthal specimens chronologically coexisted with other European Late Pleistocene specimens, to minimize taxonomic debate, we do not distinguish the separate taxon name Neanderthal from other subgroups comprising our sample of European Late Pleistocene hominins. The chronological age of \(H. floresiensis\) is within the range of our comparative samples. While some have suggested abnormal health conditions are responsible for cranial morphology in these individuals (e.g., Henneberg et al., 2014), reasonable alternative explanations exist (e.g., van den Bergh et al., 2006). To be conservative, we do not include \(H. floresiensis\) in comparative samples.

Although we do not use formal taxonomic names for comparative samples in metric comparative analyses and instead refer to regional or temporal labels (Table 1), we still refer to some widely used taxonomic names in nonmetric trait comparisons for the sake of clarity. Many Middle Pleistocene hominins have been called archaic \(H. sapiens\). Although this is not a strictly formal taxonomic term, we still recognize the term archaic \(H. sapiens\) to facilitate comparisons with HLD 6 because it is commonly used in the published literature on our comparative samples. Ultimately, we merged both criteria stratifying geographical regions within chronological periods to maximize general states of key facial characters for comparison with those of HLD 6. In addition to the fossil comparative sample, 86 modern human crania were chosen from three regions worldwide, namely China, Europe, and Africa. Table 1 summarizes details on the comparative samples used in this study.

2.4. Anatomical descriptions and measurements

In the present study, we follow Rightmire (1998b) and define the face as supraorbital structures and surrounding areas, the zygomatic arch, the nasal bridge, the piriform aperture, the subnasal region, and the hard palate. Because HLD 6 preserves nearly the complete face, any notable thickenings, suture courses, size proportions, eminences or tubercles, shapes of specific subregions, and other nonmetric features are described. Nonmetric facial traits described in the present study follow definitions provided by Weidenreich (1943), Rightmire (1988b), and Arsuaga et al. (1999). Dental morphology of HLD 6 is not addressed in the present study. Linear and angular measurements of the facial skeleton taken in the present study are listed in Table 2. Measurement definitions

2.5. Multivariate analysis

Based on metric trait comparisons, we conducted principal component analyses (PCAs) to assess overall morphological affinities of HLD 6 to comparative samples. Typically, the comparative specimens were incomplete. Thus, to maximize the number of specimens available for inclusion in PCAs, we conducted separate analyses using both five-variable and seven-variable data sets that emphasized different anatomical regions of the facial skeleton. The five-variable analysis included measurements located around the supraorbital torus, including glabellar projection, minimum frontal breadth, supraorbial torus breadth, mid-orbital supraorbital torus thickness, and lateral supraorbital torus thickness. The seven-variable analysis included measurements located on the middle and lower face, including nasospinale-prosthion height, upper facial height, orbit height, orbit breadth, nasal breadth, nasal height, and malar height. All PCAs were conducted on correlation matrices to standardize intragroup variation. Statistical analyses were performed with PAST v. 2.12 (Hammer et al., 2001).

3. Results

3.1. Anatomical description

Prognathism: The reconstructed partial cranium of HLD 6 (Wu et al., 2019; Fig. 2) permits reliable estimation of the extent of facial prognathism, which is assessed both with respect to sagittal and coronal planes. Sagittal prognathism of the HLD 6 face is quantified as entire prognathism (total prognathism angle), nasal prognathism (middle prognathism angle), and alveolar prognathism (alveolar profile angle), while flatness in the coronal plane is measured as nasomalar angle (Table 2). The HLD 6 face exhibits moderate prognathism in both sagittal and coronal views (refer to later section for details).

Supraorbital region: The HLD 6 partial cranium has well-developed supraorbital tori bilaterally (Figs. 1–3). In anterior view, the supraorbital tori are double arched and rounded with their thickest regions being in the medial halves. Supraorbital tori of HLD 6 are not uniformly thick or continuous through the glabellar region.

### Table 1

<table>
<thead>
<tr>
<th>Geographical groups and chronology</th>
<th>Specimens</th>
<th>Data sources</th>
</tr>
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<tbody>
<tr>
<td><strong>East Asia</strong></td>
<td></td>
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<tr>
<td>Early Pleistocene (n = 23)</td>
<td>Sangiran (4, 10, 17, 27), Sangiran Skull IX (Tji-1993.05), Bukuran, Trinil 2, Lantian (PA105), Yunnan 2</td>
<td>Rightmire (1996); Hublin et al. (2017); Present study (measured on original fossils)</td>
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<tr>
<td>Middle Pleistocene (n = 7)</td>
<td>Sambungmacan (1, 3, 4), Ngandong (1, 2, 5, 6, 7, 10, 11, 12), Ngawi 1, Narmada, ZKD 2, 3, 5, 10, 11, Nanjing 1, Hexian 1, Dali, Jinniushan, Maba</td>
<td>Arsuaga et al. (2014); Present study (measured on casts)</td>
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<tr>
<td>Late Pleistocene (n = 7)</td>
<td>Xuchang 1, Lujiang 1, Upper Cave (101, 102, 103), Minatogawa (1, 4)</td>
<td>Trinkaus and Svoboda (2006); Present study (measured on original fossils)</td>
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<tr>
<td><strong>Africa</strong></td>
<td></td>
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<tr>
<td>Early Pleistocene (n = 7)</td>
<td>KNM-WT 15000, KNM-ER 3733, KNM-ER 3883, OH9, OH12, Daka, Buia</td>
<td>Rightmire (1998b); Asfaw et al. (2002); Present study (measured on original fossils)</td>
</tr>
<tr>
<td>Middle Pleistocene (n = 12)</td>
<td>Bodo, Broken Hill, Ndutu, Saldanha, Elie Springs 11693, Florisbad, Jebel Irhoud (1, 2), Herto 21/BOU-VP-16/1, Laetoli 18, Onno-Ribesh (1, 2)</td>
<td>Rightmire (1998b); Hershkovitz et al. (2018); White et al. (2003); Present study (measured on casts)</td>
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<td>Late Pleistocene (n = 1)</td>
<td>Fish Hoek</td>
<td>Present study (measured on original fossils)</td>
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<td><strong>West Asia</strong></td>
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<td>Early Pleistocene (n = 5)</td>
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<td>Arsuaga et al. (2019); Present study (measured on casts)</td>
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<tr>
<td>Late Pleistocene (n = 12)</td>
<td>Misiya 1, Qafzeh (3, 6, 9, 10, 11), Skhul (2, 4, 5, 6, 9), Amud 1</td>
<td>Present study (measured on casts)</td>
</tr>
<tr>
<td><strong>Europe</strong></td>
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<tr>
<td>Early Pleistocene (n = 1)</td>
<td>ATD6-69</td>
<td>Arsuaga et al. (2014); Present study (measured on casts)</td>
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<tr>
<td>Middle Pleistocene (n = 10)</td>
<td>Atapuera Sima De Los Huesos (4, 5, 6), Steinheim, Petralona, Ehringsdorf H, Biache-Saint-Vaast 2, Zuttiyeh, Arago 21-47 Sw, Ceprano 1</td>
<td>Present study (measured on casts)</td>
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<td>Late Pleistocene (n = 84)</td>
<td>Tabun I, Shandar (1, 2, 4, 5), Lazaret 24, Saccapestore (1, 2), Spy (1, 2), Neandertal 1, Le Moustier 1, La Ferrassie 1, La Chapelle 1, Quatari 1, Gibraltor 1, La Quina 5, Krapina (1, 3, 4, 6, 23, 28, 37.1, 37.4, 37.7), Vindija (202, 224, 227, 259, 260, 261, 262, 279), Sa'ara 1, Dame du Cavillon 1, Barma Grande (1, 2, 3, 4, 5), Grotte-des-Enfants (4, 5, 6), Aricne Candide IP, Abri Patatau 1, Cro-Magnon (1, 2, 3), Chancelade 1, Brno (2, 3), Oberkassel (1, 2), Prédemonti (1, 3, 4, 9, 10), Maladie (1, 2, 5, 6, 8), Combe Capelle, Mas d’Azil III, Lafaye, Saint-Germain-La-Riviere, Les Cotes, Montdarit 1, Cheix, Rond-du-Barry, Sorde L’Abbey 2, Culoz, Dolni Vestonice (3, 13, 14, 15, 16), Pavlov 1, Oase 2, Sunghir (1, 5), Ohalo 2</td>
<td>Present study (measured on casts)</td>
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<td>Modern humans (n = 86)</td>
<td>China: n = 51; Europe: n = 17; Africa: n = 18</td>
<td>Present study (Chinese, European, and Africans)</td>
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*a* Original casts curated at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP).  
*b* Collections curated at the IVPP.  
*c* High-quality casts curated at the American Museum of Natural History (AMNH), New York, US.  
*d* Original fossils curated at the National Museum of Kenya, Nairobi, Kenya.  
*e* Collections curated at the AMNH.  
*f* Collections curated at the University of the Witwatersrand, Johannesburg, South Africa.  
*h* Bolded specimen names indicate juvenile or subadult individuals.
Because the glabellar region of HLD 6 is slightly concave, a weak midline depression at the glabella divides the HLD 6 supraorbital tori into left and right portions (Fig. 4). The supraorbital tori extend posterolaterally to follow a more oblique than lateral course with respect to the coronal plane. On each side, the torus gradually weakens laterally and is further divided into medial and lateral superciliary arches. On the better preserved left side, the torus is superoinferiorly thick and overall massive, forming a ‘trigone’ at the lateral margin of the orbit. In anterior view, the left and right supraorbital tori of HLD 6 appear asymmetric, with the supraorbital torus on the left side being more heavily built and positioned higher than on the right side. Above or behind the supraorbital tori of HLD 6, there is a shallow but broad supratoral sulcus (Figs. 3 and 4). The supratoral sulcus of HLD 6 is divided into a medial glabellar segment, including the superciliary arches, and lateral segments. The supratoral sulcus of HLD 6 is more pronounced in the lateral regions of the frontal bone, and postorbital constriction is apparent.

![Diagram of HLD 6 facial region](image)

**Figure 3.** Supraorbital region of HLD 6. A) Frontal view; B) left lateral view. Black lines indicate the processus supraorbitalis (left, upper), lacrimal fossa (left, lower), and lateral trigone (right), respectively.
The orbits of HLD 6 are tall and square-shaped with relatively straight upper margins that follow a horizontal plane. This is reflected in the HLD 6 partial cranium having an orbital index of 94.4 (refer to Section 3.3 and Table 2). There are no supraorbital notches or foramina on HLD 6. In the middle region of the left orbit of HLD 6, the superior margin of the orbit exhibits a clear tubercle or ‘processus supraorbitalis’ (Fig. 3) as described by Weidenreich (1943).

The left orbit is more completely represented in HLD 6 than the right orbit (Fig. 1). The surface of the superolateral portion of the left orbit is well preserved. The left lacrimal fossa is visible as a distinctively depressed area (Fig. 3). In the inferolateral corner and on its lateral wall, there is a large, depressed foramen of zygomatico-orbital inferior, as described by Weidenreich (1943). The position of this foramen in HLD 6 has ascended onto the lateral wall of the orbit. As opposed to the relatively straight superior margin of the orbit, the inferior margin is more rounded (Fig. 2A).

Nasal region The HLD 6 nasofrontal and maxillofrontal sutures are preserved. After mirroring preserved parts of the left maxilla, such as its frontal process, reasonably accurate estimation of some nasal bone dimensions is possible (Fig. 2A). Collectively, the nasal bones of HLD 6 appear extremely narrow (i.e., the estimated breadth for the combined nasal bones is 2 mm) and exhibit a consistent rather than tapered width from their superior to their inferior portions (Figs. 1–3).

HLD 6 exhibits a large upper face height with an upper facial index of 71.4 (refer to Section 3.3 and Table 2). The HLD 6 cranium has a high and narrow nasal aperture (piriform aperture; Table 3; Fig. 2A). The lateral margin of the nasal aperture (crista nasalis) follows a nearly vertical plane (Fig. 2B). The HLD 6 cranium exhibits a well-defined and moderately developed anterior nasal spine (Fig. 5).

In the preliminary assessment of the HLD 6 cranium (Wu et al., 2019), the transition between the nasal floor and the nasoalveolar clivus was broadly characterized as ‘sill-like’, as described by Weidenreich (1943) on the left side and smoother on the right side. In further evaluating this region, additional detail is available from both the left and right sides (Fig. 5). The border between the nasal floor and the nasoalveolar clivus on the right side is well preserved. Here, it is confirmed that there is a clear and thin (sharp) nasal transverse crest along the right border. Anterior to this crest, there is a semicircular depression (prenasal groove) situated on the upper portion of the nasoalveolar clivus. Thus, on the right side of the nasal aperture, the transverse crest and prenasal groove separate the nasal floor from the nasoalveolar clivus. While the homologous region on the left side is broken, what has been preserved suggests the presence of a sharp transverse crest but the absence of a prenasal groove. A transverse crest on both sides coupled with the unilateral presence of a prenasal groove (right side only) appears to correspond to the ‘sill-like’ elevation and ‘fossa or sulcus prenasalis’ described by Weidenreich (1943).

The nasal floor of HLD 6 is sloped posteriorly, with the lowest point of the nasal margin being slightly higher than the floor of the posterior region of the nasal cavity. Because the transition from the lowest point of the nasal margin to the internal nasal cavity floor is smooth and gradual, this results in a relatively subtle posterior sloping (Fig. 5).

Malar region In anterior, lateral, and superior views, the infraorbital surface of HLD 6 is slightly inclined anteroinferiorly (Fig. 6). Infraorbital regions situated between the piriform aperture and either zygomatic process are largely mediolaterally flattened with slight depressions on both the left and right sides. These depressions encompass the entire infraorbital regions on both sides. On the right side, there are two infraorbital foramina: a large main foramen and a smaller one located more mediusuperiorly (Fig. 5). On the left side, there is a single infraorbital foramen (Fig. 6). Infraorbital foramina coincide with the deepest areas of the infraorbital depressions.

Lateral to the nasal aperture on both sides, there is a weakly developed canine jugum (Figs. 5 and 6). Both canine jugums are confined to the canine root areas in the alveolar process. Neither of the infraorbital regions exhibits a canine fossa, although above the premolar root areas of the alveolar process there is a clear groove-like depression extending superiorly toward infraorbital foramina on each side. Each groove corresponds to the ‘sulcus maxillaris’, as described by Weidenreich (1943) for the Zhoukoudian crania (Figs. 5 and 6). As with the infraorbital foramina, the sulcus maxillaris on each side is located in the deepest area of the infraorbital depression. There is a weakly developed maxillary exostosis on both buccal sides in the M1 – M2 region of HLD 6, but a similar exostosis is bilaterally absent on the lingual side (Figs. 5 and 6).

The incisura malaris is very weakly developed on the right side of HLD 6 (Fig. 5) and absent altogether on the left side (Fig. 6). On the left side, the maxillary zygomatic process is weakly reinforced, and a well-developed malar tuber is present adjacent to the zygomatico-maxillary suture. In addition, there is a distinct zygomaticofacial foramen on the preserved portion of the left zygomatic surface (Fig. 6).

The superoinferior origin of the left anterior zygomatic root in HLD 6 is located approximately in the same transverse plane as the...
lower rim of the left orbit, and the anteroposterior origin of the zygomatic root follows the same coronal plane as the left M1 (Fig. 6). The inferior surface of the zygomatic arch extends approximately 14 mm superior to the buccocervical margin of the M1.

Hard palate Although the right side of the HLD 6 hard palate is broken along its midline from the alveoli of the central incisors to approximately midway along the palatine process, most is preserved. Specifically, the complete palatine process of the right maxilla and a portion of the right palatine adjacent to the alveolar process are present (Fig. 7). On the left side of the hard palate, the alveolar process is present from the central incisor approximately to the distal edge of the second molar (Fig. 7). The hard palate displays a rugged surface with multiple ridges and furrows running in parasagittal planes (Fig. 7).

At the anterior end of the break on the right side of the hard palate, the incisive foramen is evident at the entrance of the incisive canal, which is fully exposed in connecting the surface of the hard palate with the floor of the nasal cavity. Distance from the labial edge of the incisive foramen to the alveolar process is only 4.5 mm. The longitudinal axis of the incisive canal is slightly posteriorly inclined relative to vertical as it passes through the hard palate (Fig. 7).

Maxillary alveoli are well preserved on both left and right sides in HLD 6, permitting reliable reconstruction of its dental arcade. Dental arcade shape is semirounded or parabolic due to an anterior
dentition oriented in the coronal plane and mildly curved postcanine tooth rows (Fig. 7). The dental arch is also anteroposteriorly short and mediolaterally broad (Table 3; Fig. 7).

Paranasal sinuses

Because left and right maxillary bones of HLD 6 are separated at their midline articulation, the internal surface of the maxillary sinuses can be fully visualized on both sides (Fig. 8). Through hiatuses in the medial walls of the sinuses on both sides and also with the assistance of μCT, the extent and form of the maxillary sinuses of HLD 6 can be clearly characterized. On both sides, maxillary sinuses are spacious and occupy nearly the entire maxillary body; the left maxillary sinus even infiltrates the zygomatic region (Fig. 8). Inferior boundaries of both sinuses are situated well above the nasal cavity floor, and molar root apices do not invade either sinus (Fig. 8).

3.2. Qualitative comparative descriptions

H. erectus, as broadly defined for Early and Middle Pleistocene hominins, possesses a number of distinguishing anatomical characteristics in the facial region (e.g., strong supraorbital tori,
pronounced alveolar prognathism, prominent canine juga, and robust malar regions; Weidenreich, 1943; Rightmire, 1998b). In some of these facial morphologies, the HLD 6 supraorbital and malar regions resemble those of *H. erectus*. However, there are abundant other facial features of HLD 6 (e.g., weak mid-face prognathism, flat face, and features in the nasal and hard palate regions) that resemble those of more recent Late Pleistocene hominins and modern humans (Table 3). Here, we provide region-by-region qualitative comparisons for the craniofacial anatomy that is preserved in HLD 6.

**Supraorbital region** Although some features in the supraorbital region of HLD 6 more frequently occur in Early and Middle Pleistocene hominins, such as bilaterally projecting and heavily constructed supraorbital tori, most of these features are relatively weakly expressed in HLD 6 (e.g., the supraorbital torus is comparatively gracile and less pronounced). The double-arched shape of the HLD 6 supraorbital tori differs from those of Zhoukoudian and other Middle Pleistocene *H. erectus* that exhibit variably thickened and occasionally straight tori (i.e., a bar-like torus occupying a horizontal plane; Table 3; Figs. 1, 3 and 4).

Compared with HLD 6, which resembles Dali and modern humans from China, supraorbital morphology of Jinniushan exhibits several archaic features that resemble those of Early and Middle Pleistocene *H. erectus* from Zhoukoudian, Lantian, Hexian, and Nanjing. The supraorbital tori of HLD 6 and Dali are thickened in height throughout but do not resemble the more gracile supraorbital tori of the Jinniushan cranium (Fig. 4). For example, in superior view, the left and right sides of the Jinniushan supraorbital tori are inclined posterolaterally, similar to the tori of HLD 6 (and Dali), but differ from the straightened morphology of tori in Zhoukoudian and other *H. erectus* crania. At the lateral ends, the thickened trigone of the HLD 6 supraorbital tori resembles that characterizing some later Middle and Late Pleistocene hominins in the region (e.g., Dali, Jinniushan, and probably Ngandong) and also modern humans (Wu and Athreya, 2013).

The shallow supratoral sulcus in HLD 6 resembles those in the Dali and Jinniushan crania (Fig. 4). Moreover, the HLD 6 supratoral sulcus is notably shallower than those exhibited by earlier hominins in the region and instead resembles those exhibited by modern humans. Division of the supratoral sulcus of HLD 6 into a medial supratoral sulcus and lateral segments resembles the partitioning exhibited by the Bodo cranium (Rightmire, 1996).

The glabellar region in HLD 6 exhibits a state that occurs more often in some late Middle and Late Pleistocene hominins and modern humans (Wu and Athreya, 2013; Arsuaga et al., 2014; Wu et al., 2019). Specifically, the depressed glabellar region of HLD 6 resembles that of Dali but not the clearly outwardly projecting glabellar region of the Jinniushan cranium (Fig. 4).

The square-shaped orbit of HLD 6, with an upper margin following the horizontal plane (Fig. 2), is also exhibited by most Pleistocene hominins from China (e.g., Zhoukoudian, Nanjing, Dali, Jinniushan, Liujiang, and Upper Cave; Table 3). The lobe exception is the Maba cranium, which preserves a frontal region indicating a more rounded orbital shape. The rounded inferior orbital margins of HLD 6 recall those of Zhoukoudian crania, although HLD 6 margins are not as prominently rounded.

Unlike *H. erectus* crania from Zhoukoudian, HLD 6 does not exhibit a supraorbital notch or foramen. In contrast, HLD 6 exhibits a processus supraorbitalis as described in Zhoukoudian crania X, XI, and XII (Weidenreich, 1943). In all other *H. erectus* crania in China (e.g., Lantian, Nanjing, and Yiyuan), a pronounced processus supraorbitalis or foramen is also evident, and thus, this seems to be a primitive feature (Weidenreich, 1943; Woo, 1966; Wu et al., 2002). Both features are variably expressed in European Middle Pleistocene hominins. The Arago 21 cranium exhibits both a processus supraorbitalis and a supraorbital notch, while the Petralona 1 cranium exhibits only a weak supraorbital notch and no processus supraorbitalis.

The lacrimal fossa is present as a clearly defined depression in HLD 6 (Fig. 3). The right orbit of the Dali cranium, as well as those of the Hexian and Nanjing crania, also exhibit relatively deep fossae in this region (Wu et al., 2002; Wu, 2020). Among the five Zhoukoudian frontal bones that preserve the region around the lacrimal fossa (i.e., Nos. II, X, XI, XII, and V), orbital roofs of three of them—skull X, skull XI, and skull V—are flat, with no depressions apparent in the analogous position where the depression appears in HLD 6. In skull II and skull XII, depressions are evident, but they are located further posteriorly and are situated above the sphenoorbital suture (Weidenreich, 1943). Limited previous studies (Weidenreich, 1943; Wu et al., 2002; Wu, 2020) have suggested that a deep lacrimal fossa characterizes modern humans. Thus, not only the presence of a depression at the lacrimal fossa but also the position of the zygomatico-orbital inferior foramen in the lateral wall of the HLD 6 orbit aligns it with modern human morphology.

**Nasal region** In the nasal region, only a few features in HLD 6 appear to resemble those of Early and Middle Pleistocene hominins. Some Middle Pleistocene hominins, including Dali, Jinniushan, Kabwe, Bozo, Arago 21, and Petralona (Arsuaga et al., 1999, 2014), also exhibit a depressed nasal root (Table 3). The superiorly inclined nasofrontal and frontomaxillary sutures in HLD 6 differ from those of most Pleistocene hominins in China. For example, in Zhoukoudian and other Early and Middle Pleistocene hominins, these sutures form a subtle superiorly directed curve (Weidenreich, 1943; Wu, 1990). Crania of late Middle and Late Pleistocene hominins in China also exhibit a similar curved sutureal configuration. Specifically, the frontonasal and frontomaxillary sutures in both Dali and Jinniushan crania approximately follow a transverse plane with only slight superiorly directed curvature.

Profile of the crista nasalis in HLD 6 resembles that of the nearly vertical crest in modern humans (Weidenreich, 1943; Rightmire, 1998b). Crania of earlier hominins such as KNM-WT 15000 and Zhoukoudian exhibit a crista nasalis that slopes comparatively more forward to join the floor of the aperture in a relatively anterior position. The two late Middle Pleistocene crania from China (i.e., Dali and Jinniushan) differ from one another in this feature. Dali exhibits a vertically oriented crista nasalis, such as those of HLD 6 and modern humans, while Jinniushan exhibits a forward sloping condition resembling those of earlier hominins (Wu and Athreya, 2013; Wu, 2020).

The anterior nasal spine of HLD 6 resembles the well-defined spines of modern humans (Table 3; Rightmire, 1998b). However, compared with those specifically observed in modern Chinese populations (100% presence, n = 51), the anterior nasal spine in HLD 6 is less pronounced (lower) in its height above the floor of the nasal cavity. By comparison, anterior nasal spines in Zhoukoudian, Lantian, Sangiran, and other Early and Middle Pleistocene hominins are very weak or absent (Weidenreich, 1943; Rightmire, 1998b).

The transverse crest and prenasal groove identified in HLD 6 seem to be derived features that also characterize modern humans to a greater extent than hominins predating HLD 6. Our observations on modern Chinese crania (n = 51) indicate that transverse crests and prenasal grooves occur in 62.7% and 66.7% of the individuals, respectively. Although passage of the nasal floor into the nasoalveolar clivus in Zhoukoudian specimens is not demarcated by the same form of crest or groove that is observed in HLD 6 or that is common in modern populations, this type of smooth transition does occur in some African Pleistocene fossils (e.g., KNN-ER 3733 and KMN-WT 15000) (Weidenreich, 1943; Rightmire, 1998b). Notably, a few Pleistocene specimens from eastern Asia exhibit similar morphology to HLD 6, such as Sangiran crania and perhaps...
Gongwangling as well, in exhibiting an interrupted transition (Rightmire, 1998b). The extent of regional variation exhibited by both features casts uncertainty on their diagnostic taxonomic value.

The nasal clivus in HLD 6 differs from the convex condition in Early and Middle Pleistocene hominins and resembles the flattened condition of modern humans (Weidenreich, 1943; Rightmire, 1998b; Table 3). The HLD 6 nasal floor resembles the sloping floor of many Middle and Late Pleistocene archaic and early modern humans but contrasts with the bivelvel state that characterizes other East Asian archaic humans and also Neanderthals (Wu et al., 2012, 2019). Based on extrapolation of the HLD 6 left nasal bone (Figs. 1 and 3), there appears to have been an absence of midline keeling, which would resemble the condition in modern humans. Limited available data published by Weidenreich (1943) and in this study suggest that nasal bone midline keeling is usually absent in modern humans (i.e., absent in n = 47 of 51 modern Chinese; Table 3). By comparison, some Early and Middle Pleistocene hominins (e.g., Zhokoudian specimens and KNM-ER 3733) exhibit nasal bone midline keeling at the internasal suture.

Malar region

The lateral face and cheek regions of HLD 6 exhibit a mosaic pattern comprising both primitive and derived features. Most HLD 6 features in these anatomical regions resemble those expressed in Late Pleistocene hominins and modern humans, while only a few features of HLD 6 are more frequently expressed in Early and Middle Pleistocene hominins. Among the features of the HLD 6 malar region that resemble those of earlier hominins, similarities are observed with Zhokoudian and Nanjing (Weidenreich, 1943; Wu et al., 2002). For example, the maxillary zygomatic process, well-developed malar tuber, and the absence of a canine fossa in HLD 6 (Fig. 6) resemble conditions usually observed in Zhokoudian and other Early and Middle Pleistocene hominins (Weidenreich, 1943; Rightmire, 1998b; Arsuaga et al., 1999, 2014). The maxillary sulcus observed in Zhokoudian specimens (Weidenreich, 1943) also resembles that of HLD 6. A few features in the malar region that typically characterize Early and Middle Pleistocene hominins, such as a canine jugum and malar incisure, however, are weakly developed or altogether absent in HLD 6. The diminished expression or absence of these few features aligns HLD 6 with modern humans.

Orientation of the infraorbital surface in HLD 6 more closely resembles those of modern humans than earlier hominins. In modern humans, the midsurface is characterized by an infraorbital surface that approximately parallels the coronal plane with the nose. The orientation of the infraorbital surface in HLD 6 more closely resembles those of modern humans than earlier hominins. In contrast, although the maxillary sinuses of the 1.5 mya H. erectus maxilla (Bpg, 2001.04) and the modern human cranium (Bpg, 2007.06) (Fig. 2) resemble those of earlier fossils (Fig. 9), Late Pleistocene cranial maxillary sinuses may not be entirely an age-related phenomenon.

Paranasal sinuses

Compared to those of Zhoukoudian crania or some modern humans (Weidenreich, 1943; Fig. 7). There appears to be substantial variability in the expression of rugosity of the hard palate in Pleistocene hominins. Sangiran 17 and Sangiran 4 exhibit relatively smooth palate surfaces (Rightmire, 1998b). East African H. erectus (e.g., KNM-ER 3733 and to a lesser extent KNM-WT 15000), on the other hand, shows a pattern of hard palate surface rugosity resembling that of Zhoukoudian crania (Rightmire, 1998b). In the present study, 37.3% of modern Chinese crania (n = 51) exhibit a qualitatively rugged hard palate similar to that of HLD 6. Given this degree of variability observed in hard palate rugosity, there is doubt about the diagnostic taxonomic value of different states of this trait.

Paranasal sinuses

Comparatively, greater expansion of maxillary features than exhibited in HLD 6 (Fig. 8) has been observed in Zhoukoudian and other earlier hominin crania (Weidenreich, 1943; Rightmire et al., 2006). CT scanning of the Taung Child indicates well-developed maxillary sinuses with pneumatization extending into the zygomas and hard palate (Conroy and Vannier, 1987), suggesting that although the sinuses would have undoubtedly increased with age in this individual, some expansion of the maxillary sinuses may not be entirely age-related phenomenon. Maxillary sinuses in the juvenile KNM-WT 15000 cranium also penetrated palatal processes (Walker and Leakey, 1993). Even among adult African Early Pleistocene crania, the extent of this pneumatization is variable. While OH 9 and KNM-WT 15000 are pneumatized, KNM-ER 3733 is comparatively less pneumatized. European Middle Pleistocene hominins such as Petralona 1, Broken Hill, and some Neanderthals (e.g., Forbes’ Quarry 1) exhibit well-developed maxillary sinuses (Seidler et al., 1997; Rae et al., 2011). The maxillary sinuses of the 1.5 mya H. erectus maxilla (8pg, 2001.04) from Sangiran is spacious, extending into the floor of the zygomatic arch and is perforated by the lingual roots of M1 and M2 (Zaim et al., 2011). By comparison, while modern humans combine a relatively voluminous maxillary sinus (Ogita et al., 1986) and a relatively high position of the sinus above the floor of the nasal cavity, lateralward invagination of the sinus into the zygomatic body is typically not observed to the same extent as is demonstrated in HLD 6.
given all this documented variability, the degree of similarity in spaciousness and form of the maxillary sinuses exhibited by HLD 6 and Early and Middle Pleistocene hominin crania cannot be suitably marshalled as direct evidence of taxonomic affinities (Odita et al., 1986; Conroy and Vannier, 1987).

3.3. Quantitative comparisons

In general, linear facial measurements of HLD 6 represent a mixture of smaller or larger dimensions compared with those of Early and Middle Pleistocene hominins (Table 4).

Total prognathism in HLD 6 (89.1°) most closely resembles that of Middle or Late Pleistocene hominins rather than Early Pleistocene hominins or modern humans (Fig. 10A; Table 4). Within the eastern Asian subsample, total prognathism angle of HLD 6 is most similar to that of Middle Pleistocene hominins, being less than one standard deviation (SD) above their mean angle. HLD 6 is greater than two SDs above the mean angle of Late Pleistocene hominins and 33% higher than the one Early Pleistocene cranium from this region (Table 4). Total prognathism angle of HLD 6 is also greater than two SDs above the mean angle of modern humans from eastern Asia (Table 4). Among other regions, total prognathism angle of HLD 6 consistently exceeds angles of Early Pleistocene hominins by greater than 10% (Table 4). In terms of contemporaries from other regions, HLD 6 exceeds mean angles of European Middle Pleistocene hominins by nearly two SDs and is 7% greater than the lone African Middle Pleistocene hominin (Table 4). Compared with Late Pleistocene hominins, HLD 6 exhibits a total prognathism angle that is one or fewer SDs above mean angles from other regions, except from the lone representative from Africa which is 15% lower than HLD 6 (Table 4).

The nasomalar angle of HLD 6 exceeds that of the one Chinese Early Pleistocene hominin from Lantian by 9% and also exceeds those of early Middle Pleistocene hominins from Zhoukoudian and Nanjing (i.e., 140.3°–147.2°; Weidenreich, 1943; Wu et al., 2002). By comparison, the HLD 6 facial skeleton is moderately flattened in the coronal plane, most consistently resembling Middle or Late Pleistocene hominins rather than Early Pleistocene hominins or modern humans (Fig. 10B; Table 4). Within the eastern Asian subsample, the nasomalar angle of HLD 6 (143.3°) is indistinguishably lower than the mean angle of Middle Pleistocene hominins (Table 4). There is noteworthy similarity to the nasomalar angles of Dali (143°) and Jinniushan (145.1°) crania in particular. The nasomalar angle of HLD 6 is well within one SD below the mean angle of Late Pleistocene hominins (e.g., Upper Cave and Liujiang exhibit a range between 130.0 and 140.0°; Table 4; Wu, 2009, 2020; Athreya and Wu, 2017). Compared with modern humans (144.8° ± 5.6; Table 4), HLD 6 exhibits a nasomalar angle well within one SD below the group mean. Among other regions, HLD 6 is less than one SD below the African Early Pleistocene mean and between 1 and 2 SDs above the West Asian Early Pleistocene mean. HLD 6 is consistently less than one SD above mean nasomalar angles for Middle Pleistocene hominins from other regions. Compared with Late Pleistocene hominins, HLD 6 is less than one SD above the West Asian group mean and indistinguishably smaller than the European group mean. The lone African Late Pleistocene cranium exhibits a nasomalar angle that is 3% higher than the HLD 6 nasomalar angle.

Postorbital constriction in the HLD 6 cranium (index = 95.4°) most closely resembles that of modern humans or Late Pleistocene hominins (Fig. 10C; Table 4). Within the eastern Asian subsample, HLD 6 is slightly greater than one SD above the Middle Pleistocene mean and less than one SD above the Late Pleistocene group mean. The lone Early Pleistocene cranium has a postorbital constriction index that is 20% less than that of HLD 6. The modern human mean (95.6 ± 4.4; Table 4) is indistinguishably above the HLD 6 index value. Among other regions, HLD 6 is greater than two SDs above Early Pleistocene means and within 1 SD (Europe) or 2 SDs (Africa) above Middle Pleistocene means (Table 4). Compared with Late Pleistocene hominins, the postorbital constriction index of HLD 6 is within one SD above West Asian and European means and is 2% less than the index of the lone African Late Pleistocene cranium (Table 4).

Supraorbital torus thickness of HLD 6 at the midorbital region (16.5) exceeds all Pleistocene group means (Fig. 10D; Table 4). Within the eastern Asian subsample, it is 1–2 SDs above Early Pleistocene and Middle Pleistocene group means (Table 4). HLD 6 exhibits a thickness measurement in this location that exceeds the analogous thickness on the lone Late Pleistocene cranium by 43% (Table 4). HLD 6 approaches thicknesses exhibited on Zhoukoudian cranial, as well as those on other earlier hominins from China such as Lantian, Hexian, and Nanjing. Among other regions, the thickness measurement on HLD 6 is within one SD above (African Early Pleistocene) or more than two SDs above (West Asian Early
Table 4
Summary of selected facial linear and angular measurements in HLD 6 and comparative samples (mean ± 1SD).

<table>
<thead>
<tr>
<th>Samples</th>
<th>Total prognathism angle (°)</th>
<th>Nasomalar angle (°)</th>
<th>Postorbital constriction index</th>
<th>Supraorbital torus thickness at midorbital region (mm)</th>
<th>Orbit index</th>
<th>Nasal index</th>
<th>Upper facial index</th>
<th>Nasospinale-prosthion height (mm)</th>
<th>Malar height (mm)</th>
<th>Dental arcade index</th>
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<tr>
<td>HLD 6</td>
<td>89.1</td>
<td>143.3</td>
<td>95.4</td>
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<td>94.4</td>
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<tr>
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<td>n – 8</td>
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<td>91.1 ± 3.8</td>
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<td>145.4 ± 11.5</td>
<td>93.7 ± 6.8</td>
<td>n – 6</td>
<td>n – 6</td>
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<tr>
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<td>84.7 ± 5.8</td>
<td>n – 19</td>
<td>1436 ± 6.2</td>
<td>94.9 ± 4.0</td>
<td>n – 49</td>
<td>n – 49</td>
<td>n – 30</td>
<td>n – 32</td>
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<tr>
<td>Humans</td>
<td>79.7 ± 4.4</td>
<td>n – 58</td>
<td>1448 ± 5.6</td>
<td>95.6 ± 4.4</td>
<td>n – 58</td>
<td>n – 58</td>
<td>n – 58</td>
<td>n – 58</td>
<td>n – 58</td>
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</table>
Figure 10. Facial measurements for HLD 6 and comparative samples. A) Total prognathism angle; B) nasomalar angle; C) postorbital constriction index; D) suproorbital torus thickness at mid-orbital region; E) orbit index; F) nasal index; G) upper facial index; H) nasospinale-prosthion height; I) malar height; and J) dental arcade index. Fossils comprising groups are defined in Table 1. Boxes contain cases between the first and third quartiles (i.e., 50% of cases), horizontal lines within boxes represent medians, whiskers indicate maximum and minimum values, and open circles represent outliers for the given groups.
Pleistocene) group means or 21% above the analogous thickness on the lone European Early Pleistocene cranium (Table 4). Thickness of the supraorbital torus in this location on the HLD 6 cranium is less than one SD above Middle Pleistocene group means from Africa and Europe and approximately 1.5 SDs above Late Pleistocene group means from West Asia and Europe (Table 4). Moreover, the pattern of supraorbital torus thickness on HLD 6 differs from those on Early and Middle Pleistocene crania that usually exhibit uniform thickness throughout the whole course of the supraorbital torus. For example, the thickest region of the Middle Pleistocene Jinniushan supraorbital torus is in its medial portion, but the thickness measurements of medial, central, and lateral regions of its torus are not comparatively different (i.e., 14.3 mm, 10.4 mm, and 13.8 mm, respectively; Wu, 2020; Fig. 4).

The orbit index of HLD 6 (94.4) also exceeds mean indices of all Pleistocene groups and modern humans (Fig. 10E; Table 4). Within the eastern Asian subsample, the orbit index of HLD 6 is only 1% larger than that of the lone Early Pleistocene cranium, while it is nearly 1.5 SDs above the Middle Pleistocene group mean and greater than two SDs above the Late Pleistocene group mean (Table 4). The HLD 6 orbit index exceeds the modern human group mean by slightly more than one SD (Table 4). Among other regions, HLD 6 exhibits a 12% orbit index less than the SD of the lone African Early Pleistocene group mean and more than two SDs above the West Asian Early Pleistocene group mean (Table 4). The HLD 6 orbit index is approximately 1.5 SDs above the African Middle Pleistocene group mean and greater than two SDs above the European Middle Pleistocene group mean (Table 4). Compared with Late Pleistocene group means, HLD 6 has an orbit index that is more than two SDs above the European orbit index and slightly less than two SDs above the West Asian orbit index (Table 4). The lone African Late Pleistocene cranium has an orbit index that is 21% lower than that of HLD 6 (Table 4).

The nasal index of HLD 6 (46.0) most closely resembles those of modern humans (Table 4). Neolithic populations in East China exhibit relatively high nasal apertures and thus relatively low nasal indices that range between 47.3 and 51.7 (Wu, 2020). The mean nasal index of modern humans from China is 47.8 ± 5.6 (n = 51; Table 4). Middle and Late Pleistocene hominins from China (e.g., Nanjing, Dali, Jinniushan, and Zhouchoudian Upper Cave) all exhibit relatively broad nasal apertures with nasal indices ranging between 50.8 and 62.3 (Fig. 10F). Irrespective of region, the nasal index of HLD 6 (46.0) is approximately 1.5 SDs above the West Asian Early Pleistocene group mean and nearly 1.5 SDs higher than that of the lone African Early Pleistocene group mean and more than two SDs above the West Asian Early Pleistocene group mean (Table 4). The HLD 6 nasal index has an orbit index that is more than two SDs above the European nasal index and slightly less than two SDs above the West Asian orbit index (Table 4). The lone African Late Pleistocene cranium has a nasal index that is 21% lower than that of HLD 6 (Table 4).

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The upper facial index of HLD 6 (71.4) most closely resembles those of Middle Pleistocene groups (Table 4; Fig. 10G). Within the eastern Asian subsample, the upper facial index of HLD 6 is within one SD above Middle and Late Pleistocene group means and 3% greater than the upper facial index of the lone Early Pleistocene cranium (Table 4). HLD 6 exhibits an upper facial index that is greater than two SDs above the modern human mean (Table 4). Among other regions, HLD 6 exhibits an upper facial index that is less than one SD above the West Asian Early Pleistocene group mean, but it is 12% below the upper facial index of the lone African Early Pleistocene cranium (Table 4). HLD 6 has an upper facial index that is within one SD below (African) or above (European) Middle Pleistocene group means. Compared with Late Pleistocene groups, HLD 6 is less than one SD below European and West Asian means and 16% above the lone African Late Pleistocene cranium (Table 4).

Nasophaenom-prosthion height in HLD 6 (14.3) is much smaller than means of all Pleistocene groups and most closely resembles the mean of modern humans (Table 4; Fig. 10H; Wu et al., 2012). Within the eastern Asian subsample, HLD 6 is more than two SDs below the Early Pleistocene group mean, nearly two SDs below the Middle Pleistocene group mean, and 1.5 SDs below the Late Pleistocene group mean (Table 4). HLD 6 is noticeably smaller in this dimension than are eastern Asian hominins, such as Chaoxian 1 (28.4 mm), Sangiran 4 (28.1 mm), and Changyang 1 (24.5 mm), and also well below Neanderthals (24.2 mm; Wu et al., 2012). The nasoalveolar clivus of the Dali cranium has been damaged, but its minimum height has been estimated at 20 mm (Wu, 2020). Height of the nasoalveolar clivus in the Jinniushan cranium is 27.0 mm (as measured on a cast), which resembles heights measured on earlier hominin crania from the region. Among other regions, the nasophaenom-prosthion height of HLD 6 is more than two SDs below African Early and Middle Pleistocene means and 25% below the lone African Late Pleistocene cranium. HLD 6 is slightly less than two SDs below the group mean of West Asian Early Pleistocene hominins and slightly more than two SDs below the group mean of West Asian Late Pleistocene hominins (Table 4). HLD 6 generally exhibits a nasophaenom-prosthion height that is closest among Pleistocene groups to European Late Pleistocene hominins, which exhibit a group mean that is less than one SD above HLD 6 (Table 4). Middle Pleistocene Europeans exhibit a group mean that is approximately 1.5 SDs higher than that of HLD 6, while the lone European Early Pleistocene cranium is 19% higher in its nasophaenom-prosthion height than HLD 6.

Malar height in HLD 6 (25.0) is consistently smaller than Early and Middle Pleistocene group means, except for the smaller lone European Early Pleistocene cranium, and greater than Late Pleistocene group means and modern humans (Table 4; Fig. 10I). Within the eastern Asian subsample, HLD 6 most closely resembles Middle Pleistocene hominins, being less than one SD below the group mean. By comparison, HLD 6 is greater than two SDs below the Early Pleistocene group mean and slightly less than one SD above the Late Pleistocene group mean (Table 4). Compared with modern humans, HLD 6 exhibits a malar height that is nearly two SDs above the group mean (Table 4). Among other regions, HLD 6 is less than one SD below the African Early Pleistocene group mean, nearly 1.5 SDs below the West Asian Early Pleistocene group mean, and 4% greater than the lone European Early Pleistocene cranium (Table 4). HLD 6 exhibits a malar height that is slightly more than one SD below the European Middle Pleistocene group mean and within one SD below the African Middle Pleistocene group mean. Compared with Late Pleistocene groups and irrespective of region, HLD 6 exhibits a malar height that is consistently within one SD above group means.

Finally, while the dental arcade index of HLD 6 (81.6) is lower than those of all Pleistocene group means and also modern humans, it most closely resembles those of Late Pleistocene eastern Asian hominins and modern humans (Table 4; Fig. 10J). Within the eastern Asian subsample, while HLD 6 is within one SD below the Middle and Late Pleistocene group means, it more closely resembles the latter group (Table 4). The lone Early Pleistocene cranium exhibits a dental arcade index that is 8% higher than that of HLD 6. The dental arcade index of HLD 6 is also within one SD below the modern human group mean (Table 4). Among other regions, HLD 6 exhibits a dental arcade index that is slightly more than one SD below the West Asian Early Pleistocene group mean and 17% lower than the lone African Early Pleistocene cranium (Table 4). HLD 6 is nearly 1.5 SDs below the European Middle Pleistocene
group mean and within one SD below the African Middle Pleistocene group mean (Table 4). Compared with Late Pleistocene groups, HLD 6 exhibits a dental arcade index that is within one SD below the European Late Pleistocene mean and greater than two SDs below the West Asian mean (Table 4). HLD 6 exhibits a dental arcade index that is approximately 8% below the dental arcade index of the lone African Late Pleistocene cranium (Table 4).

3.4. Multivariate analyses

To assess overall trends within the quantitative comparisons of HLD 6 and other crania, we conducted two different PCAs. In the five-variable PCA, measurements emphasize the supraorbital region (Table 5; Fig. 11). The first three principal components (PCs) cumulatively explain 83.5% of total variance in the sample (Table 5). The first PC in particular explains 46.3% of total variance and has positive loadings on all variables. The variables that have the highest loadings on PC1 include supraorbital torus breadth, midorbital supraorbital torus thickness, and minimum frontal breadth (Table 5; Fig. 11). By comparison, PC2 explains 20.2% of the total variance and is primarily associated with an increase in minimum frontal breadth and lateral supraorbital torus thickness (Table 5; Fig. 11). PC3 explains 17.0% of the total variance and is primarily associated with a deep glabellar projection (Table 5; Fig. 11). Additional PCs explained less than 16.5% of the cumulative variance and fall below any conventional threshold of reliability; they will
not be considered further. Within this PCA space, although HLD 6 overlaps with each Pleistocene cluster, it is positioned most securely in Middle Pleistocene hominins along PC1 and equally securely in Middle and Late Pleistocene hominins along PC2 and PC3 (Fig. 11). HLD 6 exhibits no overlap with the Early Pleistocene cluster along PC2 reflecting smaller minimum frontal breadth and lateral supraorbital torus thickness in HLD 6 and is on the edge of the Late Pleistocene cluster along PC1.

In the seven-variable PCA, which includes modern humans as a group, measurements emphasize the craniofacial region below the supraorbital torus (Fig. 12). The first three PCs cumulatively explain 79.2% of total variance in the sample (Table 5). PC1 explains 54.0% of the total variance and again has positive loadings on all variables. The variables that have the highest loadings on PC1 include upper facial height, malar height, and nasal height (Table 5; Fig. 12). By comparison, PC2 explains 14.4% of the total variance and is primarily associated with an increase in orbit height (Table 5; Fig. 12). PC3 explains 10.8% of the total variance and is primarily associated with orbit breadth (Table 5; Fig. 12). Additional PCs explain less than 20.8% of the cumulative variance and fall below any conventional threshold of reliability; they will not be considered further. Within this PCA space, HLD 6 is positioned securely in an area of overlap of all Pleistocene groups along PC1, within the upper positive area of the modern human cluster along PC2, and firmly among Middle Pleistocene, Late Pleistocene, and modern human clusters along PC3 (Fig. 12). Interestingly, HLD 6 exhibits no overlap with any Pleistocene cluster along PC2, which may be related to a uniquely modern human-like orbit height in HLD 6, nor with the Early Pleistocene cluster along PC3 reflecting its similar orbit breadth to those of Middle and Late Pleistocene hominins and modern humans.

4. Discussion

Descriptive and comparative analyses of the HLD 6 facial skeleton in this study underscore the observation that HLD 6 facial morphology bears similarities to the morphologies of other Early and Middle Pleistocene hominins in the supraorbital and zygomatic regions. Specifically, these features included bilaterally projecting and heavily constructed supraorbital tori, a processus supraorbitalis and rounded inferior margin of the orbit, the form of the maxillary zygomatic process, a well-developed malar tuber, and the absence of a canine fossa in the malar region. However, while HLD 6 tended to express these archaic-like features, the extent to which they were pronounced was not as marked as in typical Early or Middle Pleistocene hominin crania. Additional features of HLD 6 appear to
firmed draw connections to Late Pleistocene hominins and even modern humans in the eastern Asian region (Tables 3 and 4). These derived modern facial features in HLD 6 include a tall orbit, less pronounced postorbital constriction, a nearly vertically oriented derived modern features in HLD 6 include a tall orbit, less pronounced postorbital constriction, a nearly vertically oriented derived modern facial features (Liu et al., 2013; Wu and Athreya, 2013; Athreya and Wu, 2017; Xing et al., 2019). It is noteworthy that studies of other hominin fossils, such as from Xujuayao, Xuchang, and Xiahe, have revealed unusual morphological patterns that led some to suggest multiple distinct groups coexisted in China during the Middle Pleistocene, including late archaic hominins, early modern humans, Denisovans, and an unidentified group (Xing et al., 2015; Li et al., 2017; Chen et al., 2019). For example, extraction and analysis of paleoprotein from a hominin mandible recovered from Xiahe linked the mandible to Deniso-
savans (Chen et al., 2019). In addition, the dental, mandibular, and cranial morphological patterns in Xujuayao and Xuchang fossils exhibit mixed combinations of primitive and derived features (Xing et al., 2015; Li et al., 2017). Even considering the aforementioned progress, the morphological diversity in late Middle Pleistocene hominins of China and its implications for evolutionary relationships and taxonomy of regional populations are still not fully understood.

Facial morphologies of HLD 6 are characterized by a suite of derived features that closely resemble those of Late Pleistocene hominins and modern humans. Although previous studies have indicated that the Dali cranium and Panxian Dadong teeth possess features resembling those of Late Pleistocene hominins and mod-
ern humans, respectively (Wu, 2009, 2014, 2020; Liu et al., 2013), compared with HLD 6, all these late Middle Pleistocene hominins exhibited comparatively more limited numbers of such derived features. In contrast, HLD 6 is the first late Middle Pleistocene hominin to exhibit such a substantial number of facial morphological features bearing strong similarities to modern human features. In fact, the facial morphological pattern identified in HLD 6 has never before been recorded in the Chinese Middle Pleistocene hominin fossil assemblage. Therefore, HLD 6 is currently the first late Middle Pleistocene hominin in eastern Asia to exhibit such a dominant and firmly established modern signal in facial morphology. Ultimately, the HLD 6 facial morphological pattern further substantiates the existence of morphological diversity in late Middle Pleistocene hominins in East Asia as it increases the sample exhibiting derived features during this time period.

### 4.1. Morphological diversity in the Middle Pleistocene Chinese hominin fossil assemblage

Recent hominin fossil discoveries from present-day China plus additional work on dating and morphological studies of Xuchang, Xiahe, Panxian Dadong, and Xujuayao have revealed a complicated pattern of morphological diversity and the possible coexistence of several hominin taxa during the Middle Pleistocene (Liu et al., 2013; Xing et al., 2015, 2019; Li et al., 2017; Chen et al., 2019). This regional diversity is manifested as different coexisting morphological patterns comprising primitive, derived, or some individual-specific unique features. In addition to its hominin contemporaries in China (e.g., Dali and Panxian Dadong), HLD 6 adds another example of a clear mosaic or mixed pattern of archaic and derived craniofacial morphologies (Liu et al., 2013; Wu and Athreya, 2013). By contrast, some Chinese late Middle Pleistocene hominins (e.g., Jinniushan, Tongzi, and Chaoxian) are characterized predominantly by archaic features such as those more frequently observed in Early and Middle Pleistocene hominins (Bailey and Liu, 2010; Wu and Athreya, 2013; Athreya and Wu, 2017; Xing et al., 2019). It is notable that studies of other hominin fossils, such as from Xujuayao, Xuchang, and Xiahe, have revealed unusual morphological patterns that led some to suggest multiple distinct groups coexisted in China during the Middle Pleistocene, including late archaic hominins, early modern humans, Denisovans, and an unidentified group (Xing et al., 2015; Li et al., 2017; Chen et al., 2019). For example, extraction and analysis of paleoprotein from a hominin mandible recovered from Xiahe linked the mandible to Deniso-
savans (Chen et al., 2019). In addition, the dental, mandibular, and cranial morphological patterns in Xujuayao and Xuchang fossils exhibit mixed combinations of primitive and derived features (Xing et al., 2015; Li et al., 2017). Even considering the aforementioned progress, the morphological diversity in late Middle Pleistocene hominins of China and its implications for evolutionary relationships and taxonomy of regional populations are still not fully understood.

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### 4.2. Transition from archaic to modern morphologies and emergence of modern humans in eastern Asia

Current fossil evidence (e.g., the Dali cranium and the Panxian Dadong teeth) conservatively indicates that some derived

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**Table 6** Summary of quantitative comparisons of group means and HLD 6.

<table>
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<tr>
<th>Resemblances&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Total</th>
<th>Nasomalar angle</th>
<th>Postorbital constriction index&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Supraorbital torus, mid-orbit</th>
<th>Orbit index</th>
<th>Nasal index&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Upper facial index</th>
<th>N–P height&lt;sup&gt;b&lt;/sup&gt;</th>
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<th>Dental arcade index</th>
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<sup>a</sup> Overall resemblances represent the closest chronological group means to HLD 6 values across all regions. Regional resemblances represent the closest chronological group means to HLD 6 values within each specific region. Bold indicates the chronological group from any region with the closest mean value to that of HLD 6 for a given trait.

<sup>b</sup> HLD 6 is closest in this trait to the modern human group, which predominantly comprises individuals from China.
morphological features resembling those of modern humans first appear in eastern Asia as early as 130–300 ka (Wu and Athreya, 2013; Liu et al., 2013). However, the derived features that characterize these fossils are limited, and there is still more abundant evidence of archaic features resembling those of Early and Middle Pleistocene hominins identified in Dali and Panxian Dadong. These fossils provide only hints as to when modern morphology may have appeared in the region. Based on the modern human-like craniodental features exhibited in the HLD 6 partial cranium (Wu et al., 2019), the timing of this transition must be reconsidered. The hominin population to which HLD 6 belonged is a potential candidate for the first modern human-like group in the region, with an intermediate position between more primitive (plesiomorphic) and more derived morphological patterns.

Both the number of its modern facial features and their pronounced expressions in HLD 6 exceed those of all other late Middle Pleistocene hominin crania currently known from China. This would suggest that the transition from archaic to modern morphology in eastern Asia occurred earlier than current convention dictates, possibly as early as 300 ka. In addition, the HLD 6 partial cranium, with its multiple derived modern facial features, suggests not only that its population included the earliest transition to the morphologically archaic and early modern humans in the region but also that the initial transition to modernity happened in some isolated regions of China while more archaic hominins contemporaneously occupied other areas (Stringer, 2016; Li et al., 2017; Chen et al., 2019; Mounier and Lahr, 2019). The available fossil evidence suggests that the modern morphologies in HLD 6 were derived from the contributions of earlier hominins in eastern Asia. Thus, we must continue to examine the scenario that such modernization could have occurred independently in eastern Asia compared with other regions.

Recent fossil discoveries and analyses suggest that the origin of modern H. sapiens may be traced back to the late Middle Pleistocene (White et al., 2003; McDougall et al., 2005; Hublin et al., 2017; Hershkovitz et al., 2018). However, genetic studies suggest that the separation between archaic and modern human lineages may have occurred even earlier than the fossil record currently indicates, e.g., between 550 ka and 765 ka (Meyer et al., 2016). Thus, the genetic evidence implies that some earlier members of the modern human lineage must have predated what the fossil record currently indicates as the earliest appearance, although this idea remains debated (Trinkaus, 2006; Weaver et al., 2008; Hershkovitz et al., 2011; Weaver, 2012; Weaver and Stringer, 2015). The presence of modern human-like features in HLD 6 by the late Middle Pleistocene of China supports this genetic evidence in suggesting an origin of our species probably even earlier than 300 ka.

5. Conclusions

Detailed morphological analyses of the HLD 6 cranium confirm preliminary analyses of the cranial, mandibular, and dental morphologies (Wu et al., 2019) in identifying a suite of derived features linking HLD 6 to modern humans. While it is important to be mindful of the developmental age of HLD 6, considering its date at 300 ka and the suite of modern human-like features that it exhibits, we conclude that HLD 6 represents the earliest occurrence of the modern human face in the fossil record of eastern Asia. Thus, based on fossil evidence, the hominin population represented by HLD 6 may have been the earliest member of the H. sapiens lineage in eastern Asia or at least the earliest example of pre-modern humans in the region. Shared similarities in craniofacial morphology between HLD 6 and Middle and Late Pleistocene groups from eastern Asia further corroborate existing evidence for evolutionary continuity in the region.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence this work reported in this paper.

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References


