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RESEARCH ARTICLE

The Terminal Pleistocene Human Skull From Yahuai Cave: Craniofacial Morphological Variation and Complex Population History in Southern East Asia

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ABSTRACT

Objective: The terminal Pleistocene is a crucial stage in the formation and differentiation of modern populations. Recent studies show that the population during this period had significant morphological variability and regional divergence. The objective of this study was to investigate the Yahuai-1 (YH1) from the Yahuai Cave site in southern China to understand human morphological diversity and population dynamics during the terminal Pleistocene in Southern East Asia.

Materials and Methods: The YH1, which dated back to 16.0k years ago, was the main material of this study. The analytical approach involved a comprehensive comparison of both metric and non-metric craniomandibular traits of YH1. The comparison samples included those from the Late Pleistocene and Early Holocene, as well as recent-modern specimens from Asia and Oceania.

Results: The YH1 cranium exhibits large overall size, substantial cranial capacity, and more developed craniomandibular superstructures. Multivariate analysis of craniometric traits reveals that YH1 is morphologically congruent with Maritime Southeast Asians, Polynesians, and Micronesians among recent and modern groups. Among ancient specimens, YH1 clusters more closely with Late Pleistocene fossils. The combined results of two multivariate analyses reveal YH1's craniofacial mosaicism, characterized by a larger, primitive facial skeleton juxtaposed with a derived neurocranial vault.

Conclusion: (1) YH1 exhibits mosaic craniofacial traits, serving as an evolutionary transition between Late Pleistocene hominins and Holocene populations. (2) Around 16.0k years ago, the north–south differentiation in East Asian craniofacial morphology had not yet been completed. (3) YH1 may have contributed to the Austronesian-speaking populations' origin.

In this study, Southern East Asia refers to the region south of East Asia, delineated by the Qinling-Huaihe line (excluding Southeast Asia). It encompasses provinces such as Guangxi, Guangdong, Fujian, Guizhou, and Yunnan.

1 | Introduction

The terminal Pleistocene–Early Holocene was a key stage in the formation and differentiation of modern human populations. As the end of the Last Glacial Period led to a warming of the global climate, significant changes in human culture and technology occurred, including a wide range of food sources and the domestication of plants and animals (Mithen 2003; Chen 2014). The morphological features of terminal Pleistocene–Early Holocene human skulls and teeth predominantly exhibit modern human patterns when compared to early Late Pleistocene (LP) human fossils. However, inter-population variation remains higher than in present-day populations (Crevecoeur et al. 2009; Demeter et al. 2003). Additionally, it has been proposed that the terminal Pleistocene–Early Holocene may have been a crucial period for the formation of distinct regional populations and the morphological characteristics found in contemporary populations (Lahr 1995, 1996).

In China, some human remains dating from the terminal Pleistocene to the Early Holocene have been unearthed since the turn of the last century. Scholars have articulated their perspectives on the morphological traits of these specimens and population affinity during this epoch. During the 1980s and 1990s, the analysis of human remains at sites such as Liyuzui, Donghulin, Zengpiyan, Chongtang, Jiahu, and Hemudu revealed that individuals in this era already exhibited the majority of modern human traits and some regional differentiation (Liu et al. 1994; Zhou and You 1972; Zhang et al. 1977; M. H. Wang 2003; B. Y. Wei et al. 1994; Wei et al. 1997; Chen and Zhang 1998; Han and Pan 1983). In the 21st century, studies of recently discovered human remains from various sites in southwestern China, including Longlin, Maludong, Dushandong, and Laoyadong, have further revealed that these individuals display a mosaic morphology of archaic and modern features. Some researchers have proposed the possibility of residual archaic or unique hominin populations forming in isolated environments in southwestern China during this period (Curnoe et al. 2012; Liao et al. 2019; Xing et al. 2017). However, the Zhaoguo-1 (ZG-1) specimen from the same period and region exhibits craniofacial features of fully modern humans (Y. Zhang et al. 2021).

These human remains also hold profound value for studying the population history of East and Southeast Asia. The "two-layer" model was proposed by Matsumura et al. (2019) to provide some insights into understanding the population history in East and Southeast Asia. This model suggests that the "first layer" groups may have migrated into East Asia via mainland Southeast Asia between 65.0k and 50.0k years ago. These groups are closely linked to the ancestors of the Andaman, Australian-Papuan, and Jomon populations. The "second layer," which is linked to Northeast Asian populations, emerged in central China approximately 9.0k years ago and subsequently migrated to Southeast Asia after 4.0k years, effectively displacing the "first layer" groups.

Recently, scholars have conducted the extraction and analysis of ancient DNA from the aforementioned human remains, leading to new insights. Examinations of the ancient DNA from the Qihe-3 (from the Fujian region of coastal China) reveal a distinct genetic connection to both modern and ancient individuals/groups linked with Austronesian (Yang et al. 2020). The paleogenomic analysis of the Longlin-1 (from the Guangxi region of southern China) suggests that they made no discernible genetic contribution to contemporary populations and are part of an unidentified archaic hominin population that diverged before the differentiation of southern and northern East Asian populations (T. Wang et al. 2021). A recently published study on an Early Holocene individual (Xingyi_EN) from the Xinyi site in the Yunnan region (southwestern China) reveals that the unidentified ancient component in Longlin-1 diverged from other Asian populations at least 40.0 kyr ago (T. Wang et al. 2025). Otherwise, studies of the mtDNA from the MLDG-1704 specimen (from the Maludong site in southwestern China) indicate its affiliation with a Southern East Asian population and demonstrate genetic continuity with contemporary populations (X. Zhang et al. 2022).

These new findings reveal a high degree of morphological and genetic diversity among the terminal Pleistocene to Early Holocene populations in southern China, and make it possible to explore the morphological characteristics, population affinities, migration, and integration processes that generated this diversity (Matsumura et al. 2019, 2021; T. Wang et al. 2021; Yang et al. 2020; Y. Zhang et al. 2021). Despite these insights, researchers still grapple with numerous questions and controversies about human evolution and population history in East Asia. For instance, the origins and differentiation of regional morphological traits (Zhang 1997; Liu 2006), the effects of climatic fluctuations and subsistence strategy shifts on population phenotypes (P. Wei 2021; P. Wei et al. 2020; Zhao et al. 2022), and the morphological and genetic continuity/discontinuity between ancient and modern populations are still not clear (Matsumura et al. 2019; Yang et al. 2020; Y. Zhang et al. 2021).

Yahuai Cave, situated in Nanning City, Guangxi, China, lies in the lower reaches of the Youjiang River (Figure 1). Between 2015 and 2018, the Guangxi Institute of Cultural Relics Protection and Archaeology, in collaboration with the Cultural Relics Management Office of Long'an County, carried out archaeological excavations at the site. A Paleolithic burial was unearthed under the sixth layer of Area B, containing human remains, including a nearly complete cranium post-restoration, partial mandible, and a few postcranial bones (YH1) (Xie et al. 2025). The burial is dated back to 16.0k years ago according to AMS (accelerator mass spectrometry) radiocarbon dating of charcoal samples from the burial and dendrochronological calibration (Xie et al. 2025; Shui et al. 2025). Some researchers conducted attempts to extract ancient DNA from YH1, albeit unsuccessfully. Matsumura et al. (2021) conducted a preliminary analysis of the YH1 skull and observed that, similar to the LP to Early-to-Mid Holocene hunter-gatherers of Southern East Asia and mainland Southeast Asia, YH1 exhibited closer affinities to the Australian, Papuan, and Jomon groups.

Building on this foundation, this study expands the scope to include the cranium and mandible of YH1, aiming to conduct a comprehensive morphological description and systematic comparative analyses not previously performed. This approach deepens the earlier morphological insights, providing a more nuanced understanding of YH1's morphological traits and population affinities. The specific research objectives are as follows: (1)

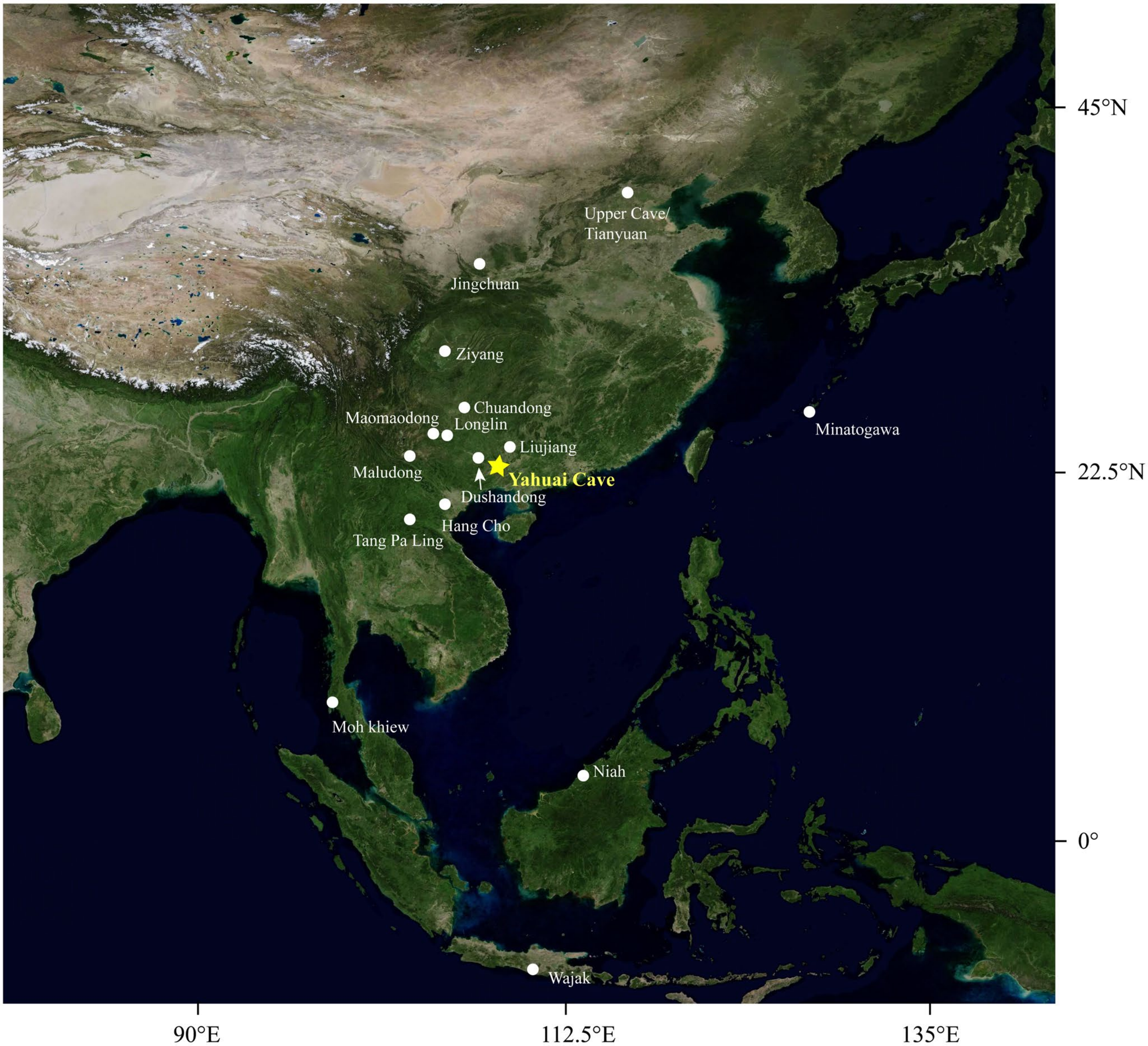

FIGURE 1 | Geographical locations of YH1 (yellow) and other Late Pleistocene specimens (white) in East Asia and Southeast Asia.

to characterize the key morphological features of YH1 with the view to assessing its taxonomic placement within the context of LP human evolution in East Asia; (2) to investigate whether East Asian populations exhibited regional differentiation approximately 16.0k years ago; (3) to explore population-level craniofacial affinities of YH1 by comparing it with both recent/modern populations and LP/Early Holocene archaeological populations, to provide insights into the regional population connectivity and evolutionary continuity/discontinuity in Southern East Asia.

2 | Materials and Methods

2.1 | Materials

The materials examined in this study were the cranium and mandible excavated from the Yahuai Cave site. The cranium and mandible were excavated from the same archaeological unit and in close proximity (Xie et al. 2025). Moreover, the maxillary and mandibular teeth exhibit a similar level of wear and a corresponding oblique wear pattern. Based on this evidence, it is believed that the cranium and mandible belong to the same individual (YH1).

The YH1 skull was mostly well-preserved. The missing parts included the bilateral nasal bone, the bilateral frontal process of the maxilla, the posterior alveolar process of the left maxilla, the frontal process of the left zygomatic bone, a portion of the left zygomatic arch, the portion around the foramen magnum of the occipital bone, and the cranial base portion of the sphenoid bone. Additionally, the maxilla exhibits marked resorption and atrophy in the posterior alveolar regions (from the left canine distally and from the right premolar distally). The anterior alveolar region also shows evidence of resorption from CT slices, but alveolar sockets remain mostly intact, with most anterior teeth having been lost postmortem. The

FIGURE 2 | Frontal and lateral views of the restored cranium and mandible of YH1.

mandible is preserved with the symphysis, a portion of the left corpus, an intact right corpus, and a region of the right mandibular angle. However, ante-mortem loss of the right P4 and M1 is evident, with marked resorption of the corresponding alveolar process. There are no preserved bilateral condyles or coronoid processes (Figure 2).

Based on metric and non-metric traits of the cranium and mandible, it is likely that YH1 is a female individual. For age estimation, considering the synostosis of cranial sutures, multiple features of the cranium, and calibration of the relationship between dental wear and age, we estimate the YH1's age at death to be 30–40 years old (L. T. He et al. 2025).

The main comparison materials can be categorized into three groups. The first group consists of either original or high-quality casts of crania and/or mandibles from the LP of East and Southeast Asia (Figure 1 and Table 1). The second group includes individuals or groups from the Early Holocene of Northern China, Southern China, and Southeast Asia (Hoabinhian). Lastly, the third group comprises recent and modern groups that contain female crania from Asia and Oceania (see Table 1 for details).

2.2 | Methods

The nonmetric traits utilized in this study are primarily based on the definitions from Franciscus (2003), Weidenreich (1943), Lahr (1996), and Maureille (1994), while the non-metric features of the mandible are informed by the works of Weidenreich (1936), Dobson and Trinkaus (2002), Franciscus and Trinkaus (1995), Mounier et al. (2009), X. J. Wu and Trinkaus (2014) (Table 2). Additionally, the occurrence of non-metric traits in YH1 was compared to the range of occurrence in the LP hominins and recent-modern East Asian populations.

The metric characteristics of both the cranium and mandible are illustrated in Table 3, following the measurement criteria of W. W. Howells (1973), Martin and Saller (1957), and Brauer (1988). Moreover, the YH1 cranium was subjected to micro-CT scanning, and 3D reconstruction was performed using Mimics 20 (Materialise NV, Leuven) to generate an endocast, assess cranial capacity, and examine the vault thickness as well as endocranial features.

Drawing on the linear morphometric traits of the cranium, this study employed principal component analysis (PCA) and linear discriminant analysis (LDA) to delineate the morphological distinctions and similarities between the craniofacial characteristics of YH1 and the comparative samples. However, as the measurement criteria used for the comparison group samples were not uniform, two separate analyses were performed to maximize the sample size. Ten linear measurements (GOL, BBH, XCB, minimum frontal breadth [MFB], ZYB, NPH-2, OBB, OBH, NLB, NLH) were utilized to compare YH1 with the LP and Early Holocene groups. Additionally, 17 linear measurements (GOL, BNL, BBH, XCB, ZYB, AUB, ASB, BPL, NPH-1, NLH, NLB, OBH, OBB, ZMB, FRC, PRC, ORC) were employed for the comparison of YH1 with recent-modern groups. Given that size varies greatly between Pleistocene hominins and modern humans, multivariate analyses were carried out on the size-adjusted metric data (i.e., where each metric measurement was divided by the geometric mean of all measurements). Furthermore, we employ the geometric mean as a representative measure of cranial

TABLE 1 | Comparative samples and specimens used for the YH1 cranial and mandibular non-metric and metric analyses.

Samples	Individuals	Sources
Late Pleistocene		
East Asia ($n=20$)	Zhiren[a], Tianyuan[a], **Upper Cave 101**[b], **103**[b], 104[b], 108[b], **Liujiang**[a], Jingchuan[b], Ziyang[a], Chuandong-1[b], Maludong 1704[b], 1706[c], 1679[c], Longlin-1[b], **Minatogawa 1**[b], 2[c], 4[c], GM7502[b], GM7505[b], GM7503[b]	Curnoe et al. 2012; Kaifu et al. 2011; Liu et al. 2010; Shang et al. 2007; Woo 1958; Li et al. 2010; X. Z. Wu 1961; Woo 1959; Cao et al. 2015; Huang 1989; Suzuki 1982; present study
Southeast Asia ($n=6$)	**Wajak-1**[b], **Wajak-2**[b], **Hang Cho Cave**[c], **Moh Khiew**[c], **Niah**[c], **Tam Pa Ling-2**[b]	Curnoe et al. 2016; Demeter et al. 2015; Matsumura et al. 2008; Matsumura and Zuraina 1999; Storm 1995; present study
Neolithic Age		
North China ($n=8$)[c]	Donghulin.M1[b], Jiahu[c], Xinglongwa[c], Baoji[c], Banpo[c], Huaxian[c], Xiawanggang[c], Jiangzhai[c]	J. N. He et al. 2020; Chen and Zhang 1998; Yen 1962; Yen, Liu, and Gu 1960; Yen, Wu, et al. 1960; M. H. Wang 2003; Z. B. Zhang and Chen 1984; Xia et al. 1983; present study
South China ($n=9$)	Qihe-3[b], Zhaoguo-1[b], Zengpiyan[c], Liyuzui[c], Huiyaotian[c], Liyupo[c], Hemudu[c], Liangdao 1[c], Liangdao-2[c]	Matsumura et al. 2019; Y. Zhang et al. 2021; Liu et al. 1994; X. J. Wu et al. 2014; Zhang et al. 1977; Han and Pan 1983; Matsumura et al. 2017; present study
Southeast Asia/Hoabinhian ($n=7$)	MDN.M1[c], MDD.M1[c], Gua Cha[c], Hang Lang Gao[c], Hang Lang Bon[c], BacSon[c], Gua Gunung Runtuh[c]	Cuong 1986; Matsumura et al. 2019
Recent-modern humans[c] ($n=565$)	Buriat, Andaman, Ainu, N.Japan, S.Japan, Hainan, Atayal, Guam, Mokapu, Easter I, Moriori, Australia, Tasmania, Tolai	W. W. Howells 1973, 1995, 1996

Note: Bolded Late Pleistocene specimens are involved in the multivariate analysis. Underlined specimens are (or include) mandibles.
[a]Original fossil curated at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP).
[b]High-quality casts curated at IVPP.
[c]Data cited from literature.

size to compare the YH1 with those of modern female samples. All statistical analyses and graphing in this study were performed with PAST v. 4 (Hammer et al. 2001) and R v. 4.5 (R Core Team 2025).

3 | Results

3.1 | Comparative Description

The YH1 cranium is distinguished by large size, surpassing the majority of recent modern female samples (Figure S1). Regarding overall cranial morphology, the YH1 cranium exhibits a more rounded contour than the other LP crania (Figure 3). The cranial capacity was estimated to be 1587 cm^3 (Figure 4). This is within the range of LP hominins in China (1300–1750 cm^3) (X. J. Wu et al. 2008) and modern humans (1140–1600 cm^3) (Leigh 1992; Rightmire 2004), yet notably exceeds the modern human average of 1390 cm^3. At the bregma and parietal eminence, the thickness of the YH1 vault is comparable to that of LP hominins and Neolithic populations in China (Table 4).

The frontal bone is broad and high, featuring a well-developed frontal eminence in the absence of a sagittal crest. The MFB of YH1 exceeds that of all LP hominins discovered in East and Southeast Asia. It is also larger than the range of variation in Neolithic and modern humans (Tables S1 and S2), approaching the Early modern humans of Africa (Curnoe et al. 2012). The glabella projects to a greater degree than in modern East Asians but is comparable to that of LP crania (Table 2). The YH1's orbital region exhibits discontinuity (Figure S2), where a supraorbital sulcus separates the supraciliary arch and supraorbital arch, a derived character of LP hominins and modern humans (Athreya 2012; Russell et al. 1985). The posterior position of the bregma is considered an archaic trait (Woo 1958, 1959). The position of YH1's bregma is quantified using the ratio of the frontal arc to the cranial sagittal arc, with a value of 33.6, indicating that the bregma is roughly located at one-third of the sagittal arc, which is very close to the average value of the modern

TABLE 2 | Discrete traits observation of the YH1 crania and mandible.

Discrete trait	YH1	Late Pleistocene hominins	Recent Asian population
Cranium			
Parietal view	Long and oval	Long and oval	Oval and elliptical
Position of the maximum cranial breadth	Middle 1/3	Middle 1/3	Middle 1/3
Lateral walls of crania	Slightly arc shape	Vertical shape/arc shape	Arc shape
Sagittal keel at frontal bone	Absent	Present/absent	Absent/weak
Glabellar prominence	IN2	IN2–IN3	IN1–IN2
Supraciliary arch	ST3	ST2–ST5	ST1–ST2
Supraorbital arch	Weak	Variable	Absent/weak
Supraorbital sulcus	Present	Present	Present
Zygomatic triangle	TR3	TR3–TR4	TR1–TR2
Sagittal keel at parietal bone	Absent	Present/absent	Absent/weak
Angular torus	Absent	Present/absent	Absent/weak
Transitional morphology of the nuchal and occipital plane	Curved transition	Curved transition	Curved transition
Occipital bun	Absent	High frequency	Low frequency
Occipital torus	Weak	Variable	Absent/weak
Occipital protuberance	Weak	Absent/weak	Absent/weak
Precondylar tubercle	Present	Absent	Absent
Shape of temporal squama	Rounded	Rounded (except UC101)	Rounded
Juxtamastoid eminence	Well developed	Well developed	Well developed
Supramastoid crest	Well developed	Medium/well developed	Absent/weak (female)
Extension of the supramastoid crest	End in the temporal bone	End in the temporal/ parietal bone	End in the temporal bone
Orbit shape and proportion	Square shaped, high	Square shaped, low	Variable, high
Inferior orbital margin	RO2	RO2	RO1–RO2
Canine fossa	Medium	Variable	Variable
Maxillary sulcus	Absent	Absent	Absent
Zygomatic root position	M1	M1/M1–M2	M1
Piriform aperture shape	Very narrow	Medium-wide	Medium
Lower margin of the aperture	Open	Open	Variable
Nasal floor topography	One level	One level	One level
Malar tubercle	ZT2	ZT1–ZT3	ZT1 (female)
Incisive foramen position	Anterior	Anterior	Anterior
Mandible			
Mentum osseum rank	4	4–5	4–5
Mandibular incurvature	Weak	Variable	Medium–strong
Alveolar planum	Absent	Absent	Absent
Superior transverse torus	Absent	Absent/weak	Absent

(Continues)

TABLE 2 | (Continued)

Discrete trait	YH1	Late Pleistocene hominins	Recent Asian population
Inferior transverse torus	Absent	Absent/weak	Absent
Genioglossal fossa	Absent	Absent/weak	Absent
Direction of digastric fossa	Downward–backward	Downward–backward	Downward–backward
Mental foramen position	P4-M1; lower	P4/P4-M1; lower	P4; middle
Superior lateral torus	Weakly developed	Absent/weak	Absent
Marginal torus	Weak	Absent/weak	Variable
Anterior marginal tubercles	Absent	Variable	Variable
Posterior marginal tubercles	Weak	Variable	Weak
Lateral prominence position	Weak M2	Variable M2, M2–M3	Variable M2, M2–M3
Mandibular torus	Absent	Variable	Variable
Retromolar space	Narrow	Absent/narrow	Absent/narrow
Extramolar sulcus	Narrow	Variable	Narrow
Gonial eversion	Slightly everted	Variable	Everted
Masseteric fossa	Weakly developed	Weak/medium	Variable

Chinese population (33.5 ± 1.2, Liu, He, et al. 2006; Liu, Wu, and Wang 2006).

The parietal bone of YH1 is longer and curved, with arc length following the order of parietal–frontal–occipital, a derived trait of modern humans (Hublin 1991; Liu, He, et al. 2006; Liu, Wu, and Wang 2006). The YH1 parietal bone lacks the sagittal crest and angular torus, features that are characteristic of *Homo erectus* and variably present in LP hominins (Table 2).

The YH1 occipital bone demonstrates a curved transition between the nuchal and occipital planes, devoid of an occipital bun and with a weak external occipital protuberance (Figure S2). The occipital bun is a feature that is common among Neanderthal (Condemi 1991a, 1991b) and LP specimens from East and Southeast Asia, and also has a certain occurrence rate in modern East Asia populations (Baba et al. 1998; Liu, He, et al. 2006; Liu, Wu, and Wang 2006). The YH1 exhibits a weakly developed occipital torus (Figure S3), with its level of development being consistent with that seen in most LP specimens yet more pronounced than that of modern East Asian females. The YH1 is distinguished by the presence of a precondylar tubercle on the occipital bone (Figure S3), a characteristic notably absent among the LP and Early Holocene comparative specimens (Table 2).

The temporal bones on both sides display a rounded configuration of the temporal squama and possess a deep glenoid fossa. The left mastoid process is moderately developed, with a large juxtamastoid eminence. In the YH1, the supramastoid crest, though limited in extent, is relatively sharp (Figure S2 and Table 2).

YH1 has a notably low and broad face (Figure 5 and Table S1). While YH1's upper facial height may have been somewhat influenced by maxillary alveolar resorption, the impact was likely insignificant given the anterior alveolar socket's relative integrity. The facial width of YH1, measuring 146.4 mm (ZYB), exceeds that of all LP and Neolithic samples from East and Southeast Asia (Table S2) and is more comparable to early modern humans from Africa and Western Asia (Curnoe et al. 2012). The orbits are approximately high-squared in shape. The OBH value for YH1 is 34.6 mm, with an orbital index of 84.4, which is significantly higher than that of all LP specimens in East and Southeast Asia (Figure 5 and Table S1).

A moderately developed canine fossa is present in the infraorbital region of YH1, which is a typical derived feature of modern humans (Liberman et al. 2002). The YH1 retains nasal bones only at the nasal root, with a narrow nose aperture, in contrast to the broader nose observed in LP individuals (Figure 5 and Table S1). The nasal floor of YH1 is characterized by a one-level floor, a feature prevalent in early modern humans and modern humans, diverging from the bi-level nasal floor of archaic humans and Neanderthals (Franciscus 2003; Wu et al. 2012). The bilateral zygomatic bones are large, protruding anterolaterally, and facing anteriorly, with moderately developed malar tubercles (Figure S2).

The mandible of YH1 is overall short, broad, and gracile. The degree of development of the chin is ranked 4 (Dobson and Trinkaus 2002), which is the most common pattern in LP hominins and modern humans (Table 2). The lingual face of the YH1 mandible lacks transverse tori and genioglossal fossa. The lateral prominence is weakly developed, located beneath the M2, with a weakly developed marginal torus. The mandibular ramus is slightly everted, and the extramolar sulcus is narrow (Figure S4).

The position of the mental foramen in YH1 is situated at P4/M1, unlike modern humans, where it is mostly below P4. However,

TABLE 3 | Measurements of cranium and mandible of YH1 (linear measurements in mm, angles in degrees, indices dimensionless).

Measurement	Definition	YH1
Cranial capacities		1587 mL
	Cranial linear measurements	
GOL	Distance between glabella and opisthocranion	188.9
BNL	Distance from nasion to the basion	97
BBH	The height from the basion to bregma	142.6
XCB	Maximum breadth between bilateral euryon	145.5
MFB	Minimum breadth between bilateral frontotemporale	109
ZYB	Breadth between bilateral zygion	146.4
AUB	Breadth between bilateral auriculare	137
AUH	Auricular height, vertical distance from biporion line to vertex of the skull	125.2
ASB	Breadth between bilateral asterion	109.
BPL	Distance from basion to prosthion	94.8
NPH-1	The height from nasion to prosthion	62
NPH-2	The height from nasion to supradentale	64
NLH	Distance between nasion and nasospinale	51.3
NLB	Taken as a maximum between the anterior edges of the piriform aperture	24.2
OBH	The height between the upper and lower borders of the left orbit perpendicular to its long axis	R: 34.6 L: 37.4
OBB	Distance between maxillofrontale to ectoconchion	R: 41 L: 40.8
Cranial sagittal arc	Arc from nasion to opisthion along the median sagittal plane of the cranium	405.9
FAR	Arc from nasion to bregma along the median sagittal plane of the cranium	136.6
FRC	Chord from nasion to bregma along the median sagittal plane of the cranium	118
PAR	Arc from bregma to lambda along the median sagittal plane of the cranium	138.8
PRC	Chord from bregma to lambda along the median sagittal plane of the cranium	122.9
OAR	Arc from lambda to opisthion along the median sagittal plane of the cranium	(130.8)
ORC	chord from lambda to opisthion along the median sagittal plane of the cranium	(111.8)
	Cranial angle measurements	
Middle prognathism angle	Angle between nasion and nasospinale in the FH plane	83.7
Nasomalar angle	Angle at nasion between the two sides reaching from this point to left and right frontomalare	147
	Cranial indices	
Cranial index	(XCB/GOL)*100	77

(Continues)

TABLE 3 | (Continued)

Measurement	Definition	YH1
Cranial length–height index	(BBH/GOL)*100	98
Cranial breadth–height index	(BBH/XCB)*100	75.5
Upper facial index	(UFH/ZYB)*100	42.4
Nasal index	(NLB/NLH)*100	47.2
Orbit index	(OBB/OBH)*100	84.4
	Mandibular measurements and angles	
Length of body (inferior)	Distance between infradentale to intergonion midpoint	(75)
Mandibular breadth across gonion	Distance between the left and right gonions	(105)
Alveolar arcade breadth (M_2)	Distance between the right and left intersection points of the distal contour of the M2 and the midline of the molar row	(64.9)
Alveolar arcade length (M_2)	Distance from infradentale to the line tangential to distal faces of right and left M2 crowns	(33.8)
Symphyseal angle	Angles between infradentale and pogonion in the alveolar plane	93.3
Symphyseal height	Minimum distance from the basal contour to the lateral alveolar margin, perpendicular to the alveolar line	(34.3)
Symphyseal thickness	Maximum distance taken perpendicular to the height of the symphysis	15
Symphyseal robusticity index	Ratio of the symphyseal thickness and height	43.7
Corpus height (mental foramen)	Minimum distance from the lateral alveolar margin to the basal contour at the midpoint of the mental foramen, perpendicular to the alveolar line	L: 32.8 R: unmeasurable
Corpus thickness (mental foramen)	Maximum distance taken perpendicular to the corpus height at the mental foramen	L: 13.1 R: unmeasurable
Corpus robusticity index (mental foramen)	Ratio of corpus thickness and height at the mental foramen	L: 39.9 R: no data

the position of the mental foramen in YH1 is similar to that of most LP specimens in East and Southeast Asia (77.8%, $n = 9$), which may be related to the shorter mandibular body in this population (Demeter et al. 2015) (Table 2). In addition, YH1 exhibits a superior lateral torus (Figure S4), similar to that of LP specimens (Table 2). The narrow retromolar area in YH1 may be linked to advanced tooth wear and ante-mortem tooth loss, resulting in mesial drift of the dental arch.

3.2 | Multivariate Analyses of Craniofacial Shape

This study conducted two different PCAs and LDAs to assess overall trends in the comparisons of the craniofacial metric traits of YH1 and other crania. The YH1 was initially compared with a sample of females from recent-modern samples (W. W. Howells 1996) from Northeast Asia (Buriat), Maritime Southeast Asia (Hainan, Atayal), East Asia (North Japan, South Japan, Ainu), Andaman islanders (Andaman), Polynesia and Micronesia (Guam, Mokapu, Easter Island, Moriori), Australia and Melanesia (Tasmania, Australia, Tolai).

The plot of PCA (Figure 6A) shows YH1 lies within the range of East Asia, Maritime Southeast Asia, Polynesia, and Micronesia, and the Andaman islanders, but outside the range of Australia, Melanesia, and Northeast Asia.

A similar affinity pattern was observed in the plot of the first two axes for the LDA (Figure 6B). The group centroids were calculated using principal component scores, and the smallest Euclidean distances from YH1 to group centroids are for Atayal, Hainan, and Guam (Table S4). The LDA results indicate that YH1 is most appropriately classified as the Moriori group (posterior probability of 40.99%), and the posterior probability of classifying YH1 into Guam also reaches 31.03% (Table S5). Interestingly, the precondylar tubercle, a feature found on the occipital bone of YH1, is predominantly regarded as a non-metric characteristic associated with Micronesian and Polynesian populations (Hanihara and Ishida 2001).

For comparisons with LP and Early Holocene individuals, we utilized size-corrected data from 10 linear measurements of the crania for multivariate analyses. The plots of the first two

FIGURE 3 | Lateral views of (A) YH1 and some comparative Late Pleistocene specimens; (B) Liujiang; (C) Wajak-1; (D) UC101; (E) UC103; (F) Minatogawa-1.

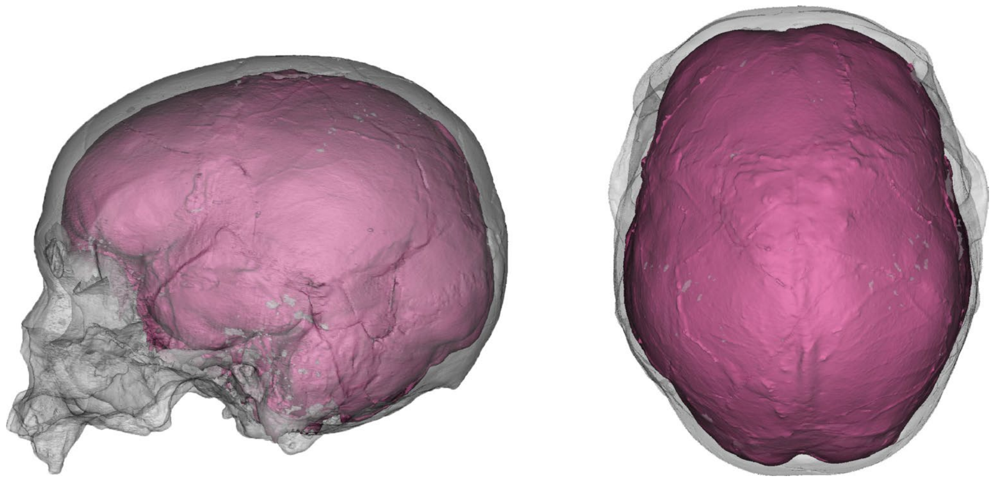

FIGURE 4 | 3D virtual reconstruction of YH1 endocast.

principal components (Figure 7A) and the first two LDA axes (Figure 7B) show that YH1 lies outside of the range of any of the LP and Early Holocene groups (but is closer to the LP group), exhibiting a broader frontal bone, face, and neurocranium (MFB, XCB, ZYB) (Tables S2 and S6). The smallest Euclidean distance from YH1 to a group centroid was for the LP group. The LDA results also suggest that YH1 best classifies as part of the LP group (posterior probability of 77%) (Table S7), which matches the distance to centroid results.

When the results of the two aforementioned multivariate analyses are combined, YH1 exhibits a mosaic morphology. YH1 exhibits the closest affinity to the LP group when only 10 facial-centered variables are considered. However, when craniometric variables encompassing the entire neurocranium are incorporated, YH1 demonstrates a stronger morphological resemblance to modern human populations from maritime Southeast Asia, Polynesia, and Micronesia. Results from multivariate analysis and qualitative analysis of the overall cranium indicate that YH1 possesses a relatively large and primitive facial skeleton, coupled with a more derived neurocranium (Figure 3 and Figure 5).

Furthermore, through the PCA and LDA plots comparing YH1 with ancient samples, a clear separation is manifested between the Neolithic South China and Neolithic North China groups. The Neolithic South China group is typified by

TABLE 4 | Comparison of the vault thickness of YH1 (mm).

	Bregma	Parietal eminence	Source
EUEHS	7 ± 3	6 ± 1	Curnoe et al. 2012
NEAND	7 ± 1	8 ± 2	
WAEHS	7	8 ± 2	
LP: MLDG-1704	7	7.6	Curnoe et al. 2012
LP: Ziyang	8.7	6.23	X. J. Wu and Yan 2020
EH: Zhaoguo-1	6.2	7.4	Zhang et al. 2021
Neolithic population in China (mean)	7.15	6.55	Zhang 1981
YH1	8.0	L 6.8/R 5.3	This study

Abbreviations: EH, Early Holocene; EUEHS, early *Homo sapiens* in Europe; LP, Late Pleistocene; NEAND, *Homo neanderthalensis*; WAEHS, early *Homo sapiens* in West Asia.

a longer cranium (GOL), lower face, and lower nose (NPH-2 and NLH) (Figure 7A and Table S2). Furthermore, the entire Neolithic South group can generally be partitioned into two subgroups: the southeast coastal and southwest inland, with a certain degree of overlap. The southwest subgroup displays a craniofacial morphology akin to that of the Hoabinhian populations and is scarcely distinguishable from them in both PCA and LDA analyses (Figure 7).

4 | Discussion

Based on the comparison of the morphological characteristics of the YH1 cranium and mandible, it is evident that YH1 exhibits mosaic morphological traits, with its evolutionary position lying at the transitional stage between LP hominins and Holocene populations.

YH1 is primitive in comparison to recent East Asian crania in some features, including the large overall size of the skull, large cranial capacity, relatively developed cranial and mandibular superstructures (glabellar prominence, supraciliary arch, zygomatic triangle, occipital torus, malar tubercles, and superior

FIGURE 5 | Facial skeleton morphology of (A) YH1 and some Late Pleistocene comparative specimens; (B) Liujiang; (C) Wajak-1; (D) UC101; (E) UC103; (F) Minatogawa-1.

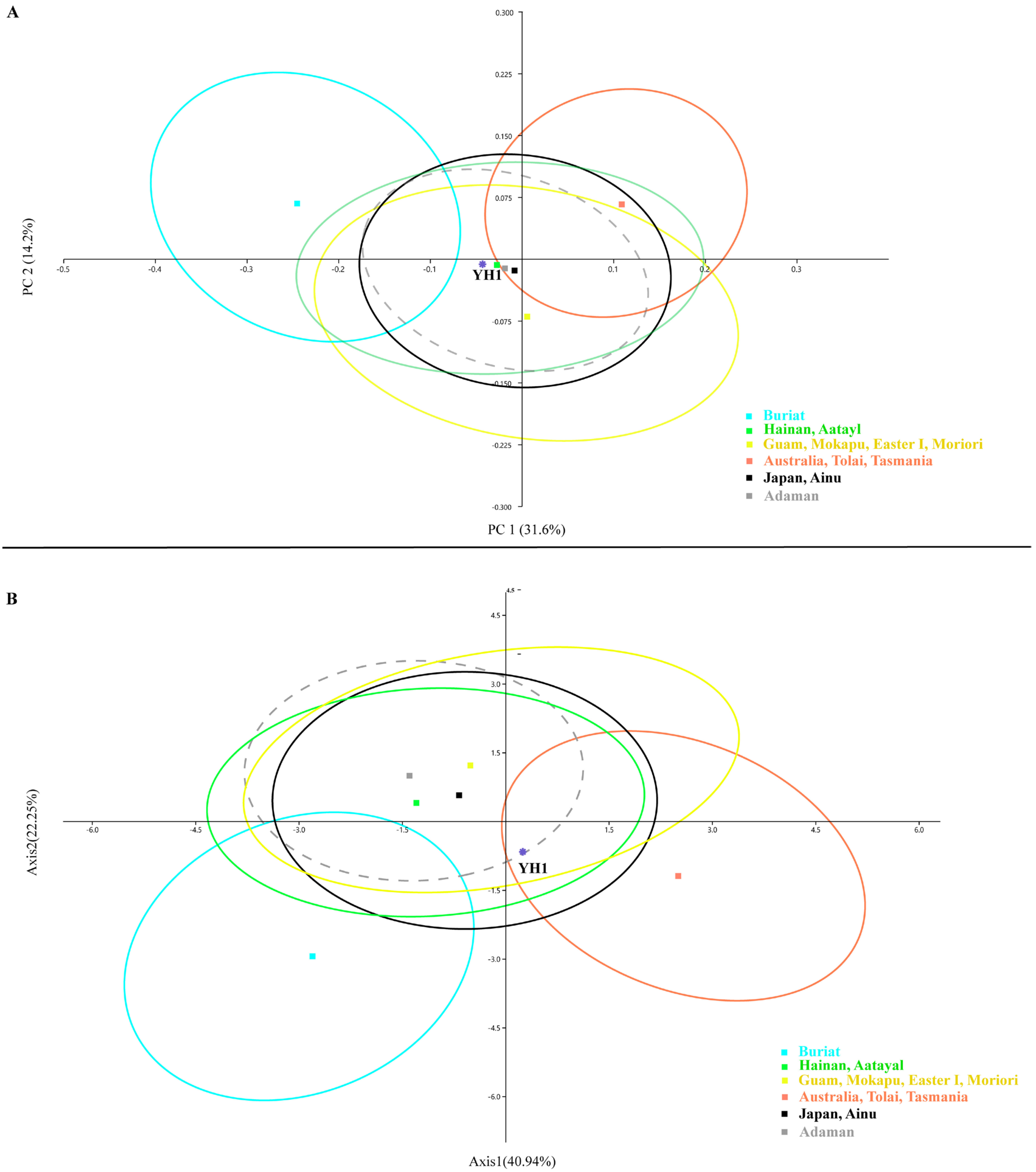

FIGURE 6 | PCA (A) and LDA (B) of YH1 and other modern samples using 17 linear measurements (the circle represents the 95% confidence interval).

lateral torus). From the craniofacial shape, YH1 possesses a large and primitive facial skeleton, exhibiting a wide frontal bone and a broad face, alongside a more derived neurocranium, evidenced by its high vault. Interestingly, the narrowness of the pyriform aperture in YH1 appears to be a unique characteristic, and its significance in LP human evolution or population affinity in East and Southeast Asia is still unclear.

4.1 | The Regional Differentiation of the Terminal Pleistocene–Early Holocene Population in East Asia

The formation and differentiation of modern humans have resulted in distinct morphological characteristics among those living in different areas. These regional morphological features may be attributed to genetic drift acting on small

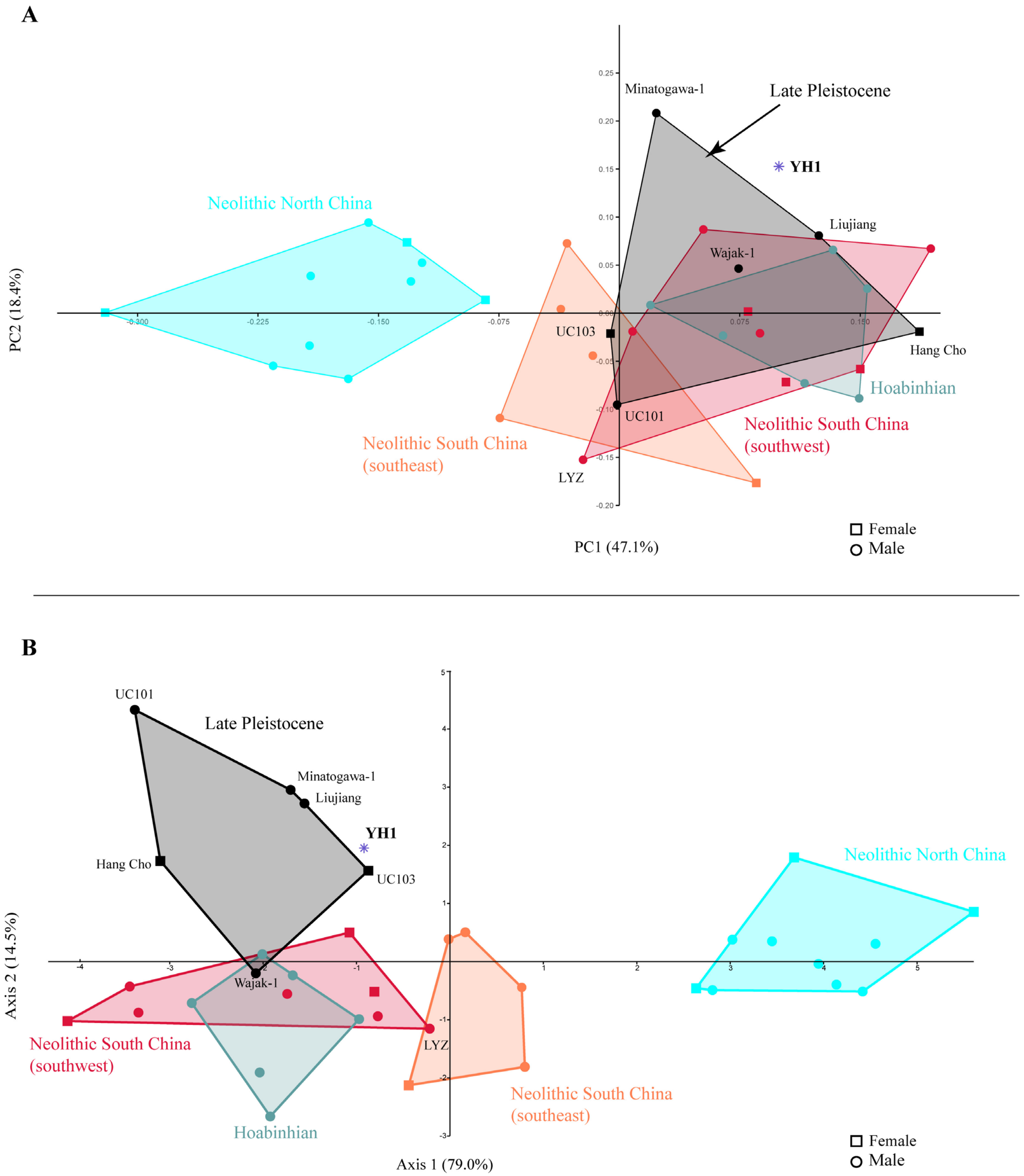

FIGURE 7 | PCA (A) and LDA (B) of YH1 and the ancient comparative samples using 10 linear measurements. Neolithic North China: Donghulin. M1, Xiawanggang, Huaxian, Baoji, Jiangzhai, Banpo, Xinglongwa, Jiahu; Neolithic South China (southeast): Liangdao-1, Liangdao-2, Qihe-3, Hemudu; Neolithic South China (southwest): Liyuzui (LYZ), Huiyaotian, Zhaoguodong, Liyupo, Zengpiyan; Neolithic Southeast Asia: MDN.M1, MDD.M1, Gua Cha, Hang Lang Gao, Hang Lang Bon, and BacSon.

founding populations of modern humans (Manica et al. 2007; von Craman-Taubadel and Lycett 2008) as well as the effects of adaptation to new environments. Some scholars suggest that the morphological features of modern humans formed no earlier than the terminal Pleistocene and Early Holocene, based on studies of LP and Early Holocene human remains around the world (Lahr 1995; Hanihara 1994). However, the natural environment, cultural development, and livelihoods vary greatly in different regions. As a result, the formation time of regional morphological features may differ in various parts of the world.

Previous studies have highlighted north–south differentiation in craniofacial morphology and genetic traits among the East Asian population during the Neolithic era (Yang et al. 2020; Z. B. Zhang 1981, 1988; L. H. Wang 1986). Additionally, it has been suggested by researchers that this differentiation can be traced back to the LP, as evidenced by the Upper Cave and Liujiang specimens (Z. B. Zhang 1988; Zhang 1997). Recently, the discourse on the differentiation between northern and southern populations in East Asia during the LP to Early Holocene period has been enriched by new fossil discoveries. The ZG-1 from southwestern China, dated to around 10.0k years, presents the quintessential craniofacial traits of southern groups (Y. Zhang et al. 2021). Conversely, the Qihe-3 from the southeastern region (11.747k–11.356k years ago) exhibits a blend of characteristics from both northern and southern populations (X. J. Wu et al. 2014). Additionally, the study of Donghulin.M1 from North China (11.17k–10.7k years) reveals traits that suggest an emerging identity of the North China population, albeit not distinctly categorized within the typical northern or southern groups (He et al. 2020).

The paleogenomic studies of terminal Pleistocene–Early Holocene human remains from various sites in China suggest that the divergence between northern and Southern East Asian populations dates back to no later than the Early Holocene period (T. Wang et al. 2021; Yang et al. 2020). In Northeast Asia, this differentiation may have occurred as early as around the Last Glacial Maximum, approximately 19.0k years (Mao et al. 2021).

From craniofacial morphology, the typical Southern East Asian population is characterized by long and low vaults, along with low, broad faces and wide piriform apertures. Based on the craniometric data, it is noted that YH1, similar to the southern population, exhibits a relatively low and wide facial skeleton, although this particular trait is prevalently found in the LP group. However, YH1 presents a relatively high neurocranium and a narrow piriform aperture. The multivariate analyses also demonstrate that YH1 is closer to the LP group. All of these factors suggest that the craniofacial morphological differentiation between the northern and southern populations in East Asia had not yet been established around 16,000 years ago. Moreover, there was a great deal of intra-population variation during this period. It was not until the Early Holocene (around 10.0k years ago, i.e., the stage of the Liyuzui, Zhaoguo-1, and Zengpiyan individuals) that the increase in craniofacial homogeneity and the craniofacial morphometric characteristics of the typical Southern East Asia population were almost completely formed.

Additionally, there was a pattern of morphological diversity among human fossils in South China during the terminal Pleistocene to Early Holocene epoch. The southwestern areas that encompass contemporary Guangxi, Guizhou, and Yunnan provinces act as a transitional belt linking the continental East and Southeast Asia. It is renowned as a "crossroads" where early human groups and cultures met and intertwined in a complex mosaic of interaction. Most or all traits of the cranium in terminal Pleistocene–Early Holocene human fossils excavated from southwestern China, including Liujiang, Zhaoguo, Ziyang, and Lijiang, exhibit a fully modern pattern (Woo 1958, 1959; Yunnan Provincial Museum 1977; X. J. Wu et al. 2014; Y. Zhang et al. 2021). Concurrently, there exist individuals unearthed from Longlin, Maludong, and Dushandong who exhibit a mosaic of archaic and derived features (Curnoe et al. 2012; Liao et al. 2019). This study also reveals that YH1 not only exhibits the mosaic features characteristic of modern humans and LP hominins but also demonstrates some unique traits. This finding contributes supplementary fossil-based evidence and morphological insights into the diversity of human evolutionary processes during the terminal Pleistocene within Southwest China.

4.2 | Population Dynamics During the Terminal Pleistocene–Early Holocene in Southern East Asia

Matsumura et al. (2019) conducted a study on the morphology of 89 groups of male skulls from Northeast Asia, Southeast Asia, and Pacific Oceania. They proposed a "two-layer" model as a hypothesis for the population history in East and Southeast Asia. Moreover, Matsumura et al. (2021) conducted an analysis of female skulls (dating from 16.0k to 5.3k years ago) excavated from seven sites in southern China and Southeast Asia, including YH1. The findings of their study support the "two-layer" model, suggesting that female samples from southern China and Southeast Asia, as well as Australian and Papuan females, exhibit relatively close affinity. However, recent research on ancient genomes from the LP to Early Holocene human remains in southern China indicates no close affinity between these ancient populations and modern Australians and Papuans. The Qihe-3 is related to ancient and modern Austronesian populations (Yang et al. 2020). The MLDG-1704 and Longlin-1 align with the genetic diversity of modern East Asian populations, belonging to the East Asian lineage within modern humans (T. Wang et al. 2021; X. Zhang et al. 2022).

Based on the analysis in this study, the YH1 cranium exhibits a mosaic pattern and features unique morphological traits that set it apart from all ancient comparative samples. It shows a closer resemblance to LP specimens than to Early Holocene southern specimens, making it difficult to define a clear affinity link between YH1 and specific Early Holocene groups. However, compared with recent-modern populations, YH1 is closer to that of Maritime Southeast Asians, Polynesians, and Micronesians, especially those from Hainan, Atayal, Guam, and Moriori. Since these three groups belong to the Austronesian, YH1, like Qihe-3, may be related to the Austronesian origin.

In the Early Holocene, there were morphological differences between populations in North and South China. However, whether these differences arose from the gradual differentiation of early modern human adaptation and genetic drift or stemmed from two distinct populations with different origins (i.e., the first and second layers of the "two-layer" theory) remains unclear. There is currently insufficient evidence to make a definitive judgment on this issue. In Southern East Asia, however, craniofacial morphological variation in Early Holocene populations does not conform to a singular pattern. Some differences in certain facial metric traits were observed between the southeast and southwest populations, which cannot be broadly classified into a "first layer" group. Specifically, the southeast specimens, including those from Qihe, Hemudu, and Liangdao sites, exhibited higher faces and noses. The southwest group, such as those from the Huiyaotian, Liyupo, and Zhaoguo Cave sites, more commonly had broad and low faces. Nevertheless, some individuals, such as the Liyuzui individual in southwest China, showed morphological intergradations, as it is situated within the range of the southeast group in both PCA and LDA plots (Figure 7) and exhibits a narrow facial width. These observations indicate the existence of gene flow between the southeast and southwest populations during the Early Holocene, a pattern corroborated by evidence from paleogenomic research (T. Wang et al. 2021).

Ancient DNA studies on the Maludong specimen have revealed that distinct genetic characteristics existed in Southwest China and Southeast Asia at the terminal Pleistocene (T. Wang et al. 2021). During the Early Holocene, it was found that the craniofacial morphology of the majority of individuals in Southwest China closely resembled that of the Hoabinhian populations in Southeast Asia. This may be due to the intensified frequency of migrations between the populations in Southeast Asia and Southwest China, which engendered a diminution in morphological disparities among them. Concomitantly, this phenomenon was accompanied by cultural exchanges (Ji et al. 2016). The underlying impetus for such alterations might be attributed to the termination of the Younger Dryas event in the initial Holocene, with the consequent stabilization and warming of the climate that spurred population growth and enhanced mobility.

5 | Conclusion

In this study, we describe and analyze the morphology of the cranium and mandible of the terminal Pleistocene Yahuai-1 from Guangxi province, southern China. We examined both non-metric and metric features and compared them qualitatively and quantitatively with recent-modern Asia and Oceania groups or specimens from the LP and Early Holocene. In terms of craniomandibular morphology, YH1 exhibits mosaic morphological traits, with its evolutionary position lying at the transitional stage between LP hominins and Holocene populations.

The study of YH1 reveals that while there were early signs of north–south differentiation in craniofacial morphology, the degree of morphological variation within the Southern Chinese specimens at this time was substantial. This variation suggests that the formation of distinct regional morphological features was a gradual process. The YH1 findings, in conjunction with other LP and Early Holocene human remains, indicate that the typical craniofacial morphometric characteristics of Southern East Asia populations were not fully formed around 16.0k years.

In examining the population dynamics within Southern East Asia, the craniofacial morphometric traits of YH1, which exhibit closer resemblance to LP specimens, obfuscate its taxonomic linkage to specific Early Holocene populations. However, analyses with recent-modern groups suggest that YH1 may have played a role in the origin of Austronesian-speaking populations. During the Early Holocene, regional morphological differentiation between northern and southern and southeastern and southwestern populations was fully established, and analogous patterns were evident in genetic studies. Concurrently, evidence for population interactions and gene flow was elucidated among populations across these regions.

In summary, the human evolutionary narrative in Southern East Asia during the terminal Pleistocene to the Early Holocene epoch is considerably more intricate than the "two-layer theory" describes. The study of the YH1 fossil provides a clearer picture of the human diversity and complexity in Southern East Asia and, indeed, across East Asia during a pivotal period in modern human differentiation.

Author Contributions

Letian He: writing – original draft, methodology, conceptualization. **Guangmao Xie:** resources, project administration, funding acquisition. **Xiujie Wu:** writing – review and editing, conceptualization. **Qiang Lin:** resources, investigation. **Jieying Lu:** investigation, resources. **Noreen von Craman-Taubadel:** writing – review and editing, methodology, conceptualization.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information of this article.

References

Athreya, S. 2012. "The Frontal Bone in the Genus *Homo*: A Survey of Functional and Phylogenetic Sources of Variation." *Journal of Anthropological Sciences* 90: 1–22. https://doi.org/10.4436/jass.90008.

Baba, H., S. Narasaki, and S. Ohyama. 1998. "Minatogawa Hominid Fossils and the Evolution of Late Pleistocene Humans in East Asia." *Anthropological Science* 106, no. supplement: 27–45.

Brauer, G. 1988. "Osteometrie." In *Anthropologie*, edited by R. Martin and R. Knussman, 160–232. Gustav Fischer.

Cao, B., L. T. He, and P. Zhang. 2015. "A Study of Human Fossils Discovered at the Maomao Cave Site, Xingyi County, Guizhou Province." *Acta Anthropologica Sinica* 34, no. 4: 451–460 (in Chinese).

Chen, D. Z., and J. Z. Zhang. 1998. "The Physical Characteristics of the Early Neolithic Humans in the Jiahu Site and the Comparison With Other Neolithic Humans and Modern Man." *Acta Anthropologica Sinica* 3: 28–48 (in Chinese).

Chen, S. 2014. *Prehistoric Modernization: An Ecocultural Investigation of the Origins of Agriculture in China*. Science Press.

Condemi, S. 1991a. "Neanderthal Man, Vol 7, Extinction [French]." *L'Anthropologie* 95, no. 4: 852–853.

Condemi, S. 1991b. "Circeo I and variability among classic Neanderthals." In *The Circeo 1 Neanderthal skull: Studies and documentation*, edited by M. Piperno and G. Scichilone. Poligrafico e Zecca dello Stato.

Crevecoeur, I., H. Rougier, F. Grine, and A. Froment. 2009. "Modern Human Cranial Diversity in the Late Pleistocene of Africa and Eurasia: Evidence From Nazlet Khater, Peştera cu Oase, and Hofmeyr." *American Journal of Physical Anthropology* 140, no. 2: 347–358.

Cuong, N. L. 1986. "Two Early Hoabinhian Crania From Thanh Hoa Province, Vietnam." *Zeitschrift für Morphologie und Anthropologie* 77, no. 1: 11–17.

Curnoe, D., I. Datan, P. S. Taçon, and M. S. Sauffi. 2016. "Deep Skull From Niah Cave and the Pleistocene Peopling of Southeast Asia." *Frontiers in Ecology and Evolution* 4: 191813. https://doi.org/10.3389/fevo.2016.00075.

Curnoe, D., J. Xueping, A. I. R. Herries, et al. 2012. "Human Remains From the Pleistocene-Holocene Transition of Southwest China Suggest a Complex Evolutionary History for East Asians." *PLoS One* 7, no. 3: e31918.

Demeter, F., F. Manni, and Y. Coppens. 2003. "Late Upper Pleistocene Human Peopling of the Far East: Multivariate Analysis and Geographic Patterns of Variation." *Comptes Rendus Palevol* 2, no. 8: 625–638.

Demeter, F., L. Shackelford, K. Westaway, et al. 2015. "Early Modern Humans and Morphological Variation in Southeast Asia: Fossil Evidence From Tam Pa Ling, Laos." *PLoS One* 10, no. 4: e0121193.

Dobson, S. D., and E. Trinkaus. 2002. "Cross-Sectional Geometry and Morphology of the Mandibular Symphysis in Middle and Late Pleistocene Homo." *Journal of Human Evolution* 43, no. 1: 67–87.

Franciscus, R. G. 2003. "Internal Nasal Floor Configuration in Homo With Special Reference to the Evolution of Neandertal Facial Form." *Journal of Human Evolution* 44, no. 6: 701–729.

Franciscus, R. G., and E. Trinkaus. 1995. "Determinants of Retromolar Space Presence in Pleistocene Homo Mandibles." *Journal of Human Evolution* 28, no. 6: 577–595.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. "PAST: Paleontological Statistics Software Package for Education and Data Analysis." *Palaeontology Electron* 4, no. 1: 1–9.

Han, K. X., and Q. F. Pan. 1983. "Early Neolithic Human Skulls From Hemudu, Yuyao, Zhejiang." *Acta Anthropologica Sinica* 2: 124–131 (in Chinese).

Hanihara, T. 1994. "Craniofacial Continuity and Discontinuity of Far Easterners in the Late Pleistocene and Holocene." *Journal of Human Evolution* 27: 417–441.

Hanihara, T., and H. Ishida. 2001. "Frequency Variations of Discrete Cranial Traits in Major Human Populations. III. Hyperostotic Variations." *Journal of Anatomy* 199, no. 3: 251–272.

He, J. N., C. H. Zhao, J. C. Yu, et al. 2020. "The Physical Evolution and Biocultural Adaptation of Human Remains in Donghulin Site, Beijing." *Archaeology* 7: 90–98.

He, L. T., G. M. Xie, Q. Lin, D. W. Li, and X. J. Wu. 2025. "Sex and Age-at-Death of the Yahuai Cave Man From the Late Pleistocene of Guangxi." *Acta Anthropologica Sinica* 44, no. 3: 389–403. https://doi.org/10.16359/j.1000-3193/AAS.2024.0034. (in Chinese).

Howells, W. W. 1973. *Cranial Variation in Man: A Study by Multivariate Analysis of Patterns of Difference Among Recent Human Populations*. Harvard University Press.

Howells, W. W. 1995. *Who's Who in Skulls: Ethnic Identification of Crania From Measurements*. Harvard University Press.

Howells, W. W. 1996. "Howells' Craniometric Data on the Internet." *American Journal of Physical Anthropology* 101, no. 3: 441–442.

Huang, X. H. 1989. "A Crania Fossil From Chuandong, Puding, Guizhou." *Acta Anthropologica Sinica* 8, no. 4: 379–382 (in Chinese).

Hublin, J. J. 1991. "L' Émergence des *Homo sapiens* Archaïques: Afrique du Nord-Ouest et Europe Occidentale." Thèse d'Etat, Université Bordeaux 1, France.

Ji, X., K. Kuman, R. Clarke, et al. 2016. "The Oldest Hoabinhian Technocomplex in Asia (43.5 Ka) at Xiaodong Rockshelter, Yunnan Province, Southwest China." *Quaternary International* 400: 166–174. https://doi.org/10.1016/j.quaint.2015.09.080.

Kaifu, Y., M. Fujita, R. T. Kono, and H. Baba. 2011. "Late Pleistocene Modern Human Mandibles From the Minatogawa Fissure Site, Okinawa, Japan: Morphological Affinities and Implications for Modern Human Dispersals in East Asia." *Anthropological Science* 119, no. 2: 137–157.

Lahr, M. M. 1995. "Patterns of Modern Human Diversification: Implications for Amerindian Origins." *American Journal of Physical Anthropology* 38, no. S21: 163–198.

Lahr, M. M. 1996. *The Evolution of Modern Human Diversity: A Study of Cranial Variation*. Cambridge University Press.

Leigh, S. R. 1992. "Cranial Capacity Evolution in Homo Erectus and *Homo sapiens*." *American Journal of Physical Anthropology* 87: 1–13.

Li, H., X. Wu, S. Li, W. Huang, and W. Liu. 2010. "Late Pleistocene Human Skull From Jingchuan, Gansu Province." *Chinese Science Bulletin* 55, no. 11: 1047–1052 (in Chinese).

Liao, W., S. Xing, D. Li, et al. 2019. "Mosaic Dental Morphology in a Terminal Pleistocene Hominin From Dushan Cave in Southern China." *Scientific Reports* 9, no. 1: 2347.

Liberman, D. E., B. M. McBratney, and G. Krovitz. 2002. "The Evolution and Development of Cranial Form in *Homo sapiens*." *Proceedings of the National Academy of Sciences of the United States of America* 99, no. 3: 1134–1139.

Liu, W. 2006. "Some Problems in the Study of Human Evolution and Modern Population Formation in the Late Pleistocene." *Progress in Natural Science* 16, no. 7: 789–796 (in Chinese).

Liu, W., J. N. He, X. J. Wu, and J. Y. LU. 2006. "The Comparisons of Cranial Non-Metric Features Between Upper Cave Skulls and Modern North Chinese Populations, and Late Pleistocene Human Evolution in China." *Acta Anthropologica Sinica* 1: 26–41 (in Chinese).

Liu, W., C.-Z. Jin, Y.-Q. Zhang, et al. 2010. "Human Remains From Zhirendong, South China, and Modern Human Emergence in East Asia." *Proceedings of the National Academy of Sciences of the United States of America* 107, no. 45: 19201–19206.

Liu, W., A. H. Luo, F. W. Zhu, W. S. Lu, C. D. Lin, and F. Q. Li. 1994. "Human Remians From the Neolithic Site of Liyuzui in Dalongtan, Liuzhou." *Guangxi Ethnic Studies* 3: 22–37 (in Chinese).

Liu, W., X. J. Wu, and S. Wang. 2006. "Some Problems for the Late Pleistocene Human Cranium Found in Liujiang of South China Based on Morphological Analysis." *Acta Anthropologica Sinica* 3: 177–194 (in Chinese).

Manica, A., W. Amos, F. Balloux, and T. Hanihara. 2007. "The Effect of Ancient Population Bottlenecks on Human Phenotypic Variation." *Nature* 448: 346–348.

Mao, X., H. Zhang, S. Qiao, et al. 2021. "The Deep Population History of Northern East Asia From the Late Pleistocene to the Holocene." *Cell* 184, no. 12: 3256–3266.e13.

Martin, R., and K. Saller. 1957. *Lehrbuch der Anthropologie in Systematischer Darstellung Mit Besonderer Berücksichtigung der Anthropologischen Methoden*. Fischer.

Matsumura, H., H. Hung, C. Higham, et al. 2019. "Craniometrics Reveal "Two Layers" of Prehistoric Human Dispersal in Eastern Eurasia." *Scientific Reports* 9, no. 1: 1451.

Matsumura, H., H. C. Hung, Z. Li, and K. Shinoda. 2017. "National Museum of Nature and Science Monograph." In *Bio-Anthropological Studies of Early Holocene Hunter-Gatherer Sites at Huiyaotian and Liyupo Guangxi, China*, No. 47. National Museum of Nature and Science.

Matsumura, H., G. Xie, L. C. Nguyen, et al. 2021. "Female Craniometrics Support the 'Two-Layer Model' of Human Dispersal in Eastern Eurasia." *Scientific Reports* 11, no. 1: 20830.

Matsumura, H., M. Yoneda, Y. Dodo, et al. 2008. "Terminal Pleistocene Human Skeleton From Hang Cho Cave, Northern Vietnam: Implications for the Biological Affinities of Hoabinhian People." *Anthropological Science* 116, no. 3: 201–217.

Matsumura, H., and M. Zuraina. 1999. "Metric Analyses of an Early Holocene Human Skeleton From Gua Gunung Runtuh, Malaysia." *American Journal of Physical Anthropology* 109, no. 3: 327–340.

Maureille, B. 1994. "La Face Chez *Homo erectus* et *Homo sapiens*: Recherche Sur la Variabilité Morphologique et Métrique [The face in *Homo erectus* and *Homo sapiens*: Research on Morphological and Metric Variability]." Ph.D. thesis, Université Bordeaux 1, France.

Mithen, S. 2003. *After the Ice: A Global Human History, 20,000–5000 BC*. Harvard University Press.

Mounier, A., F. Marchal, and S. Condemi. 2009. "Is *Homo heidelbergensis* a Distinct Species? New Insight on the Mauer Mandible." *Journal of Human Evolution* 56, no. 3: 219–246.

R Core Team. 2025. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical.

Rightmire, G. P. 2004. "Brain Size and Encephalization in Early to Mid-Pleistocene Homo." *American Journal of Physical Anthropology* 124: 109–123.

Russell, M. D., T. Brown, S. M. Garn, et al. 1985. "The Supraorbital Torus: 'A Most Remarkable Peculiarity'." *Current Anthropology* 26, no. 3: 337–360.

Shang, H., H. Tong, S. Zhang, F. Chen, and E. Trinkaus. 2007. "An Early Modern Human From Tianyuan Cave, Zhoukoudian, China." *Proceedings of the National Academy of Sciences of the United States of America* 104, no. 16: 6573–6578. https://doi.org/10.1073/pnas.0702169104.

Shui, W. Y., G. M. Xie, L. T. He, et al. 2025. "Facial Approximation of a Late Pleistocene Human Fossil in the Yahuai Cave, Southern China." *Journal of Archaeological Science* 177: 106–180.

Storm, P. 1995. *The Evolutionary Significance of the Wajak Skulls*. National Naturhistorisch Museum.

Suzuki, H. 1982. "Skull of the Minatogawa Man." In *The Minatogawa Man*, edited by H. Suzuki and K. Hanihara, 7–49. University of Tokyo Press.

von Craman-Taubadel, N., and S. J. Lycett. 2008. "Brief Communication: Human Cranial Variation Fits Iterative Founder Effect Model With African Origin." *American Journal of Anthropology* 136: 108–113.

Wang, L. H. 1986. "Secular Change and Geographical Variation in Chinese Neolithic and Modern Inhabitants: A Statistical Study of Cranial Metric Traits." *Acta Anthropologica Sinica* 3: 243–258.

Wang, M. H. 2003. "Physical Characteristics." In *Zengpiyan in Guilin*, edited by Institution of Archaeology, CASS, Cultural Relics Work Team of Guangxi, Zengpiyan Site Museum et al., 405–428. Cultural Relics Publishing House (in Chinese).

Wang, T., W. Wang, G. Xie, et al. 2021. "Human Population History at the Crossroads of East and Southeast Asia Since 11,000 Years Ago." *Cell* 184, no. 14: 3829–3841.e21.

Wang, T., M. A. Yang, Z. H. Zhu, et al. 2025. "Prehistoric Genomes From Yunnan Reveal Ancestry Related to Tibetans and Austroasiatic Speakers." *Science* 388: eadq9792. https://doi.org/10.1126/science.adq9792.

Wei, B. Y., E. S. Zhong, W. Zhu, and W. Chen. 1994. "The Discovery of the Chongtang Neolithic Site in Chongzuo County, Guangxi and a Preliminary Study of Human Skull." *Acta Anthropologica Sinica* 1: 78–80 (in Chinese).

Wei, B. Y., W. Zhu, E. S. Zhong, and W. Chen. 1997. "A Study on the Neolithic Human Remains and the Neolithic in Chongtang, Chongzuo County, Guangxi." *Acta Academiae Medicinae Guangxi* 01: 41–43 (in Chinese).

Wei, P. 2021. "Late Pleistocene Partial Femora From Maomaodong, Southwestern China." *Journal of Human Evolution* 155: 102977.

Wei, P., H. Lu, K. J. Carlson, et al. 2020. "The Upper Limb Skeleton and Behavioral Lateralization of Modern Humans From Zhaoguo Cave, Southwestern China." *American Journal of Physical Anthropology* 173, no. 4: 671–696.

Weidenreich, D. F. 1936. "The Mandible of *Sinanthropus pekinensis*: A Comparative Study." *Palaeontologia Sinica, Series D* 7: 1–132.

Weidenreich, D. F. 1943. "The Skull of *Sinanthropus Pekinensis*: A Comparative Study of a Primitive Hominid Skull." *Palaeontologia Sinica* 10D: 1–484.

Woo, J. 1958. "Tzeyang Paleolithic Man—Earliest Representative of Modern Man in China." *American Journal of Physical Anthropology* 16, no. 4: 459–471.

Woo, J. 1959. "Study on the Liujiang Man in Liujiang, Guangxi." *Vertebrata Palasiatica* 3: 97–104 (in Chinese).

Wu, X. J., C. X. Fan, S. M. Li, et al. 2014. "The Early Neolithic Human Skull From the Qihe Cave, Zhangping, Fujian." *Acta Anthropologica Sinica* 33, no. 4: 448–459 (in Chinese).

Wu, X. J., W. Liu, W. Dong, J. M. Que, and Y. F. Wang. 2008. "CT Scan and Brain Morphological Characteristics of Liujiang Human Skull Fossils." *Science Bulletin* 13: 1570–1575 (in Chinese).

Wu, X. J., and E. Trinkaus. 2014. "The Xujiayao 14 Mandibular Ramus and Pleistocene *Homo* Mandibular Variation." *Comptes Rendus Palevol* 13, no. 4: 333–341.

Wu, X. J., and Y. Yan. 2020. "Endocranial Anatomy of the Ziyang 1 Human Skull." *Acta Anthropologica Sinica* 39, no. 4: 511–520 (in Chinese).

Wu, X. Z. 1961. "Study on the Upper Cave Man of Choukoutien." *Vertebrata Palasiatica* 3: 181–211 (in Chinese).

Wu, X.-J., S. D. Maddux, L. Pan, and E. Trinkaus. 2012. "Nasal Floor Variation Among Eastern Eurasian Pleistocene Homo." *Anthropological Science* 120, no. 3: 217–226.

Xia, Y. M., Q. M. Gong, Q. Gao, and C. M. Zhou. 1983. "A Study on the Human Remains of the First Stage of Jiangzhai Culture in Lintong." *Prehistory* 02: 112–132 (in Chinese).

Xie, G. M., Q. Lin, M. H. Yu, and J. Y. Lu. 2025. "An Excavation Report of the Yahuai Cave Site in Guangxi, South China." *Acta Anthropologica Sinica* 44, no. 3: 365–388. https://doi.org/10.16359/j.1000-3193/AAS.2025.0046.

Xing, S., Y. Guan, M. O'Hara, H. Cai, X. Wang, and X. Gao. 2017. "Late Pleistocene Hominin Teeth From Laoya Cave, Southern China." *Anthropological Science* 125, no. 3: 129–140.

Yang, M. A., X. Fan, B. Sun, et al. 2020. "Ancient DNA Indicates Human Population Shifts and Admixture in Northern and Southern China." *Science* 369, no. 6501: 282–288.

Yen, Y. 1962. "Neolithic Human Skeleton Unearthed at Hua-Hsien, Shensi." *Acta Archaeologica Sinica* 2: 85–104 (in Chinese).

Yen, Y., C. Z. Liu, and Y. M. Gu. 1960. "Neolithic Human Skeleton Was Unearthed at Baoji." *Vertebrata Palasiatica* 1: 32–43 (in Chinese).

Yen, Y., X. Z. Wu, C. Z. Liu, and Y. M. Gu. 1960. "Neolithic Human Skeleton Unearthed Banpo, Xi'an." *Archaeology* 9: 36–44 (in Chinese).

Yunnan Provincial Museum. 1977. "Preliminary Study of Human Skull in Lijiang, *Yunnan*." *Vertebrate Palasiatica* 2: 157–161 (in Chinese).

Zhang, X., X. Ji, C. Li, et al. 2022. "A Late Pleistocene Human Genome From Southwest China." *Current Biology* 32, no. 14: 3095–3109.e5.

Zhang, Y., H. Lu, X. Zhang, et al. 2021. "An Early Holocene Human Skull From Zhaoguo Cave, Southwestern China." *American Journal of Physical Anthropology* 175, no. 3: 599–610.

Zhang, Y. Y., L. H. Wang, and X. R. Dong. 1977. "Human Skulls From the Neolithic Zengpiyan Site in Guilin, Guangxi (in Chinese)." *Vertebrata PalAsiatica* 15, no. 1: 4–15.

Zhang, Z. B. 1981. "On the Geographical Distribution of the Physical Features of the Neolithic Population in China (in Chinese)." *Vertebrata Palasiatica* 1: 87–97.

Zhang, Z. B. 1988. "An Analysis of the Physical Characteristics of Modern Chinese." *Acta Anthropologica Sinica* 4: 314–323 (in Chinese).

Zhang, Z. B. 1997. "The Microevolution of Cranial Characteristics in Chinese Humans and the Origin of Modern Chinese People." In *Confirmation of Evolution: Essays in Commemoration of the Centenary of Professor Yang Zhongjian's Birth (in Chinese)*, edited by Y. S. Tong. 7–21. Ocean Press.

Zhang, Z. B., and D. Z. Chen. 1984. "The Racial Types of Xiawanggang Neolithic Age Population." *Prehistory* 01: 68–76 (in Chinese).

Zhao, Y., P. Wei, X. Zhang, et al. 2022. "Structural Properties of Humeral Diaphyses of East Asian Modern Humans From the Late Pleistocene to Early Holocene." *American Journal of Biological Anthropology* 178, no. 3: 461–475.

Zhou, G. X., and Y. Z. You. 1972. "Neolithic Graves in Donghulin, Beijing." *Archaeology* 06: 12–15 (in Chinese).

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ajpa70114-sup-0001-Supinfo.docx.