

Human remains from Zhirendong, South China, and modern human emergence in East Asia

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The 2007 discovery of fragmentary human remains (two molars and an anterior mandible) at Zhirendong (Zhiren Cave) in South China provides insight in the processes involved in the establishment of modern humans in eastern Eurasia. The human remains are securely dated by U-series on overlying flowstones and a rich associated faunal sample to the initial Late Pleistocene, >100 kya. As such, they are the oldest modern human fossils in East Asia and predate by >60,000 y the oldest previously known modern human remains in the region. The Zhiren 3 mandible in particular presents derived modern human anterior symphyseal morphology, with a projecting tuber symphyseos, distinct mental fossae, modest lateral tubercles, and a vertical symphysis; it is separate from any known late archaic human mandible. However, it also exhibits a lingual symphyseal morphology and corpus robustness that place it close to later Pleistocene archaic humans. The age and morphology of the Zhiren Cave human remains support a modern human emergence scenario for East Asia involving dispersal with assimilation or populational continuity with gene flow. It also places the Late Pleistocene Asian emergence of modern humans in a pre-Upper Paleolithic context and raises issues concerning the long-term Late Pleistocene coexistence of late archaic and early modern humans across Eurasia.

Late Pleistocene | archaic humans | mandible | chin | teeth

A consensus has been building that the Pleistocene establishment of modern human morphology across the Old World involved an initial emergence in equatorial Africa in the later Middle Pleistocene and then the subsequent appearance of that biology across the remainder of the inhabited Old World during the Late Pleistocene. The processes involved are likely to have been geographically and temporally variable population dispersal with the absorption of regional late archaic humans or regional continuity with substantial gene flow (1–6). As a result, variations on an Assimilation Model (6) have become dominant in the discussions of modern human emergence, and scenarios involving strict Out-of-Africa with complete replacement or regional continuity with only minimal gene flow are less supported.

The timing and nature of those populational processes are becoming increasingly evident in the western Old World (7, 8), especially in western Eurasia, where early modern humans briefly occupied extreme southwestern Asia ~90 kya but did not extend permanently into the region until after ~50 kya, fully occupying western Eurasia by ~35 kya (9). In eastern Eurasia, the dearth of diagnostic and well-dated fossil remains (5, 10–12) has inhibited more than general statements for that region. Fully modern human morphology was established close to the Pacific rim by ~40 kya, as is indicated by the fossils from Niah Cave in Sarawak (13) and especially Tianyuan Cave in northern China (5). The actual time of the transition has remained elusive, because the age of the latest known archaic humans in the region is substantially earlier (10). The eastern Eurasian age of the transition has been generally assumed to approximate that of western Eurasia (~50–40 kya), although there have been claims

supporting earlier dates for modern human presence in East Asia (cf. 12).

This scenario implies a long term (>100,000 y) restriction of early modern humans to portions of Africa with a brief ~90 kya expansion into extreme southwestern Asia, followed by a relatively rapid expansion throughout Eurasia after ~50 kya (7). The scenario also implies some form of adaptive threshold, roughly contemporaneous with the emergence of the Upper Paleolithic (*sensu lato*), and a marked behavioral difference between those expanding modern human populations and regional populations of late archaic humans (14).

It is in this context that three fragmentary human remains were discovered in 2007 at Zhirendong, South China (15). Because it is only well-dated diagnostic human remains that can document the timing and nature of human evolution and dispersal patterns (as opposed to archeological proxies for human biology or imprecise inferences from extant genetic diversity), the Zhirendong remains have the potential to shed light on these ongoing paleoanthropological issues.

Context and Dating

Zhirendong (Zhiren Cave; *Homo sapiens* Cave) is located within the Mulanshan (Mulan Mountain), Chongzuo City, Guangxi Zhuang Autonomous Region in South China (22° 17' 13.6" N; 107° 30' 45.1" E) (*SI Appendix, Figs. S1 and S2*). It is an open karstic chamber in Triassic limestone that leads into a tubular passage at the rear left of the modern cave (*SI Appendix, Figs. S3 and S4*). It is currently 179 m above sea level, 34 m above the Hejiang River; it was probably closer to the adjacent land surface in the later Pleistocene. The rear passage filled with sediment during the Pleistocene, the majority of which was subsequently removed geologically, leaving a cemented hanging remnant along portions of the ceiling (Section A) (*SI Appendix, Fig. S5*). The open space subsequently filled with water displaced fossiliferous sediment (Section B), unconformably reaching up to the lower surface of Section A with some gaps in the contact. The Section B sediments are capped by a continuous layer of flowstone (Layer 1, *SI Appendix, Fig. S5*), and they show lithological characteristics that are distinctly different from the Section A sediments. It is likely that the Section B sediments and fossils originated from the surface near the mouth of the cave and not from a redeposition of the Section A sediments. Moreover, the Section B, Layer 1 flowstone would have prevented the intrusion of remains from later than Section B into the underlying deposits.

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The human remains were excavated in situ from Layer 2, in the upper portion of Section B (*SI Appendix, Fig. S5*). The series of flowstones in Layer 1 of Section B have provided a set of U-series dates (Table 1 and *SI Appendix, Fig. S6* and Table S1). The two upper flowstones have yielded marine isotope stage (MIS) 3 ages with mean values of ~28 and ~52 kya. The thicker, next-deeper flowstone has yielded a series of dates (samples Sa and S3 to S5) with MIS 5 to 4 mean ages ranging from ~74 kya to ~87 kya. The deepest, thin flowstone level provided an age of 106.2 ± 6.7 kya (2σ error), which provides a minimum age for Layer 2 (and the human fossils) of ~100 to ~113 kya.

The human remains were associated in Section B with an abundant if fragmentary faunal assemblage (15) (*SI Appendix, Table S2*). The faunal remains, especially the absence of the Early and earlier Middle Pleistocene *Gigantopithecus*, *Sinomas-todon*, and *Stegodon*, the appearance of *Elephas kiangnanensis* and *Eliphas maximus*, and the presence of 25% extinct macromammal species in the faunal assemblage, indicate a late Middle or earlier Late Pleistocene age for the deposits.

The combination of these U-series dates and the associated faunal remains therefore place the Zhiren Cave human remains securely in earlier MIS 5 or possibly MIS 6. The stratigraphically higher U-series dates provide a minimum age of ~100 ka BP [MIS 5c (16)], and the associated fauna constrain the deposits to be no older than late Middle Pleistocene (15). As such, these fossils are at least 60,000 y older than the early modern human remains from the Tianyuan and Niah Caves.

Zhirendong Human Remains

The Zhirendong human remains (Fig. 1) consist of two isolated molars found in November 2007 [Zhiren 1 (PA 1521) and 2 (PA 1522)] and an anterior mandibular corpus excavated a month later [Zhiren 3 (PA 1520)]. The first specimen consists of a right M_3 with the resorbed M_2 and M_3 partial alveoli, and the second element is an isolated right M_3 or (possibly) M_2 with a distal carious lesion. The mandible preserves the edentulous symphyseal region from the right P_4 to the left P_4 , with damage to the P_4 regions, minor erosion to the basal symphysis, and buccal apical lesions to both P_3 alveoli. The antemortem lesions do not affect morphological comparisons. Zhiren 1 and 2 are mature. All of the preserved alveoli of Zhiren 3 have sharp borders without resorption and contained fully erupted teeth, indicating a late adolescent or young adult age at death. Zhiren 1 and 2 are from separate individuals, as they are both right M_3 s or Zhiren 2 is an M_2 but does not fit the Zhiren 1 M_2 alveolus (*SI Appendix*). Zhiren 1 and 3 are unlikely to derive from the same individual, given the marked alveolar resorption evident on Zhiren 1 but not on Zhiren 3. Zhiren 2 and 3 could derive from one individual, but they are considered separately because the association cannot be confirmed.

Table 1. Adjusted ^{230}Th dating results of flowstones from Section B, Layer 1 of Zhiren Cave

Sample no.	^{230}Th age (kya)
S1	28.4 ± 6.6
S2	51.8 ± 22.7
S3	84.9 ± 12.9
S3*	79.4 ± 13.9
Sa	74.1 ± 21.6
S4*	84.7 ± 36.9
S5*	86.6 ± 3.3
Sb	106.2 ± 6.7

See *SI Appendix, Table S1* for details. Errors are at 2σ .

*Samples measured on a multicollector inductively coupled plasma mass spectrometer, whereas the others were run on inductively coupled plasma mass spectrometers.

Zhiren 1 and 2 Human Dental Remains. The two teeth (Fig. 1) have small crowns. Their respective buccolingual crown diameters (10.1 and 10.3 mm) fall below the central tendencies for M_3 s of all of the comparative samples, except the sub-Saharan African one, and the same pattern holds for the Zhiren 1 crown "area" (Table 2 and *SI Appendix, Fig. S7* and Table S3). If Zhiren 2 is considered an M_2 , its breadth is slightly below the range of an East Asian early modern human sample (10.4–11.8 mm, $n = 10$), within the ranges of the other samples, and on the sub-Saharan African mean (Table 2).

Despite occlusal wear [Smith (17) stages 5a and 4b, respectively], both teeth appear to have exhibited five cusps and lack anterior foveae and midtrigonid crests. The high root bifurcations indicate that they are nontaurodont. In a western Eurasian Late Pleistocene context, these features align them principally with early modern humans (18), but insufficient samples of associated unworn lower molars and the absence of identified derived late archaic features in East Asian molars (10, 19) prevent determination if the teeth are diagnostic of modern humans in South China.

Zhiren 3 Human Mandible. The Zhiren 3 mandible (Fig. 1) is a moderately small specimen for the Late Pleistocene (Table 3 and *SI Appendix, Table S4*), in that its corpus height at the mental foramen (average: 27.4 mm) is 1.30 SDs below the pooled Late Pleistocene sample mean (32.0 ± 3.7 mm, $n = 31$); none of the known East Asian early modern human mandibles are as small (29.1–33.0 mm, $n = 5$). It presents a mosaic of the features (*SI Appendix, Table S5*) that are considered characteristic of both early modern human and late archaic human mandibles (20–22).

Modern human features. The symphysis in *norma lateralis* is nearly vertical with an anterior symphyseal angle of 91° (Figs. 1 and 2A and Table 3). Its angle is above those of all Middle and Late Pleistocene archaic humans, slightly above those of the sub-Saharan African and Middle Paleolithic modern human (MPMH) samples, and exceeded only by the interquartile range of the earlier Upper Paleolithic (EUP) sample.

The profile of the symphysis approaching the mandibular base projects anteriorly, whereas the superior portion is slightly depressed forming an incurvatio mandibulae (Fig. 1B and D). In the anterior view (Fig. 1A), there is a ridge-shaped projection in the central symphyseal region running from the alveolar border (infradentale) to the mandibular base. This ridge gradually becomes wider inferiorly, merging with central keel and mental trigone. The mental trigone is moderately projecting, but it exhibits an obvious tuber symphyseos, evident in both anterior (Fig. 1A) and superior (Fig. 1C) views. Anteroinferiorly, the tuber symphyseos extends bilaterally, forming modest lateral tubercles with no clear separation between the two features. The central keel extends upward from the tuber symphyseos and weakens gradually. Along the two sides of the central keel and the tuber symphyseos, shallow but distinct mental fossae (incisura mandibulae anterior) are evident. Therefore, the anterior midline of the Zhiren 3 mandible exhibits the distinctive features of a modern human chin (20, 23), modestly developed but nonetheless distinctly projecting from the anterior contour of the mandibular symphysis. As such, it falls within the criteria of mentum osseum rank 4 of Dobson and Trinkaus (24).

The primary anterior symphyseal elements of a human chin (especially a tuber symphyseos) are variably present in genus *Homo* mandibles since the Early Pleistocene (20, 24–26), but through Middle and Late Pleistocene archaic humans ($n = 56$) they remain within the profile of the anterior mandible (mentum osseum ranks <4) (Table 3 and *SI Appendix, Table S6*). It is only with late Middle and Late Pleistocene early modern humans that there is consistent presence of at least a projecting tuber symphyseos with distinct mental fossae (a mentum osseum rank >3). This almost universal presence applies in particular to the MPMH and EUP samples, as the sub-Saharan African sample exhibits considerable variation in these features [they are present in Klasies River Mouth (KRM) 6222, Loiyangalani 1 and Omo-

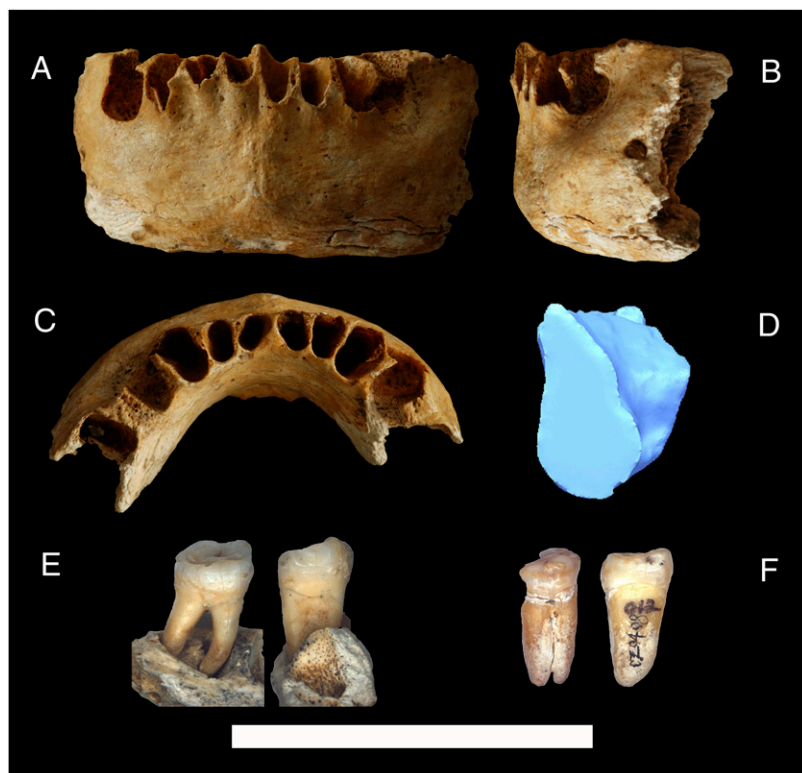


Fig. 1. The human remains from Zhiren Cave. The Zhiren 3 mandible in anterior (A), lateral left (B), and superior (C) views. The midsymphyseal cross-section of the Zhiren 3 mandible (D). The Zhiren 1 M₃ in buccal and mesial views (E), and the Zhiren 2 M₃ in the same views (F). (Scale bar, 5 cm.)

Kibish 1, but absent from the other KRM mandibles (*SI Appendix, Table S6*); each of the later East Asian early modern humans ($n = 8$) has a prominent tuber symphyseos with variably developed lateral tubercles, as do all but one of the western EUP mandibles ($n = 40$). These anterior symphyseal features on Zhiren 3, although modest, therefore fall with early modern human ranges of variation. They are more prominent than those of any known late archaic human, including those of the substantial number of late archaic humans with vertical symphyses.

This pattern is partially evident in the geometric morphometric analysis of the midline contour of the anterior symphysis (Fig. 2B and *SI Appendix, Fig. S8*); although quantifying symphyseal shape and orientation, these contours do not include the topography of the mental fossae or the lateral tubercles. Zhiren 3 falls principally with the sub-Saharan African and MPMH samples, especially with respect to the more important relative warp 1 (*SI Appendix, Fig. S8*). The sub-Saharan sample is a heterogeneous one that presents both late archaic and early modern features (7, 27–31), whereas the MPMH one is distinctly

“modern,” despite its craniofacial robustness (32–34). The Zhiren 3 contour falls within the Late Pleistocene archaic range of variation, but it is more vertical and S-curved than all but a couple of those specimens. It is separate, in opposite directions, from the Middle Pleistocene and EUP samples.

In addition to these features, the position of the mental foramen of Zhiren 3, a feature reflecting several aspects of mandibular proportions (35), is at the P₄. This position is present in all of the comparative samples (Table 3 and *SI Appendix, Table S7*). However, it has frequencies $\geq 50\%$ in the sub-Saharan, MPMH and EUP samples, but only 26.4% and 11.5% in the archaic samples. There is no evidence of an incisura submentalis, an anterior marginal tubercle, a planum alveolare, or a superior transverse torus (Fig. 1D and *SI Appendix, Table S5*), all features that are more common among archaic humans. In addition, the digastric fossae, despite a rounded inferior symphysis, are posteroinferiorly, rather than inferiorly, oriented—a more common recent human pattern.

Table 2. Comparative mandibular molar crown diameters for Zhiren 1 and 2

Samples	M ₃ MD (mm)	M ₃ BL (mm)	M ₃ “Area” (mm ²)	M ₂ BL (mm)*
Zhiren 1, 2	(10.9)	10.1, 10.3	110.1	10.3
EUP	11.3 ± 1.0 (26)	10.7 ± 0.8 (30)	121.9 ± 19.4 (26)	10.9 ± 0.7 (54)
MPMH	11.9 ± 0.8 (7)	10.8 ± 0.7 (7)	128.9 ± 15.5 (7)	11.0 ± 0.7 (9)
SAfrica	10.9 ± 1.7 (6)	9.8 ± 1.2 (6)	108.2 ± 29.4 (6)	10.3 ± 1.2 (9)
Late Pleist	11.8 ± 0.7 (56)	11.0 ± 0.8 (59)	129.8 ± 14.9 (55)	11.1 ± 0.8 (57)
Mid Pleist	11.8 ± 1.2 (33)	10.9 ± 1.0 (33)	129.3 ± 24.4 (33)	11.5 ± 1.2 (51)
P value [†]	0.061	0.030	0.064	0.002

Mean ± SD (N). “Area”, MD × BL; BL, buccolingual crown diameter; EUP, Earlier Upper Paleolithic modern humans; Late Pleist, Late Pleistocene (mostly Neandertal) archaic humans; MD, mesiodistal crown diameter; Mid Pleist, Middle Pleistocene archaic humans; MPMH, Middle Paleolithic modern humans; SAfrica, later Pleistocene sub-Saharan African sample.

*Comparative data are included for M₂ buccolingual diameters, in case Zhiren 2 should be better considered as an M₂ rather than as an M₃.

[†]ANOVA P values across the five comparative samples.

Table 3. Comparisons of discrete traits and morphometrics of the Zhiren 3 mandible and later Pleistocene comparative samples

Samples	Mentum osseum rank % >3*	Anterior symphyseal angle	Major axis symphyseal angle	Mental foramen % mesial of P ₄ /M ₁ *†	Corpus height at mental foramen (mm)	Corpus breadth at mental foramen (mm)
Zhiren 3	4	91°	78.5°	P ₄	27.4	16.0
EUP	97.9% (48)	96.5° ± 6.2° (21)	91.0° ± 7.9° (20)	69.3% (44)	31.6 ± 3.6 (22)	12.6 ± 1.7 (21)
MPMH	85.7% (7)	86.4° ± 6.4° (5)	83.4° ± 8.0° (4)	57.1% (7)	35.0 ± 4.1 (6)	14.0 ± 1.9 (6)
SAfrica	50.0% (6)	88.2° ± 1.0° (4)	78.1° ± 3.6° (4)	50.0% (4)	33.8 ± 4.6 (5)	17.1 ± 1.8 (5)
Late Pleist	0.0% (39)	79.4° ± 6.9° (26)	75.7° ± 5.8° (26)	11.5% (39)	32.0 ± 3.7 (31)	15.6 ± 1.7 (33)
Mid Pleist	0.0% (17)	70.4° ± 6.2° (14)	63.3° ± 4.6° (13)	26.4% (34)	30.4 ± 3.6 (25)	16.5 ± 1.8 (26)
P value†	<0.001	<0.001	<0.001	<0.001	0.058	<0.001

Mean ± SD (N). See Table 2 for sample abbreviations.

*For details, see *SI Appendix, Tables S6 and S7*.

†P values across the comparative samples. Exact χ^2 for discrete traits, and ANOVA for morphometrics.

Archaic human features. At the same time, there are aspects of the Zhiren 3 mandible that are unusual in an early modern human. The major axis angle of the symphyseal cross-section (78.5°) is within the interquartile ranges of the Late Pleistocene archaic, sub-Saharan and MPMH samples, above the Middle Pleistocene range but below the EUP values (Fig. 3A and Table 3). This angle reflects its full symphyseal contour, which includes a distinct inferior transverse torus (Fig. 1D), smaller than those of Middle Pleistocene humans, different from the lingual contours of the MPMH and EUP samples, and close to those of the Late Pleistocene archaic and sub-Saharan samples (Fig. 3B and *SI Appendix, Fig. S9*).

The symphyseal contour produces an elevated robustness of the mandibular corpus. Using corpus height as the independent variable, this robustness is reflected in relative anteroposterior versus superoinferior second moments of area at the symphysis (Fig. 4A and *SI Appendix, Fig. S10*) and relative corpus breadth at the mental foramen (Fig. 4B and *SI Appendix, Fig. S11*). In the former, Zhiren 3 is modest relative to Middle Pleistocene mandibles, but it is among the more robust Late Pleistocene mandibles and exceeds all of the MPMH ones. In the EUP sample, only three European specimens ($n = 20$) exceed Zhiren 3 in their relative anteroposterior rigidities, and they all have prominent chins. In the lateral corpus comparison, Zhiren 3 is among the more robust of the Middle Pleistocene, Late Pleistocene archaic, and sub-Saharan African mandibles, and it is distinctly separate from the MPMH and EUP samples.

These aspects of the mandibular corpus, in combination with weakly marked digastric fossae and no interdigastric spine, combine to align the specimen in part with the more archaic of the Late Pleistocene human mandibles.

Discussion

The Zhiren Cave human remains, securely dated to at least 100 kya (early MIS 5), therefore represent the oldest evidence of derived modern human morphology in East Asia. The Zhiren 3 mandible in particular presents an anterior symphyseal morphology and orientation which aligns it with other early modern humans and distinct from all Middle and Late Pleistocene archaic humans. It is nonetheless a robust mandible, with a lingual symphyseal contour, symphyseal cross-section, and lateral corporeal breadth that distinguish it from most (but not all) Late Pleistocene early modern humans.

Late Pleistocene human mandibles are rare in eastern Eurasia (the MIS 3 Batadomba lena, Minatogawa, Moh Khiew, Tianyuan, and Zhoukoudian-Upper Cave ones). They differ from Zhiren 3 principally in being more gracile and having a more prominent tuber symphyseos. A more global assessment of later Pleistocene human mandibular morphology aligns the Zhiren fossil primarily with the penecontemporaneous sub-Saharan African ones, a heterogeneous sample that has been noted for its complex mix of late archaic and early modern human features (7, 27–31) and whose mosaic morphology may reflect the transitional nature of the east African MIS 6 early modern human sample (30, 31) plus gene flow southward within Africa during MIS 5 (7, 28). The presence of the morphological mosaic of Zhiren 3 in the initial Late Pleistocene of East Asia, substantially earlier than the previously secure paleontological documentation of modern human morphology east of 40° E longitude, has implications for the populational and behavioral processes involved in modern human emergence in eastern Eurasia.

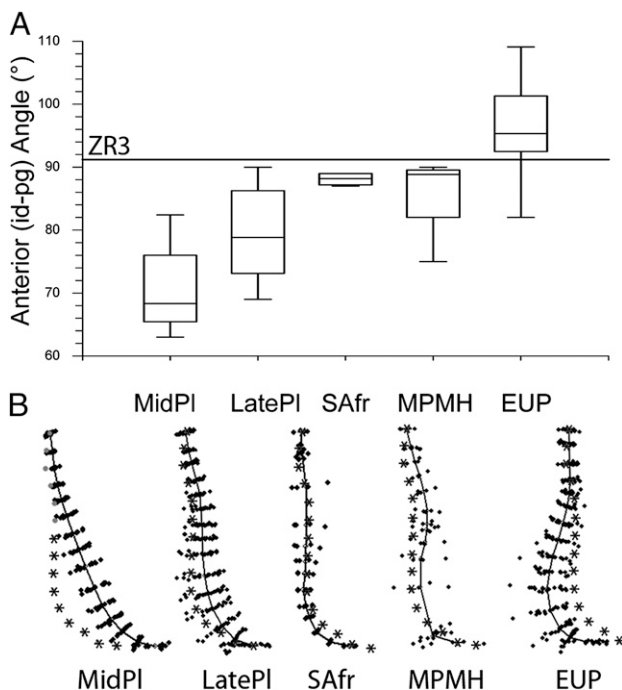


Fig. 2. The anterior (infradental-pogonion versus alveolar plane) symphyseal angle of Zhiren 3 versus comparative samples (A), and the anterior symphyseal profile of Zhiren 2 (stars) versus consensus profiles for the comparative samples (B). MidPI: Middle Pleistocene archaic humans; LatePI: Late Pleistocene archaic humans; SAfr: later Pleistocene sub-Saharan Africans; MPMH: Middle Pleistocene modern humans; EUP: earlier Upper Paleolithic modern humans. The sample sizes for the two comparisons, in left to right sample order, are: anterior angle: 14, 26, 4, 5, and 21; anterior profile: 13, 26, 4, 4, and 20.

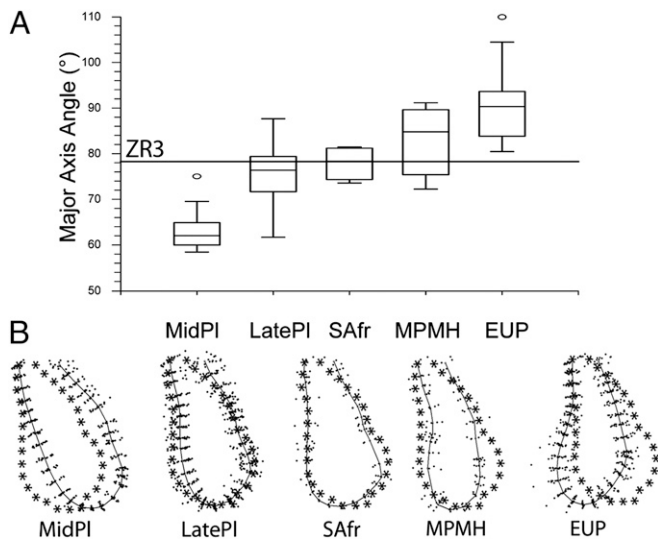


Fig. 3. The major axis symphyseal angle of Zhiren 3 versus comparative samples (A), and the symphyseal contour of Zhiren 2 (stars) versus consensus contours for the comparative samples (B). Sample abbreviations as in Fig. 2. The sample sizes for the two comparisons, from left to right, are: major axis angle: 13, 26, 4, 4, and 20; profile consensus: 13, 25, 4, 4, and 20.

Populational Implications. Assuming that modern human biology emerged initially in the late Middle Pleistocene of equatorial Africa (8, 31, 36), the presence of derived, modern human mandibular features in East Asia by early MIS 5 implies early modern human population dispersal or gene flow across at least southern Asia sometime before the age of the Zhiren Cave human remains or independent emergence of these features in East Asia. The early modern human MIS 5 dispersal into Southwest Asia may therefore have included further population dispersal or gene flow eastward across southern Asia.

However, the Zhiren 3 complex mosaic of distinctly derived, modern human features of the anterior mandibular symphysis, combined with archaic features of the lingual symphysis and overall mandibular robustness, indicates that any “dispersal” involved substantial admixture between dispersing early modern human populations (cf. 5) or gene flow into regional populations (cf. 37, 38). The paleontological data are insufficient to assess the levels of such gene flow or admixture, but the morphological mosaic of Zhiren 3 is most parsimoniously explained as the result of such populational processes. It is not easily accommodated into any Out-of-Africa with populational replacement scenario.

Behavioral Implications. At the same time, the evidence from Zhiren Cave indicates that the appearance of modern human morphology across Asia, by whatever populational process, took place in the context of a pre-Upper Paleolithic (*sensu lato*) cultural (technological and adaptive) system. At least in East Asia, modern human morphology was present >50,000 y before the emergence of Upper Paleolithic (*sensu lato*) archaeological assemblages (12, 39–41), whatever elements of “behavioral modernity” (42, 43) may or may not have been present in those pre-Upper Paleolithic cultural systems (12, 44).

In addition, the Zhirendong remains in South China during early MIS 5 imply a distribution of modern human biology across portions of East Asia in MIS 5 and subsequently up to the time of the pan Old World establishment of modern human biology in the middle of MIS 3. It therefore indicates a prolonged (>50,000 y) coexistence of late archaic and early modern humans across portions of Eurasia, and not just between Africa and Eurasia. Those late archaic humans include the Neandertals in western Eurasia until mid-MIS 3 (11). They also encompass MIS 3 archaic humans in central Asia and Siberia (45, 46) and into at

least MIS 5 in northern China (10, 47). This emerging pattern raises the question of what subtle behavioral patterns may have limited genetic exchange between these two morphologically defined groups of human across portions of Eurasia for tens of millennia.

Conclusion

The recent discovery of fragmentary human remains in Zhirendong (Zhiren Cave) in South China, securely dated to ≥ 100 kya, indicates that derived aspects of modern human morphology were present in East Asia in the early Late Pleistocene. It is in particular the anterior symphyseal morphology of the Zhiren 3 mandible, with its distinctly projecting tuber symphyseos, associated mental fossae, and modest lateral tubercles that aligns it with the derived morphology of early and recent modern humans. These features nonetheless occur in the context of a robust mandibular corpus.

These fossils therefore support previous populational scenarios for the emergence of modern humans that include populational continuity (to whatever degree) and admixture in East Asia, a version of the Assimilation Model. They indicate that the appearance of modern human biology in portions of western and eastern Eurasia occurred in the early Late Pleistocene, long before the appearance of Upper Paleolithic (*sensu lato*) behavioral complexes. They also further raise the question, long apparent for the western Old World, as to behavioral parameters underlying the apparent geographic separation of morphologically late archaic versus early modern human populations for tens of millennia.

Materials and Methods

The comparative assessment of the Zhiren Cave human remains was done using distributions of discrete traits [mentum osseum rank (24) and mental foramen position (35)], linear and angular morphometrics (48), symphyseal

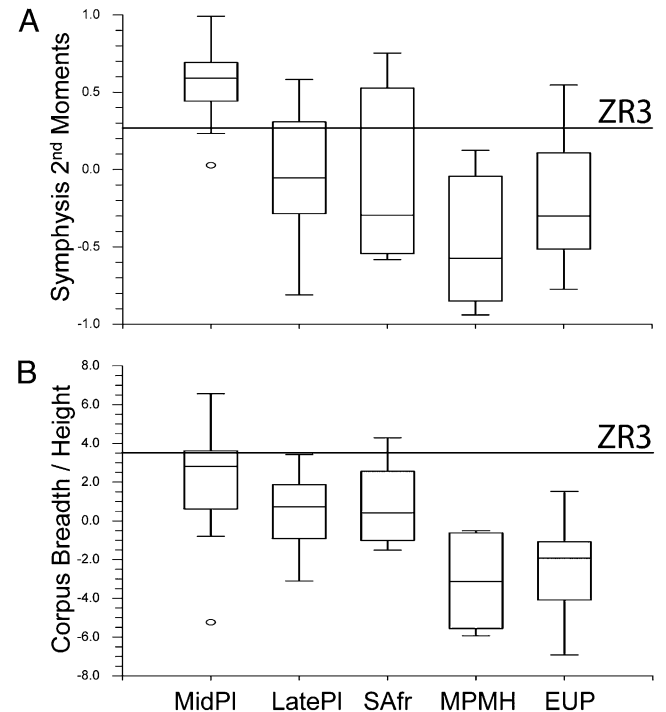


Fig. 4. (A) Residuals from the RMA line of the anteroposterior versus superoinferior second moments of area, and (B) residuals from the RMA line of the corpus breadth versus height at the mental foramen, for Zhiren 3 (ZR3) and comparative samples. Scatterplots of the original data are in *S1 Appendix*, Figs. S10 and S11. Sample abbreviations as in Fig. 2. The sample sizes for the two comparisons, from left to right, are: symphyseal second moments: 13, 25, 4, 4, and 20; lateral corpus breadth versus height: 25, 31, 5, 6, and 23.

cross-sectional geometry modeling it as a solid beam (24), and geometric morphometrics (49, 50) of the anterior and full symphyseal subperiosteal profiles. For the last two analyses, symphyseal cross-sections were obtained from the literature or from sections generated on original fossils or casts using either polysiloxane putty (Cuttersil Putty Plus; Heraeus-Kulzer Inc.) or a NextEngine Model 2020i Desktop 3D Scanner and Rapidworks software (NextEngine Inc.). In both sets of analyses, the symphyseal contours were analyzed oriented relative to the alveolar plane without Procrustes rotation (*SI Appendix*, Figs. S12 and S13).

The cross-sectional geometric properties were generated by projecting the cross-sections enlarged $\sim 10\times$ onto a Summagraphics 1812 tablet, digitizing the contour and computing the parameters with SLICE/SLCOMM (51, 52). The geometric morphometric analyses used landmarks (infradentale for the anterior profile and infradentale plus linguale for the full contour) plus equally spaced semilandmarks (14 and 28 respectively) and Generalized Procrustes Analysis (GPA) (but without rotation), Thin Plate Spline (TPS), and principal components analysis to generate relative warp scores by sample and specimen and consensus lines for each a priori sample. TpsDig2 (<http://life.bio.sunysb.edu/morph>) was used to generate the coordinates for the landmarks and semilandmarks, and TpsRelw (<http://life.bio.sunysb.edu/morph>) was used to carry out the relative warps analysis.

The Zhirendong human remains were compared principally to five paleontological samples (see *SI Appendix* for sample details): a pan-Old World

Middle Pleistocene sample, a western Old World Late Pleistocene archaic human sample (principally Neandertals), a later Pleistocene (MIS 6–4) sub-Saharan African sample, a Southwest Asian Middle Paleolithic early modern human sample, and a pan-Old World prelast glacial maximum earlier Upper Paleolithic modern human sample. The sub-Saharan African sample includes specimens which have been variously referred to as “late archaic” versus “early modern,” as they variably exhibit derived modern human versus generalized (but non-Neandertal) archaic human features (7, 8, 27–31). The Upper Paleolithic sample pools together specimens frequently separated into Early Upper Paleolithic and Mid Upper Paleolithic samples in western Eurasia (3). In the GPA and TPS analysis, a small sample of recent (mostly East Asian) humans are included for reference (*SI Appendix*, Figs. S12 and S13).

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