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Late Middle and Early Late Pleistocene Hominin Systematics

Diversity and Evolution of Archaic Eastern Asian Hominins: A Synthetic Model of the Fossil and Genetic Records

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ABSTRACT

With the discoveries of new hominin fossils from historically well-studied as well as poorly sampled regions, and thanks to great advances in paleogenetic studies, Asian paleoanthropology has now entered a new phase of research. In particular, fossil discoveries from insular Southeast Asia demonstrate unique pathways of hominin evolution that contrast markedly with the continental pattern, while new fossils from the latter region reveal the hitherto unrecognized great range of morphological diversity that characterized pre-*sapiens* Asian *Homo*. Furthermore, extensive analyses of Denisovan genomes offer a new framework in which the existing Asian fossil record can be interpreted. In this paper, we review these developments by first summarizing our current knowledge about each of the major hominin fossils from eastern Asia. We then present a large scaled craniometric analysis to determine the basic pattern of spatiotemporal variation of eastern Asian hominins from the late Calabrian (late Early Pleistocene) through the Late Pleistocene. Based on this, we discuss four issues: the question of *H. erectus* evolutionary continuity on Java during the Pleistocene, evidence for regional continuity vs. discontinuity in continental East Asian archaic *Homo*, which of the existing fossils from eastern Asia represent Denisovans, and whether there is fossil evidence for Denisovans across the Sunda Shelf of Southeast Asia, implying an oversea distribution.

INTRODUCTION

The 21st century has been a period of great advances in Asian paleoanthropology. There have been discoveries of hominin fossils from unexpected places such as the islands of Flores and Luzon off the Sunda Shelf, and the seabed off the coast of Taiwan (Brown et al. 2004; Chang et al. 2015; Detroit et al. 2019). Collectively, these and other findings reveal the great diversity of Pleistocene archaic hominins in this region (Figures 1 and 2). Additionally, paleogenetics has confirmed the previous claim for the presence of Neanderthals in the Russian Altai and demonstrated their co-occurrence—and indeed their genetic interaction—with another archaic hominin group called 'Denisovan' in this subarctic region (Krause et al. 2007; 2010; Kuzmin et al. 2022; Reich et al. 2010). Based on much of this information, one of us previously synthesized the knowledge of the time and formulated an evolutionary model of archaic hominin groups in eastern Asia (Kaifu 2017).

Since then, further discoveries of fossils and new analyses on the existing fossil collections were made, the chronology of some of these sites was refined and updated, and importantly, paleogenomic analyses have offered intriguing insights into the genetic structure of archaic Asian hominins. Particularly interesting is the molecular evidence that

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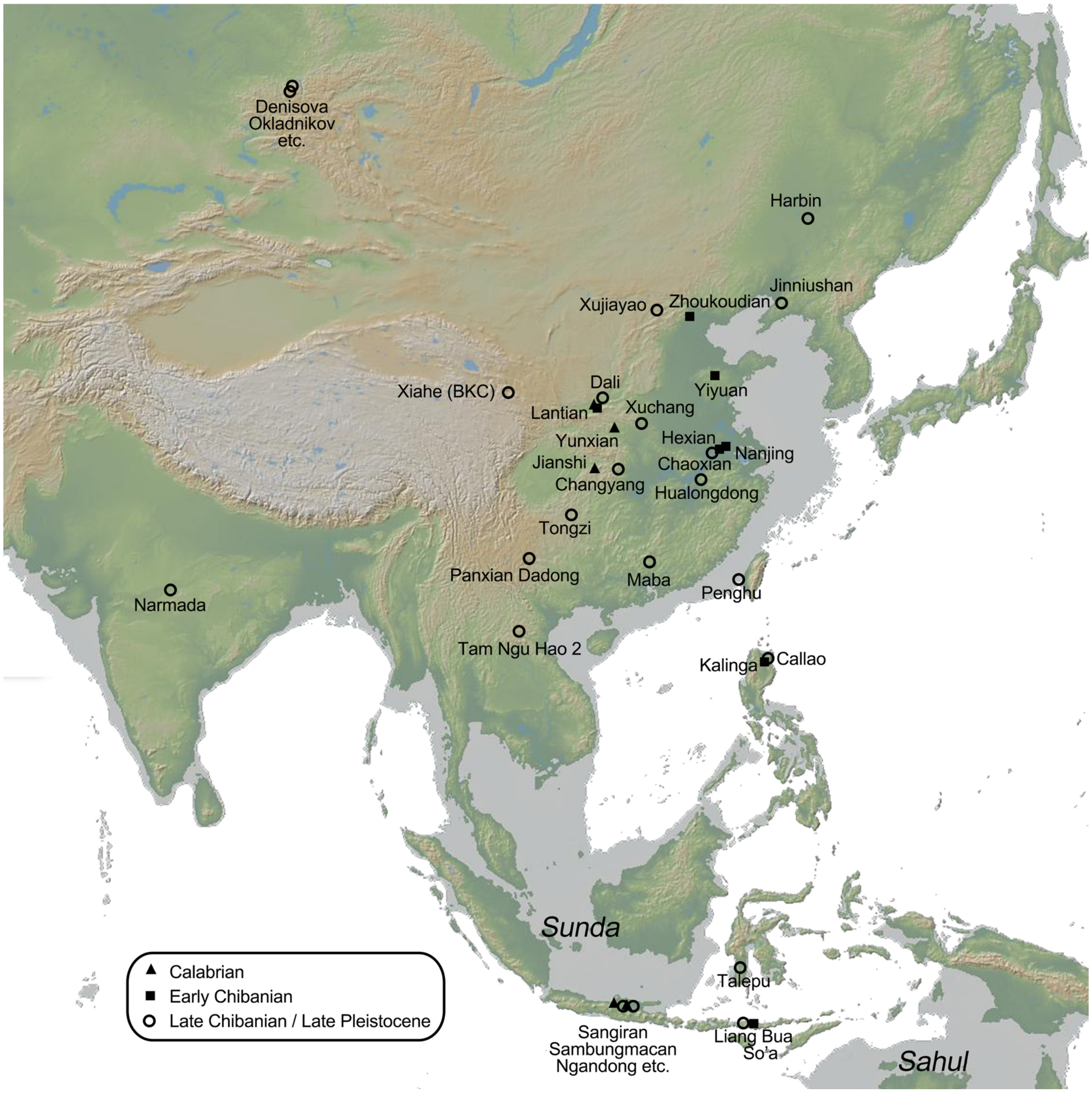


Figure 1. Map of the fossil localities discussed in this paper. The light gray areas are the continental shelves 0–100m below sea level. 'Lantian' includes Gongwangling and Chenjiawo. 'Yunxian' includes Quyuan River Mouth and Meipu. The base map was created using the GeoMapApp (www.geomapapp.org) / CC BY / CC BY (Ryan et al. 2009).

Denisovans were widespread in Late Pleistocene eastern Asia when there was a dispersal into this region by outside *Homo sapiens* group(s); that Denisovans were not a homogenous entity but included multiple genomically distinguishable regional populations; that several living populations share up to ~6% of DNA derived from Denisovans; and that the Altai Densiovans themselves experienced gene flow not only from Neanderthals but also from hitherto unidentified, 'super-archaic' hominins (Browning et al. 2018; Choin et al. 2021; Jacobs et al. 2019a; Jinam et al. 2017; Koganebuchi and Oota 2021; Larena et al. 2021a; Massilani et al. 2020; Peyrégne et al. 2024; Prüfer et al. 2014; Reich et al. 2011; Sawafuji et al. 2024; Teixeira et al. 2021). Furthermore, Denisovans were originally defined based on genomic sequences derived from fragmentary bones and teeth excavated from the Denisova Cave in the Russian Altai; since then, an archaic mandible from Tibet and a tooth from Laos have been assigned to this mysterious archaic hominin group—the former on the basis of ancient protein analysis and the latter based on dental morphology (Chen et al. 2019; Demeter et al. 2022). This departs from the way that ancient hominin populations such as Neanderthals and *Homo erectus* have historically been defined—i.e. morphologically—and we address this in later sections.

Paleoanthropologists have traditionally recognized that most eastern Asian archaic *Homo* fossils from late Chibanian contexts are morphologically different from local *H. erectus*. For example, cranial specimens from East and South Asia (Dali, Jinniushan, Maba, Narmada, etc.) still exhibit primitive traits such as a low lateral profile and variably developed supraorbital torus, but tend to have enlarged cranial capacity, slightly more rounded cranial vault, reduced postorbital constriction, more or less gracile supraorbital torus, etc. (Athreya and Wu 2017; Etler 1996; Kenne-

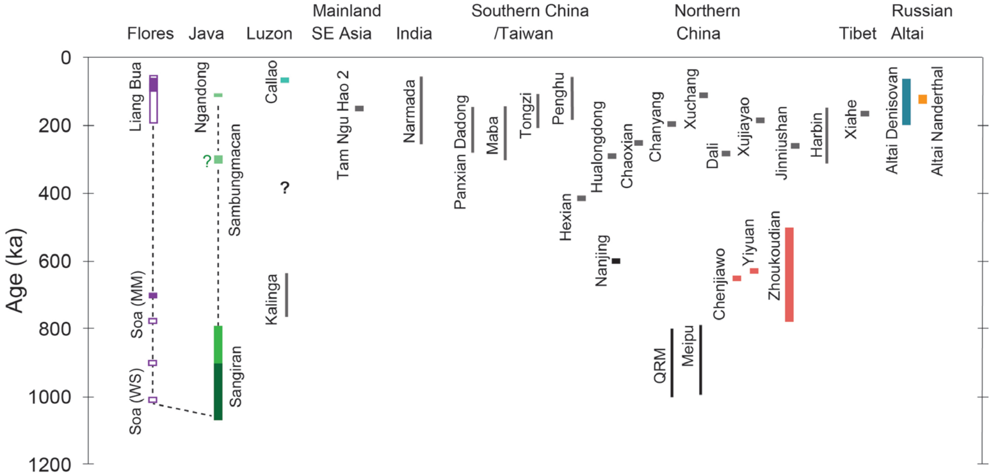


Figure 2. Chronology of the archaic Asian hominin fossils discussed in this paper. Filled squares represent fossil specimens, and open squares cultural remains. Specimens with uncertain provenance and/or numeric age with a very large error range are indicated by "?". Error ranges are not shown. The long squares are probable time ranges. Selected proposed p-demes are indicated by the same colors. See the text for the sources of the chronological data.

dy et al. 1991; Li et al. 2017; Wolpoff 1999; Wu and Athreya 2013; Wu and Poirier 1995; Wu and Wu 1985; Wu et al. 2019; 2022). These 'late' or 'post-*erectus* grade' archaic *Homo* have been interpreted in several different ways (Athreya and Hopkins 2021). Some researchers regard them as descendants of local *H. erectus* with possible gene flow from western Eurasia following a braided-stream model of hominin evolution for this time period in East Asia (Athreya and Wu 2017; Etler 1996, 2006; Pope 1992; Roseberg and Wu 2013; Wolpoff 1999; Wu 2014). Others have cautiously suggested that some of them (Dali, Jinniushan, etc.) belong to *H. heidelbergensis*, a taxon defined for Euro-African fossils such as Mauer, Arago, Petralona, Bodo and Kabwe (Rightmire 1998, 2015; Stringer 2012; Tattersall and Schwartz 2009). Those researchers who emphasize the variation within the East Asian sample have suggested that Dali, Jinniushan, and Maba belonged to their own paleodemes (p-demes), respectively (Howell 1999). Additionally, there is a controversy as to whether *H. erectus* persisted in Java throughout the Chibanian or if the local terminal Chibanian hominins from Ngandong and other sites represent their own evolving lineage unrelated to *H. erectus* (as defined by the Trinil 2 skullcap) (Zeitoun et al. 2010).

Now, genetic information offers us a useful premise to further advance this discussion. The evidence of multiple Denisovan introgressions into the genomes of modern Asia-Pacific populations strongly suggest that Denisovans — a sister group to Neanderthals that emerged ~390–440 ka (Prüfer et al. 2017) — were once present as multiple regional lineages in a wide area of this region during the late Chibanian (Browning et al. 2018; Jacobs et al. 2019a). Therefore, if we can identify Denisovan remains in the existing hominin fossil sample from this region, we will be able to discuss their genetic structure and evolutionary history using the available genetic information about Denisovans. Morphological identification of Denisovan fossils in the absence of direct genetic data from these specimens can be approached from two different directions. First, with reference to the fossils whose Denisovan identity is confirmed/suggested from molecular evidence, we can examine in detail to identify uniquely Denisovan morphological characters. In this context, the isolated molars from Denisova cave (Denisova 2, 4, and 8) as well as the Xiahe mandible can be used as reference fossils. Second, if we accept the genetic inference that Denisovans formed a sister clade with Neanderthals with their population split time around the mid Chibanian (Prüfer et al. 2014; 2017), those hominins that can be safely supposed to have descended from local *H. erectus* cannot be Denisovans (see Discussion for alternative interpretations). The latter approach does not directly identify Denisovans but is useful to narrow down candidate members of this group within the sample. The question as to which fossils represent Denisovans leads to further interesting questions. For example, how widespread were they? Did they live in the Sunda Shelf and its nearby islands? If the robust Xiahe mandible represents a Denisovan, what does it imply in terms of age, geographic distribution, and evolutionary history of this population?

Given the importance of these new questions that follow on the latest finds, we update the model offered by Kaifu (2017). The major purpose of this synthesis is to construct a reasonable scheme about paleodemes (p-demes: Howell 1999) in Asia based on fossil morphology. We then discuss possible evolutionary relationships among such p-demes and seek candidates of Denisovans and descendants of local *H. erectus* among the Chibanian hominin fossils from eastern Asia. In other words, by superimposing genetic evidence onto the fossil record from this region, we attempt to advance our knowledge about the Pleistocene hominin evolution in eastern Asia and refine hypotheses regarding the evolutionary history of *Homo* in eastern Eurasia for future testing.

SPECIES OR PALEODEMES?

Chibanian hominins in this region display a high level of craniodental variability that has defied efforts to categorize and name groups along morphological lines. Among paleoanthropologists, there is no consensus on how many species are present in the sample, and where the species boundaries should be drawn; we are not seeking to weigh in on these questions in this paper. This lack of consensus does not, to us, have a chance of being resolved by more or better arguments because the concept of species is itself a culturally constructed one (Athreya and Hopkins 2021). Given the subjectivity and uncertainty around the species question, we prefer to focus on reconstructing what *can* be known from the current data. We therefore follow Howell (1999) and will explore paleodemes (p-demes) in the fossil record. A deme is a communal interbreeding population within a species, and p-deme refers to local populations of fossil taxa that are inferred to have shared a closer gene pool than their geographically and temporally more distant relative populations (Antón et al. 2016; George 1971).

We first formulate how p-demes are recognizable in Pleistocene eastern Asia based on a literature survey. We then present our own craniometric analysis to discuss possible evolutionary scenarios for these hominins. Following convention, we call fossils from Java and northern China (Zhoukoudian Locality 1 and nearby sites) *H. erectus*, but do not propose taxonomic names for a series of post-*erectus*-grade archaic hominins from China and India ('late archaic *Homo'* from Dali, Jinniushan, Narmada, and so on).

ARCHAIC HOMININ PALEO-DEMES IN EASTERN ASIA

LATE CALABRIAN *H. ERECTUS* FROM JAVA (SANGIRAN LOWER AND SANGIRAN UPPER P-DEMES)

Craniodental Variation at Sangiran

A large number of cranial, mandibular, and dental remains are available from the radiometrically and paleomagnetically dated sequences from Sangiran, Trinil, and Mojokerto. Among them, the fossil collection from Sangiran is central to this discussion. However, we first discuss Trinil due to its taxonomic and historical significance in establishing the species *Homo erectus*.

Trinil is the site from where the type specimen of *H. erectus* (the Trinil 2 skullcap) was excavated in 1892. Recent bibliographic surveys coupled with field and laboratory studies have successfully reconstructed some details about the original excavations of the 1890s and 1900s (Huffman et al. 2022; Pop et al. 2023). These studies demonstrate the site's complex stratigraphy and the presence of multiple fossiliferous layers at Trinil. The latter holds the keys to obtaining reliable depositional ages for the fossil remains (Berghuis et al. 2021; Hilgen et al. 2023; Pop et al. 2023). Pop et al. (2023) and Hilgen et al. (2023) have cautiously concluded that Trinil 2 and four hominin leg bones (Femora II-V) were probably from the basal conglomerate 'Bone-Bearing Channel 1,' which is tentatively dated by magnetostratigraphic and ^{40}Ar/^{39}Ar dating methods to 830–773 ka.

The Sangiran Dome area in Central Java has a rich hominin fossil record that spans over ~300,000 years. Two geological formations provide geological context for the Sangiran hominin fossils—the younger Bapang formation and the older underlying Sangiran formation. All of the hominin fossils were recovered from ~50-m-thick sediments between the Upper Tuff complex in the Bapang Formation, and Tuff 11 at the topmost part of the underlying Sangiran Formation (Itihara et al. 1985) (Figure 3). The Grenzbank zone is a key lithostratigraphic marker bed situated at the bottom of the Bapang Formation. The older hominin fossils collected from either the Grenzbank zone or the underlying Sangiran Formation exhibit some primitive craniodental morphology compared to the younger fossil assemblage from the levels above the Grenzbank zone (Kaifu et al. 2005; 2010). We refer to them here as the 'Sangiran Lower (Grenzbank/ Sangiran)' and 'Sangiran Upper (Bapang-AG)' hominin fossil assemblage, respectively with the latter being geologically younger.

The two assemblages are usually regarded as reflecting temporal variation within *H. erectus* because their cranial morphology is generally similar to that of Trinil 2, but the chronological difference is so substantial that we believe the two samples should be treated separately. Compared to the Gelasian (early Early Pleistocene) early *Homo* in East Africa (*H. habilis sensu lato*) and ~1.77 Ma *Homo* from Dmanisi, Georgia, the Lower Sangiran fossils are derived. They show larger cranial capacity, increased cranial robusticity, advanced cranial form (see below), a slightly wider dental arcade, non-elongated first molars, and reduced postcanine tooth size. However, this sample is distinctly more primitive compared to the Sangiran Upper group of *H. erectus*—the Sangiran Lower group exhibit a smaller cranial capacity, a more robust mandibular body and everted mandibular lateral corpus, and larger postcanine tooth size, among other traits.

Schwartz and Tattersall (2005) also noted great morphological diversity in the Sangiran sample and recognized two closely related but different morphs within it, which they called the Trinil/Sangiran 2 morph and the Sangiran 17 morph. Sangiran 17, the best-preserved cranium of Javanese *H. erectus*, has been noted by many researchers as morphologically unique, and there is general agreement that it represents transitional morphology that links between Sangiran and post-Sangiran *H. erectus* in Java (Jacob 1973b; Kaifu et al. 2008; 2013; Santa Luca 1980; Sartono 1975). As a support for this view, this is one of the youngest hominin cranial specimens recovered from the Sangiran Dome area (Itihara et al. 1985; Matsu'ura 1982).

Additional features characterizing the Sangiran Lower group are the great degree of variation in cranial bone thickness, cranial surface structures (e.g., strong vs. mild development of sagittal keel, occipital protuberance, etc.), and mandibular robusticity (Kaifu et al. 2010). This elevated diversity led some researchers to claim the coexistence of multiple hominins in the Lower Sangiran fossil sample

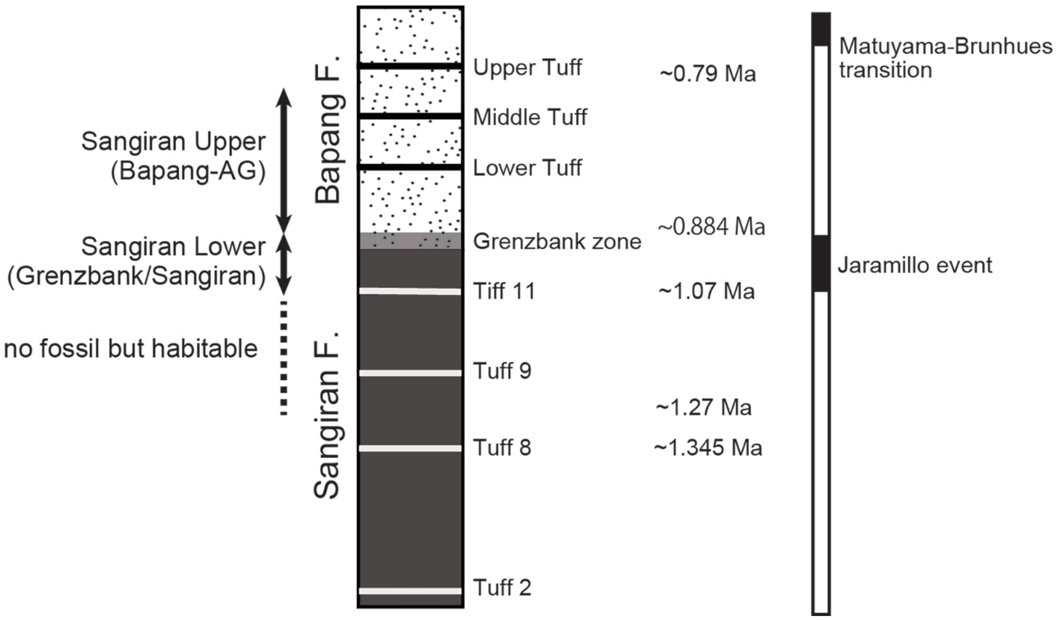


Figure 3. Hominin fossil-bearing zone (the double arrows) and chronology in the Sangiran Dome area. Chronological data based on Matsu'ura et al. (2020).

(e.g., *Meganthropus palaeojavanicus*, *Pithecanthropus* (*Homo*) *dubius*: Von Koenigswald 1950; Weidenreich 1945) and even the occurrence of a non-hominin species within the sample (Zanolli et al. 2019), although this last view is based solely on post-canine dental features and without any comparison to early African *Homo*. An alternative, more likely interpretation is that the assemblage consists only of *H. erectus* with a high degree of sexual dimorphism which is a primitive feature of the genus *Homo* (Kaifu et al. 2010) and is similar to what has been suggested for Dmanisi (Lordkipanidze et al. 2013). At a minimum, we can be sure that a primitive form of *Homo* is present in the lowest hominin-bearing zone of Sangiran. The cranial morphology suggests that Trinil 2 may have been a gracile member of the population represented by this Sangiran Lower group (Kaifu et al. 2010), but their contemporaneity has not been established (Hilgen et al. 2023) so at the present stage of research this is an inference.

To summarize what we know about the oldest Javanese assemblages from Sangiran and Trinil, two chronologically successive p-demes can be proposed—Sangiran Lower and Sangiran Upper. The two share similar cranial form and have been traditionally grouped together as a single regional population of *H. erectus*, but the morphological differences between the two chronological samples are considerable as summarized above. They probably represent different time bands of the single evolving lineage of *H. erectus*. Trinil 2 may belong to the older group, but this association remains tentative until a more reliable age is obtained.

Geochronology at Sangiran

An important recent advance regarding the Sangiran fossil record is its updated chronology. The Matuyama-Brunhes polarity transition has been securely identified within the Upper Tuff complex of the Bapang Formation based on densely sampled palaeomagnetic analyses (Hyodo et al. 2011). These ages indicate that the uppermost hominin-bearing sediments at Sangiran are ~0.78 Ma. Ages for two other key beds below—the Grenzbank zone and Tuff 11—are more contentious, but probably do not far exceed 1.1 Ma based on a few lines of evidence. In 2001 Larick and colleagues (2001) reported hornblende ^{40}Ar/^{39}Ar ages of ~1.51 Ma for pumice samples collected from immediately above the Grenzbank zone. However, these may have been affected by natural reworking and/or a temporal gap between mineral crystallization and volcanic eruption. So, to overcome this potential problem and find out the eruption age of the targeted tuff horizons, Matsu'ura et al. (2020) later combined fission track and U-Pb dating. Taken together with the magnetostratigraphy and ^{40}Ar/^{39}Ar ages for the bottom of the Sangiran Formation (Lower Lahar), their results strongly suggest that the Grenzbank zone is ~0.9 Ma and the Jaramillo subchronozone (1.07 Ma) lies near Tuff 11. This chronology is also supported by an astronomical age model recently attempted by Hilgen et al. (2022).

Given this evidence, the terrestrial Cosmogenic Nuclide ages for the Grenzbank zone reported by Husson et al. (2022) of 1.78±0.35 Ma are difficult to reconcile. As Husson et al. (2022) themselves noted, if this extremely old age is correct, we then have to explain the dramatic change in the local sedimentation rate. It would require that the ~100-m-thick Sangiran Formation was deposited in less than 0.1 Ma in a shallow marine/swampy environment (>1mm/a) while the ~40-m-thick middle-lower Bapang Formation accumulated during ~1.0 Ma in a fluvial environment (~0.04mm/a) (Brasseur et al. 2015; Itihara et al. 1994). More to the point of this paper, the larger cranial capacity and advanced cranial form in Java (~860 cc) would be older than the ~1.77 Ma *Homo* from Dmanisi, which exhibits far more primitive traits and has a cranial capacity of ~634 cc (Kaifu et al. 2010). Therefore, the current best estimates for the Sangiran Lower and Upper hominin assemblages are 1.1–0.9 Ma and 0.9–0.8 Ma, respectively.

One final note: Matsu'ura et al. (2020) suggested the possibility that the lower age limit for these fossils could extend back to ~1.3 (<1.45) Ma if habitability (and dating error rage) is considered. This means that the area became habitable for terrestrial mammals around that time through a transition from marshy to drier environments (Brasseur et al. 2015), although hominin fossils are yet to be discovered/demonstrated from this lower stratigraphic zone in Sangiran. However, the absence of fossils here, as well as the above hominin chronology for Sangiran, do not mean that there were no hominins on Java by that time. Other areas in this part of the uplifting Sunda Shelf may have been accessible and habitable by hominins substantially earlier than the Sangiran evidence, although such evidence is weak at present (Huffman et al. 2006; Hyodo et al. 1993; Morwood et al. 2016).

LATE CHIBANIAN *H. ERECTUS* FROM JAVA (NGANDONG/SAMBUNGMACAN/NGAWI P-DEME)

After the Sangiran Upper assemblage, a large chronological gap exists in the Javanese hominin fossil record. Specimens from the Chibanian contexts of Java are known from Ngandong (12 crania and 2 tibiae), Sambungmacan (3 crania and 1 tibial fragment), and Ngawi (1 cranium). The depositional age for the Ngandong hominin assemblage was recently constrained to 117,000–108,000 years ago by an elaborate combination of uranium-series, luminescence, ^{40}Ar/^{39}Ar, and electron-spin resonance dating techniques (Rizal et al. 2020). The ages of Sambungmacan and Ngawi still remain controversial, but they are generally regarded as contemporaneous with or older than Ngandong on the basis of limited geological survey, morphological similarities with Ngandong, and some radiometric dating (Antón 2003; Baba et al. 2003; Kaifu et al. 2008; 2015c; Yokoyama et al. 2008). Because our ongoing field study indicates that these fossils are likely derived from the fluvial deposits formed by the ancient Solo River, we assume that they are somewhat older than the Ngandong fossils that were excavated from the terrace deposits along the present-day Solo River (Huffman et al. 2010). In Figure 2, the ages of Sambungmacan and Ngawi are tentatively placed at the later Chibanian (~0.3 Ma).

Because no facial (except for the supraorbital region and nasal root), mandibular, or dental remains have been reported from Ngandong, Sambungmacan, and Ngawi, their taxonomy must rely on the neurocranial morphology. Within this limit, researchers agree that these specimens are distinguishable from the Sangiran/Trinil group and similar to each other. Such shared cranial features include, but are not limited to, a larger cranial capacity, a wide frontal squama (reduced postorbital constriction), laterally thickened supraorbital tori that are bar-like and laterally continuous, an elongated midcranial base region, a prominent postcondyloid tuberosity, a V-shaped posterior margin of the foramen magnum (opisthionic recess), and the loss of postglenoid process and other specialized morphologies in the mandibular fossa (see Kaifu et al. 2008 for more details). Therefore, there is general agreement that the hominins from Ngandong, Sambungmacan, and Ngawi constitute a single morph or p-deme (Ngandong/Sambungmacan/Ngawi p-deme) (e.g., Antón 2002; Baab and Zaim 2017; Baba et al. 2003; Delson et al. 2001; Durband 2006; Jacob 1978; Kaifu et al. 2008; 2015c; Kubo 2022; Schwartz and Tattersall 2005; Widianto and Zeitoun 2003).

Current issues in dispute are how to interpret the minor variation observed within this group (i.e., within-population vs. diachronic variation), and their evolutionary relationship with the earlier Sangiran/Trinil *H. erectus* (i.e., evolutionary continuity vs. discontinuity in Java). For the supporters of evolutionary continuity, the Ngandong/Sambungmacan/Ngawi p-deme is a temporal variant of Javanese *H. erectus* that had experienced gradual evolution in this region beginning at least one million years ago (since the late Calabrian) (Antón 2002, 2003; Baba et al. 2003; Kaifu et al. 2008; Kidder and Durband 2004; Weidenreich 1943; Wolpoff 1999), although not necessarily in a linear way (see Baab and Zaim 2017). A different version of this view is anagenetic speciation in this Javanese lineage (Durband 2008) but we here do not take this standpoint.

For the supporters of evolutionary discontinuity, this p-deme is another species, *Homo soloensis*, which had replaced *H. erectus* sometime during the Chibanian. This view was most recently put forth based on a combination of morphometric and cladistic analyses (Zeitoun et al. 2010) but has not received widespread support for several reasons. First, the majority of studies of the Pleistocene Javanese material have not found clear evidence for morphological discontinuity, as detailed above. In addition, this conclusion is driven mostly by cladistic analyses, which rest on a few deeply problematic assumptions. The 123 morphological and 345 metric features scored in Zeitoun et al.'s 2010 study, for example, illustrate how cladistics treats multiple correlated traits as independent lines of evidence for a given conclusion, while statistical studies can account for this basic violation of the assumption of independence using Principal Components Analysis (Athreya and Glantz 2003). Second, the subtle or overlapping range of variation present between the earlier and later Javanese samples cannot be observed when using cladistic methods. In theory ,the ambiguity would be reflected in several different but equally parsimonious trees. However, in practice, the researcher focuses on a single tree—either a consensus one, or a single "most" parsimonious one, that is, in reality, not necessarily representative of the true phylogeny and may not even be statistically supported. In addition, cladistics rests on the assumption that evolutionary change takes the most parsimonious path, but on an island such a Java, variation very well could have been shaped by drift due to geographic isolation and small population sizes—meaning character state reversals are more likely. In sum, within the current limit that no facial, mandibular, and dental materials are available from the Chibanian contexts of Java, there is no sufficient evidence to support the argument for evolutionary discontinuity in Java, so here we treat them as a younger variant of the Javanese *H. erectus* p-deme.

OFFSHORE ISLANDS IN SOUTHEAST ASIA (LIANG BUA AND CALLAO P-DEMES)

The Liang Bua p-deme is defined by the skeletal remains of *H. floresiensis*, a small-brained, diminutive hominin species excavated from a limestone cave at Liang Bua on the island of Flores (Brown et al. 2004; Morwood et al. 2005; Morwood and Jungers 2009; Morwood et al. 2004). The recently revised chronostratigraphy suggests that these skeletal remains date to between ~100–60 ka, and the cultural remains attributed to this species are between ~190–50 ka (Sutikna et al. 2016; 2018). The skeleton of *H. floresiensis* displays a distinct combination of primitive, derived, and unique morphological features (Brown and Maeda 2009; Brown et al. 2004; Jungers et al. 2009a; b; Kaifu et al. 2011a; 2015a; Larson et al. 2007; Larson et al. 2009; Morwood et al. 2005; Orr et al. 2013; Tocheri et al. 2007), although the unknown effect from insular dwarfism complicates efforts to interpret them.

In the past 12 years, several detailed examinations of the craniodental morphology as well as craniometric analyses have demonstrated *H. floresiensis*'s close affinities with *H. erectus*, particularly the more primitive Sangiran/Trinil group (Baab et al. 2013; Kaifu et al. 2011a; 2015b). Studies based on cladistic and Bayesian phylogenetic approaches using numerous character states and/or measurements tend to suggest its close relationship with *H. habilis/rudolfensis* (Argue et al. 2009; 2017; Dembo et al. 2015; 2016). Expanding on our discussion above, we believe that character state studies will need to account for the influence of size on shape, confirm repeatability across researchers, and incorporate the issue of character correlation in order to be more reliable (see, for example, Rightmire 2013), for an endeavor to resolve this issue).

A fragmentary but much older hominin fossil collection is from the Mata Menge site in the So'a Basin, central Flores. It is comprised of an adult mandibular fragment, eight isolated teeth, and an adult humeral fragment belonging to at least four individuals (Kaifu et al. 2024; van den Bergh et al. 2016a), which were excavated from a fluvial sandstone layer securely dated to ~0.7 Ma (Brumm et al. 2016; van den Bergh et al. 2022). These fossils are similar to Liang Bua *H. floresiensis* in dimensions and morphological characteristics except for the mandibular first molar that retains a more primitive condition (Kaifu et al. 2024; van den Bergh et al. 2016a). Although the lack of hominin cranial and other elements has hampered a firm taxonomic classification, an allocation as one of the time-successive p-demes of the local *H. floresiensis* lineage is reasonable and well-supported within the limited data from the region. Interestingly, the Mata Menge mandible, molars, and humerus are even smaller in size than those of the two existing *H. floresiensis* individuals from Liang Bua (Kaifu et al. 2024; van den Bergh et al. 2016a). In addition, simple stone artifacts from the same basin were discovered at Wolo Sege, Mata Go, Kobatuwa, Boa Leza, and Mata Menge and are dated to between ~1.0 and ~0.7 Ma, but no artifacts are known from the deposits older than 1.27 Ma. The local faunal record suggests a turnover of *Stegodon* species between 1.27 and 1.0 Ma, after which the faunal elements remain relatively stable on Flores until the arrival of *H. sapiens* in the Late Pleistocene (van den Bergh et al. 2022).

Taken together, and with reference to the recently revised chronology for Javanese *H. erectus* summarized above, a plausible scenario is that *H. floresiensis* was a continuous evolving lineage that spanned about one million years on Flores. Its ancestral population was closely related to early Javanese *H. erectus* and arrived on Flores shortly after Java was occupied by the latter. That ancestral population experienced insular dwarfism within a relatively short period but retained some primitive cranial, mandibular, and mandibular premolar morphologies through the Pleistocene (see also below). Ongoing field research in the So'a Basin will further illuminate the origin and evolution of this insular species. Interestingly, stone artifacts have also been found from late Chibanian contexts further north at Talepu, Sulawesi, confirming the presence of hominins there during this period as well (van den Bergh et al. 2016b).

At the northernmost reach of Island Southeast Asia is the Philippines' island of Luzon, where flaked stones and cores as well as a cut-marked skeleton of a rhinoceros were unearthed from the ~0.7 Ma sediments at Kalinga, Cagayan Valley (Ingicco et al. 2018). Not far away from this site, at Callao Cave, extremely small-sized hominin teeth and postcranial elements were excavated and directly dated by uranium-series ablation to >50–67 ka. These were reported as a new species, *H. luzonensis* (Detroit et al. 2019; Mijares et al. 2010). The anatomical remains, although quite limited, show a combination of primitive, derived, and unique features. Overall, the authors report that its small size parallels *H. floresiensis* and that the maxillary premolar-molar row shows reductive trends that recall *H. erectus*, *H. floresiensis*, and *H. sapiens*, while the phalanges show some affinities with *Australopithecus*.

A more recent detailed study on the Callao Cave dental remains emphasized affinities with Sangiran *H. erectus* and concluded that *H. luzonensis* probably evolved from some *H. erectus* groups that dispersed to the various islands of Southeast Asia and became isolated, leading to endemic speciation (Zanolli et al. 2022). Although morphological differences between *H. floresiensis* and *H. luzonensis* are slight in the available limited fossil sample, such a speciation event is plausible given the geographic separation between Flores and Luzon and the natural isolation of island populations (see Figure 1). That is why, on this basis, we identify an independent Callao p-deme in the Late Pleistocene of Luzon. Taken together, these recent discoveries demonstrate that there was a wide geographic distribution of archaic hominins in insular Southeast Asia during the late Calabrian and throughout the Chibanian periods.

CALABRIAN *HOMO* FROM CONTINENTAL EASTERN ASIA

Calabrian archaic hominin fossils from continental eastern Asia are restricted to several fragmentary and/or distorted specimens from China. These include isolated teeth from Jianshi, Yuanmou, and Yunxian (Meipu), and distorted cranial remains from Lantian (Gongwangling) and Yunxian (Quyuan River Mouth), which have been dated by using biostratigraphy, magnetostratigraphy, and radiometric methods. The most complete of these are the one partial and two nearly complete cranial remains recovered from Lantian/Gongwangling (~1.63 Ma) and Yunxian/Quyuan River Mouth (~1.0–0.8 Ma?), respectively. Unfortunately, all three are heavily distorted so it is difficult to draw meaningful morphological information.

The Gongwangling specimen (PA 105), as reported by Wu (1966) and Wu and Dong (1985), appears to be primitive relative to Zhoukoudian *H. erectus* showing pronounced postorbital constriction. In addition, its thickened cranial bones are comparable to the thickest crania from Java (Sangiran 27 and Sangiran 31, both of which are from the lowest hominin fossil bearing zone: Y.K., personal observation), although this character may have been influenced by the taphonomic distortion (Brown 2001) and the published low-resolution CT scan does not help to dismiss this concern (Shang et al. 2008). The reported small cranial capacity (~780cc: Wu 1966) is a (very) rough estimate from a complex reconstruction. The bony labyrinth of Gongwangling is typical for the genus *Homo* with none of the specialized morphology observed in Neanderthals or Xujiayao (Wu et al. 2014). As for the Yunxian/Quyuan River Mouth specimens (EV 9001 and EV 9002), the digital reconstruction gives an endocranial capacity for EV 9002 as ~1050cc (Vialet et al. 2012) and also supports the original report that postorbital constriction for this specimen is less pronounced than in Zhoukoudian *H. erectus* (Li and Etler 1992). Both are said to exhibit *H. erectus*-like receding frontal squama and robust supraorbital tori, and to share this with Gongwangling. However, the cranial shape of the Yunxian/Quyuan River specimens is still difficult to analyze due to the remaining distortion.

As for the dental materials, detailed morphological analyses have so far been performed for the maxillary teeth associated with the Gongwangling cranium (~1.63 Ma) and the four isolated teeth from Yunxian/Meipu (0.99–0.78 Ma). Pan et al. (2022) described the former and reported that the Gongwangling M^2 and M^3 are characterized by moderate crown size and EDJ morphology similar to mid-Chibanian Chinese fossils such as Hexian, Yiyuan, and Zhoukoudian. However, their highly divergent molar roots are different from Zhoukoudian and more similar to other Calabrian *Homo* specimens as well as the Chibanian fossil from Hexian which, as we discuss in more detail below, exhibits several unusual morphologies for its geological age. According to Xing et al. (2021), the maxillary premolar and molar from Meipu share primitive occlusal crown shape with African early *Homo* (a mesiodistally broad lingual cusp of P^4 and a squarish crown contour of M^1), whereas the incisors are similar to *H. erectus* from Zhoukoudian, Sangiran, etc., showing moderate (I^1) or strong (I_2) labial surface convexity.

In summary, the eastern Asian continental fossil evidence is far too poor to deduce the local Calabrian p-demes and their evolutionary relationship with the succeeding Chibanian hominins. Still, recent detailed studies suggest the presence of some primitive cranial features at ~1.63 Ma (Gongwangling), and the persistence of some primitive dental morphologies until the terminal Early Pleistocene (Meipu), with sporadic signals of possible derived morphologies that prefigure the Chinese Chibanian hominins.

EARLY CHIBANIAN *H. ERECTUS* FROM NORTHERN CHINA (ZHOUKOUDIAN P-DEME)

Zhoukoudian

The vast cranial, mandibular, dental, and some postcranial remains from Zhoukoudian Locality 1 are both historically and qualitatively central to defining a regional group of *H. erectus* in northern China. This fossil sample, excavated from the ~40-m-thick sequence that records the local evolutionary history during the early Chibanian (~0.78–0.45 Ma) (Shen et al. 2001; 2009; but see Chen and Zhou 2009 who suggested younger ages), display little, if any, chronological variation (Etler 1996; Pope 1992; Weidenreich 1943; Wolpoff 1999; Wu and Dong 1985; Wu and Poirier 1995; Wu et al. 2010). The inclusion of all fossil specimens into 'Zhoukoudian *H. erectus*' is thus uncontested. A question that cannot be answered clearly is the geographic range of 'northern Chinese *H. erectus*' represented by the Zhoukodian assemblage, as summarized below.

The Zhoukoudian cranial remains are distinguishable from all specimens of Javanese *H. erectus* by a series of features such as a marked supratoral sulcus, a steeply rising frontal squama with salient tuberosities, a narrow occiput, a laterally projecting suprameatal crest, and markedly inclined temporal walls (Antón 2002; Baab 2010; Kidder and Durband 2004; Reightmire 2013; Santa Luca 1980; Weidenreich 1943, 1951). This, in addition to the geographic distance of ~5000km, is the primary basis that distinguish them as two regional groups or demes of *H. erectus*.

Yiyuan, Chenjiawo (Lantian), Nanjing, and Zhoukoudian (ZKD) p-deme

Previous preliminary reports and craniometric analyses emphasized morphological similarities between Zhoukoudian and other specimens from China, specifically: a) a partial cranium from Yiyuan (Etler 1996), b) a mandible from Lantian/Chenjiawo (Woo 1964), c) a partial crania from Nanjing (Tangshan) (Antón 2002; Etler 1996; Wu and Li 2002; but see Cui and Wu 2015; Liu et al. 2005; Vialet et al. 2010 for opposing views), and, d) the distorted Yunxian/Quyuan River Mouth specimens described above (Li and Etler 1992; Pope 1992; Wu and Poirier 1995). These inferences are now being tested by detailed descriptions and comparisons, micro-CT-based imaging, and geometric morphometric analyses of the dental remains. Through a series of such studies, Xing and colleagues (2014; 2016; 2018) suggest that the following dental features characterize East Asian Chibanian *H. erectus* represented by Zhoukoudian and other sites:

1. I^1 with moderately convex labial surfaces, tuberculum dentale associated with several finger-like prolongations, and pronounced shoveling;
2. subequal mesiodistal breadths of the buccal and lingual cusps of P^3 and P^4;
3. M^1 and M^2 have trapezoidal contour with an oblique buccal side (buccally expanded mesiobuccal corner);
4. rounded and bucco-lingually expanded M_2;
5. rare occurrence of the middle trigonid crest on M_1;
6. shelf-like protostylid and mesial protoconid ridge at the EDJ on M_1 and M_2;
7. robust "column-like" dental roots in general; and,
8. highly developed crenulation on the outer enamel surface, enamel-dentine junction (EDJ), and the underlying roof of the pulp cavity on M_1 and M_2.

Although these features are more or less shared with other archaic hominin groups, according to these authors, the last feature, which is expressed as wrinkled I^1 labial surface and "dendrite-like" crenulation in the occlusal basin of mandibular molars, is unique to Zhoukoudian, Yiyuan, Hexian, and Xuchang. Therefore, this feature may be a key dental character that defines "Chinese *H. erectus*" (Xing et al. 2018) (but see below for a different placement of Hexian).

Considering the above situation, it is probably safe to include Yiyuan and Chenjiawo into northern Chinese *H. erectus* (primarily represented by Zhoukoudian). Given the spatio-temporal proximity among them, this group can be regarded as the 'Zhoukoudian (ZKD) p-deme' following the terminology of Howell (1999), although the contents are somewhat different from his delineation. Depending on if Nanjing is included or excluded from this group, the fossil-based geographic range of the Zhoukoudian p-deme is restricted to the Yellow River basin or could extend southward to the Yangtze River basin. The situation south of the Yangtze River basin is presently unknown due to the lack of fossil evidence. How the Yunxian/Quyuan River Mouth and other Calabrian fossils from China are related (or not related) to the Zhoukoudian p-deme, as well as their evolutionary origin are also among the unresolved questions at the current stage of research.

MID-CHIBANIAN HOMO FROM HEXIAN

A well-preserved neurocranium (PA 830), fragmentary mandible (PA 831), and isolated dental remains (PA831-839) excavated from the cave of Longtandong, Hexian Country in southern China, deserve attention here because of their unique morphologies. These fossils have been dated by ESR and U-series methods on the associated faunal teeth to the mid-Middle Pleistocene, probably about 400 ka (Grün et al. 1998; Liu et al. 2014; Wu and Poirier 1995). The PA830 cranial specimen was a major focus of the earlier studies because of its unique morphology relative to the ZKD sample, which is considered "classic" Chinese *H. erectus*. In particular, Hexian is very wide posteriorly in the occipital region, which contrasts remarkably with the consistently narrow occiput of Zhoukoudian *H. erectus* (Kaifu 2017). At the same time, it resembles other Chibanian Chinese fossils (Zhoukoudian, Dali, etc.) in such features as the form of supraorbital arches and frontal keel, as well as the midsagittal profile of the frontal squama (Wu and Athreya 2013). Some earlier studies explained its morphology as a product of its inferred chronologically younger age, calling it a morphologically "progressive" member of the evolving Chinese *H. erectus* lineage (Wu and Dong 1985). Subsequent studies have focused on its unique cranial form among the Chinese Chibanian hominins (Antón 2002; Cui and Wu 2015; Durband et al. 2005; Etler 1996; Kaifu 2017; Kidder and Durband 2004; Wolpoff 1999; Wu et al. 2006).

The mandibular (PA 831) and dental remains from Hexian are likewise morphologically confounding. As described in Liu et al. (2017), the mandible is characterized by a very thick and robust lateral corpus. None of the Chinese mandibles from the early Chibanian contexts, including the chronologically older Zhoukoudian and Lantian/Chenjiawo, approach this condition (Chang et al. 2015), so it may be a primitive retention comparable to the Calabrian *Homo* from Africa and Java (the Sangiran Lower assemblage). However, the Hexian mandible does not consistently display a full set of primitive features that characterizes these Calabrian *Homo*. For example, it lacks a narrow dental arcade and an anteriorly located lateral prominence. The occurrence of multiple mental foramina in Hexian is also not common among the early members of *Homo*. In terms of its dental morphology, as mentioned above, Xing et al. (2018) highlighted similarities between Hexian and Zhoukoudian but also noted marked differences between the two, namely in tooth size, hypocone development on M^1 (in both cases Hexian is larger), and root morphology (Hexian has three-rooted P^3 and more robust and divergent molar roots).

Within the Hexian sample the M3s are variable. A marked reduction or agenesis of M3s is observed widely in the East Asian Chibanian hominins. One Hexian specimen, the PA 831 mandible, displays such reduction (Liu et al. 2017), while the other, PA 834—part of an isolated molar pair believed to be left M_2 and M_3—is very large (Xing et al. 2014). However, it is equally plausible that PA 834 is an M_1 and M_2 pair, given the squarish occlusal contour and mesially positioned mesial root of the mesial molar (Y.K., personal observation). If this is the case, the absence of distal interproximal facet and rounded distal crown contour of M_2 suggests that the left M_3 was congenitally absent in this individual, consistent with what is seen in other eastern Asian hominins.

Taken together, the above cranial and dentognathic characters led some researchers to suggest that Hexian may have been the survival of a primitive form of hominins distinct from the *H. erectus* deme represented by Zhoukoudian (Kaifu 2017; Liu et al. 2017; Xing et al. 2014). Alternatively, its primitive-looking dentognathic characters may have been an evolutionary reversal. In either case, we do not group it with the ZKD p-deme. We will further discuss its affiliation later in this paper.

LATE CHIBANIAN *HOMO* FROM CONTINENTAL EAST ASIA

Hominin fossils from this time period have been collected from Jinniushan, Dali, Xujiayao, Maba, and other sites such as shown in Figures 1 and 2. Useful reviews of the studies in the 20th century are available in Brown (2001), Etler (1996), Liu et al. (2014), and Wu and Poirier (1995), so these are not repeated here. The recent discoveries of fossils from Hualongdong, Xuchang, Harbin, Penghu, and other sites, coupled with reanalysis of the existing collection spark renewed discussion on how to recognize and interpret the "complicated patterns of morphological diversity" observed in the East Asian hominin fossil record (Liu et al. 2022). In this section, we mainly review such recent advances as well as new discoveries during the last two decades, in chronological order from the older to younger specimens for the northern and southern continental regions, respectively (see Figure 2).

Chaoxian

The Chaoxian fossils consist of a hominin occipital and maxillary fragment found in 1982 and 1983 in eastern China, in the upper part of the collapsed cave (or fissure) deposits in Chaoxian Country, Anhui. Mass spectrometric U-series dating suggests that these are 310–360 ka or somewhat older, based on speleothem intercalated at the presumed provenance of the hominin fossils (the middle or slightly higher level of Layer 2) (Shen et al. 2010). Wu et al. (2012) reported the nasal floor topography of the maxilla as being 'bi-level,' which is common in Neanderthals. At the same time, Bailey and Liu (2010) note the lack of Neanderthal-like skewed M^1 crown shape in Chaoxian, its generally large premolar crown dimensions, and its complex premolar and molar occlusal surface morphology, all of which are shared with other Chibanian fossils from China such as Changyang, Tongzi, and Xujiayao. A more recent geometric morphometric analysis demonstrates that the Chaoxian P^3 has a primitive oval crown configuration with a mesiodistally broad lingual cusp, which is comparable to the early Chibanian northern Chinese *H. erectus* (the square symbol on the lefthand side of Figure 7 in Xing et al. (2019).

Hualongdong

At Hualongdong in southern China, hominin cranial fragments, isolated teeth, femoral fragments, and a remarkably well-preserved, partial skull of an adolescent were excavated between 2006 and 2017 from brecciated deposits in association with mammalian remains and stone artifacts (Wu et al. 2019). The age of the fossiliferous breccia was constrained to 331–275 ka by numerous U-series dates on speleothem, fossil tooth, and other samples, as well as biochronology. The craniofacial morphology of HLD 6 is not easy to put into context due to its subadult status. Acknowledging this fact, Wu et al. (2021) emphasized its modern-looking facial features (e.g., small size, a tall orbit, less pronounced postorbital constriction, weak prognathism, flattened malar regions, a well-developed anterior nasal spine, an anteriorly positioned incisive foramen, and a parabolic-shaped dental arcade) and concluded that "HLD 6 represents the earliest occurrence of the modern human face in the fossil record of eastern Asia." Also, the Hualongdong dental remains lack the complex molar occlusal morphology that characterizes Zhoukoudian, Hexian, and Xujiayao. The M^3s of HLD 6 are congenitally absent (right) or markedly reduced (left), as observed in some Chinese fossils such as Chenjiawo and Jinniushan (Wu et al. 2019).

Dali

An almost complete cranium from Dali was found in 1978 by a geologist at a loess terrace along the Luo River in Dali Country, Shaanxi Province in northwestern China. The minimum age of the fossil, based on a correlation between the fossil bearing unit and the Chinese loess sequence, is ca. 247 ka (MIS 7) (see Wu and Athreya 2013 for detailed discussion). Detailed nonmetric and morphometric analyses converged upon the conclusion that Dali shares aspects of overall cranial expansion with late-Chibanian *Homo* from Europe and Africa (Athreya and Wu 2017; Wu and Athreya 2013), such as reduced postorbital constriction, a relatively short and arched parietal with bossing, a high and arched temporal squama contour, and a longer occipital vs. nuchal plane; it also has a derived supraorbital torus that is divided into distinct medial and lateral portions. At the same time, it retains certain traits that are seen in Chinese *H. erectus*: namely, a weakly pneumatized supraorbital torus, the absence of a supraorbital notch, short parietal profile, presence of a weak angular torus, relatively thick parietal bones and a moderately thick tympanic plate. Its overall affinities align it with the Afro-European Chibanian sample, but it also has some similarities with Chinese *H. erectus*.

Jinniushan

In 1984, a hominin partial skeleton was excavated from a limestone cave at Jinniushan, Liaoning Provence, northeastern China, by a research team from Beijing. The preserved parts include a cranium with most of the maxillary dentition, a left ulna, a left os coxae, vertebrae, and other postcranial elements. ESR and U-series dating of five animal teeth suggested that the human remains are 200 ka or older (Chen et al. 1994). Rosenberg et al. (2006) examined its postcranial bones and reported its sex as female (based on the pelvic morphology), estimated stature being ~168cm (calculated from the ulnar length), estimated body mass ~78.6kg, and noted the pelvic breadth, which was very broad (as found in west Eurasian archaic specimens from La Chapelle-aux-Saints, Kebara, and Atapuerca). The cranium had been broken into more than one hundred pieces during excavation but was later meticulously restored in the laboratory (Wu 1988), with later adjustment at Peking University (Brown 2001). Brief English descriptions of the cranium are available in (Wu and Poirier 1995) and Brown (2001). The M^3 shows a marked reductive trend relative to M^1 and M^2 (He 2000).

Harbin

An almost perfectly preserved cranium, HBSM2018-000018(A), was discovered in 1933 during construction work in Harbin City, which is the capital of Heilongjiang in far northeastern China. Ji et al. (2021) recently reported it as a new species, *Homo longi*. Because the exact site and stratigraphic context of this specimen are uncertain, its age was inferred from a series of geochemical analyses and direct U-series dating (Shao et al. 2021). First, its derivation from the local Pleistocene context was supported through element profiling of both the cranium itself and mammalian fossils collected locally. Then, the sediments adhered in its nasal cavity were examined, yielding evidence that its nature and $^{87}Sr/^{86}Sr$ ratio were similar to those of the upper part of the core drilled near the original construction site. This may in turn be correlated to the upper part of the Upper Huangshan Formation in the local standard stratigraphic sequence, which has an OSL date of ~309–138 ka (Wang et al. 2020). On the grounds of this evidence, the Harbin cranium was dated to the late Chibanian, an inference supported by direct U-series ages measured on the hominin fossil (>146 ka).

In order to determine the phylogenetic position of Harbin within the genus *Homo*, Ni et al. (2021) performed parsimony-based phylogenetic analyses using a large phenetic character data matrix, which was constructed by 234 discrete and 400 continuous character data taken from a global (Afro-Eurasian) sample of fossil *Homo*. The results suggested that Jinniushan, Hualongdong, Dali, Xiahe (see below), and Harbin form a monophyletic group with a sister relationship with *H. sapiens*. The former was set apart from Maba, Xuchang, and Narmada (which forms another monophyletic group), as well as the paraphyletic *H. heidelbergensis/rhodesiensis* group (Bodo, Broken Hill, Arago, Petralona, etc.). These authors further suggested that the clade to which Harbin belongs was Denisovan because this clade includes the Xiahe mandible, whose paleoproteomic profile is reportedly similar to the Altai Denisovan (Chen et al. 2019). However, the suggested link between Harbin (cranium) and Xiahe (mandible) is weak because it is based solely on the character state of large molar size and M3 agenesis. Additionally, as with previous critiques of studies based on cladistic methods, the results failed to account for character correlation and thus are weaker than multivariate analyses that have yet to be performed on this specimen.

Changyang

The Changyang hominin fossil consists of a left hominin maxillary fragment with P^3 and M^1 preserved *in situ* as well as an isolated left P_4. They were recovered from a cave in Changyang Country, Hubei, central China. The reported U-series date of ~195 ka on the associated vertebrate teeth, bones, and travertines (Yuan et al. 1986) gives us only a rough idea about its antiquity. Wu et al. (2012) described, as in the case for the Chaoxian maxilla, its nasal floor topography as being 'bi-level.' Bailey and Liu (2010) noted general similarities of its premolar and molar morphology to those of Chaoxian.

Xujiayao

Hominin craniomandibular fragments and isolated teeth from the Xujiayao site in the Nihewan Basin, northern China, were excavated during the late 1970s. Various dates have been proposed, but recent OSL and $^{26}Al/^{10}Be$ burial dating of sedimentary samples, coupled with faunal and palynological evidence suggesting colder climate, point to the hominin fossils and the associated cultural layer belonging to Marine Isotope Stage (MIS) 6 (~190–130 ka) (Li et al. 2014; Tu et al. 2015); but see Ao et al. (2017) for an older age estimate (~370–260 ka).

Morphology of the specimen was recently reanalyzed from several different perspectives, yielding new insights. First, a computer-based reconstruction of the parietal, temporal, and occipital bones, which are presumably from the same adolescent or young adult individual (XJY 6), demonstrated a low, broad posterior cranial form and offered a rough endocranial capacity estimate of ~1700cm^3 (Wu et al. 2022). Although a slight change in the orientation of the occipital bone to make the nuchal plane more horizontal like Dali and Harbin would decrease this figure, the large cranial capacity of this individual is apparent. The reconstructed specimen is similar to Xuchang 1 in these respects, although the occipital bone does not display a Neanderthal-like suprainiac fossa as is evident in Xuchang 2. Second, the temporal bone included in this reconstruction (Xujiayao 15) exhibits a bony labyrinth morphology typical of Neanderthals—the anterior semicircular canal is low and narrow, the posterior is small and circular, and the lateral portion is high and wide (Wu et al. 2014). When the semiciruclar canal dimensions were analyzed metrically, Xujiayao 15 was placed in the middle of the range of variation exhibited by Neanderthals, while the Xuchang temporal bones were in the zone of overlap between Neanderthals and other Afro-Eurasian fossil and recent *Homo* samples. Finally, the teeth from Xujiayao are generally large with non-reduced M3s (Xing et al. 2015). The M^1 crown outline is trapezoidal, and the molar roots are robust and divergent even in the M3s. In these and a few other features, these specimens are different from *H. sapiens* and Neanderthals, but closer to Calabrian-Chibanian hominins from Java and China. At the same time, the Xujiayao teeth are derived in comparison with chronologically earlier Chinese specimens from Yiyuan, Zhoukoudian, Hexian, and Chaoxian in showing less-pronounced finger-like projections in the I^1, a weaker canine essential ridge, simpler occlusal and buccal surfaces in P^3 and P^4, a more symmetrical P^3 crown outline with much smaller lingual cusp, a reduced M^3 metacone, and an elliptical M_3 crown outline (see also Xing et al. 2019). The above combination of primitive, derived, Neanderthal-like, and other features (see also Wu and Trinkaus 2014)) observed in the Xujiayao craniodental remains has led some authors to propose that Xujiayao represents a previously unreported, primitive hominin group that survived into the late Chibanian of China (Wu et al. 2022; Xing et al. 2015).

Xuchang

The open-air site of Lingling, in Xuchang, Henan Province, is situated between the Yellow and Yangtze Rivers in central China. Excavations in the past decade have yielded a well-preserved neurocranium (Xuchang 1) and one partial posterior neurocranium (Xuchang 2), as well as three other cranial fragments (Xuchang 3 to 5) from Layer 11, which was OSL dated to ~125-105 ka (Li et al. 2017). Like the Middle Pleistocene archaic *Homo* fossils from eastern Eurasia, these early Late Pleistocene specimens share a primitive, low cranial shape, but quite notably exhibit derived (extremely) expanded cranial capacities (~1800cm^3) and somewhat reduced cranial hypertrophy as seen in the supraorbital torus, cranial bone thickness, nuchal torus, and angular torus. They exhibit marginally "Neanderthal-like" mid-occipital and temporal semicircular canal morphologies. According to Li et al. (2017), the derived features in the Xuchang sample point to "pan–Old World trends;" the primitive cranial form suggests genealogical continuity from local Chibanian hominins; and, the distinctive Neandertal features reflect populational interactions across Eurasia during the late Middle and early Late Pleistocene. In a broad sense, this conclusion follows the traditional standpoint that supposes local evolution of Chinese Chibanian *Homo* with possible gene flow from western Eurasia (Athreya and Wu 2017; Etler 1996; 2006; Pope 1992; Wolpoff 1999; Wu 2014).

Maba

A partial cranium from a karst cave located on the outskirts of Maba town, Guangdong, southern China, was dug up by a local farmer in 1958 (Wu and Poirier 1995). Dating of this specimen (Maba 1) is extremely challenging primarily because of its unknown provenance in the cave system as well as the removal of much of the fossiliferous sediments during the past activities of fertilizer mining, excavations, and reconstruction for tourism (Shen et al. 2014). Earlier arguments suggesting terminal Chibanian ages were disputed due to the unwarranted association of the dated flowstone and faunal samples with the hominin fossils, among other reasons. To overcome this problem, Shen et al. (2014) reconstructed the cave sedimentation history and concluded that the U-series age for its capping flowstone (~230 or ~278 ka) can be used as the minimum age for all the fossiliferous deposits of the site. However, even this approach does not convince all researchers. Some of the mammalian taxa represented from Maba (e.g., *Crocuta crocuta ultima* and *Cuon javanicus*) support a late Chibanian/Late Pleistocene age (Wu et al. 2011).

The Maba 1 cranium is from an adult individual with substantial cranial suture closure. It suffers from an antemortem lesion on the right frontal squama and postmortem porcupine gnawing at the supraorbital region, but is relatively complete (Wu et al. 2011). Maba 1 is unique among the Chinese Chibanian hominins, showing a markedly round orbit with no supraorbital notch, a narrow, pinched and prominent nasal saddle, and a rounded posterior neurocranial profile. It somewhat resembles Neanderthals in these features (Pope 1992; Wu and Bruner 2016; Wu and Wu 1985; Wu et al. 2011). Its endocranial capacity is estimated at around 1300cc (Wu and Bruner 2016).

Tongzi and Panxian Dadong

The hominin fossil assemblage from Tongzi consists of several isolated teeth excavated by Chinese research teams at Yanhui Cave, Tongzi county, Guizhou, southern China, between 1972 and 1983 (Wu and Poirier 1995). Based on U-series dates obtained from the associated mammalian teeth, flowstone, and stalagmite samples, these teeth are dated to 240–206 ka or more broadly 240–113 ka (Liu et al. 2022; Shen and Jin 1991; Xing et al. 2019). The cave of Panxian Dadong is also located in Guizhou Province. Four isolated hominin teeth were found by a series of excavations conducted between 1992 and 2005, together with stone artifacts and fossil remains of *Ailuropoda-Stegodon* fauna, from the stratigraphic level dated to 280–130 ka (Liu et al. 2013; the age range cited from Liu et al. 2022). Although caution about possible intrusion is required for isolated teeth recovered from cave deposits (Kaifu et al. 2022), these constitute an important part of the small hominin dental collection currently available from the late Chibanian contexts of China.

Detailed morphological description and comparisons for four Tongzi teeth and the four Panxian Dadong teeth were published by Xing et al. (2019) and Liu et al. (2013), respectively. These teeth do not display primitive configurations typically observed in northern Chinese *H. erectu*s and Hexian, such as a mesiodistally broad lingual cusp of the upper premolars and asymmetric P_3 crown shape; The premolar and molar crown shapes of Tongzi and Panxian Dadong are generally encompassed in the range of variation exhibited by *H. sapiens*; the Tongzi M^1 lacks the Neanderthal-like crown configuration characterized by a distally protruded hypocone. Overall, both the modern-looking crown morphology of these teeth, as well as their moderate to large crown dimensions, are comparable to Xujiayao and possibly Jinniushan (Xing et al. 2015; 2019).

Penghu

The Penghu 1 specimen, a robust archaic hominin mandible from Taiwan, was dredged from the seabed of the ~60–120m deep Penghu Channel and subsequently reported by Chang et al. (2015). Attempts to directly date the specimen using laser-ablation U-series and radiocarbon methods were unsuccessful, so other mammalian fossils collected from the same seabed were used to narrow down the possible age, and it was concluded that the mandible is from the terminal Chibanian or early Late Pleistocene. Considering the times of lowered sea level when the channel would have been low enough to expose a land bridge between present-day China and the island of Taiwan, the plausible age for the specimens is MIS 6 (190–130 ka) or MIS 4-2 (~70–10 ka). The Penghu mammalian fauna includes *Palaeoloxodon*, *Elaphurus*, and *Usrus arctos* but lacks *Ailuropoda*, *Stegodon*, *Tapirus*, and *Pongo*. This is consistent with the assumption of episodic migration, not along the same latitude (i.e., from southernmost China eastward), but from the mid-latitude regions southward to the Taiwan area in colder climate (Chang et al. 2015).

The Penghu 1 mandible is strikingly similar to the Hexian mandible, showing a very thick and robust corpus, a wide dental arcade, large tooth size, and robust premolar and molar roots with a tendency of branching (in P_3 and M_2 of Penghu 1 and in P^3 and P_4 of Hexian) (Chang et al. 2015; Liu et al. 2017; Xing et al. 2014). The M_2 of Penghu 1 is of particular interest—its root is considerably longer than that of M_1, and it has a distinct extra root in-between the lingual aspects of the mesial and distal roots. Additionally, the right M_3 of Penghu 1 is congenitally absent, a feature which may also have been present in Hexian (see above).

LATE CHIBANIAN *HOMO* FROM THE RUSSIAN ALTAI, TIBET, LAOS, AND INDIA

Russian Altai (Altai Neanderthal and Altai Denisovan p-demes)

Since 2007, paleogenetic and paleoproteomic analyses using thousands of fragmentary bones and teeth have identified the presence of Neanderthals and another enigmatic archaic hominin called Denisovan in the Russian Altai cave of Denisova. Such studies have also confirmed the presence of Neanderthals alongside Denisovans, expanding the evidence of the former population to three sites in the Altai (along with Okladikov and Chagyrskaya caves) (Buzhilova 2013; Krause et al. 2007; 2010; Kuzmin et al. 2022; Mafessoni et al. 2020; Meyer et al. 2012; Prüfer et al. 2014; Reich et al. 2010; Sawyer et al. 2015; Slon et al. 2017; Turner 1990). Careful studies of the stratigraphy of Denisova Cave and dating with radiocarbon, uranium series, and optical methods as well as molecular age estimations of the hominin mtDNA, together suggest that Denisovans intermittently occupied the site from ~200 to 50 ka, while Neanderthals were present ~134–100 ka (Brown et al. 2022; Douka et al. 2019; Jacobs et al. 2019b; Morley et al. 2019). Paleogenomic analysis confirm that at least one case of admixture occurred between the two populations (Slon et al. 2018).

Morphological analyses of the two isolated molars from Denisova (Denisova 4 and 8: M^2 or M^3) emphasized their large size, complex occlusal surface morphology, massive roots, and lack of Neanderthal-like reduced distal cusps among other features, which are together somewhat similar to Xujiayao (Buzhilova et al. 2017; Reich et al. 2010; Sawyer et al. 2015; Zubova et al. 2017). A distal manual phalanx from the adolescent female individual (Denisova 3) does not show a Neanderthal-like wide apical tuft and shaft morphology (Bennett et al. 2019). Despite the evidence of admixture and possible cohabitation at Denisova Cave, the observed distinct differences in their genomic and morphological characters point to largely independent population histories between the Altai Neanderthals and Altai Denisovans. Because of this, we regard them as two independent p-demes.

Xiahe

This robust, archaic hominin mandible was found in 1980 at Baishiya Karst Cave, Xiahe County, Gansu Province, on the northeastern margin of the Tibetan Plateau (3,280m altitude). The cave preserves >16m-thick sediments containing abundant stone artifacts and faunal remains, which were deposited during the last ~190,000 years according to optical and radiocarbon dating (Zhang et al. 2020). The exact provenance of the Xiahe mandible within the cave is unknown but U–Th dating performed on samples of carbonate crust adhered to the fossil suggest that the specimens is ~160 ka (Chen et al. 2019). The endogenous proteins extracted from the dentine sample suggested its closer affinities with Altai Denisovan (Chen et al. 2019); a later sedimentary DNA analysis found Denisovan mitochondrial DNA from the cave's sequence and was dated to the early Late Pleistocene (Zhang et al. 2020). Together these suggest a long-term occupation of the Baishiya Karst Cave by Denisovans who could exploit a wide range of animal taxa (Xia et al. 2024), and provide support for the earlier proposition that the population had genetically adapted to life at high altitudes, even transmitting such genes to modern humans on the Tibetan Plateau (Huerta-Sanchez et al. 2014; Zhang et al. 2020).

The Xiahe mandible is primarily characterized by a low and robust body, a wide dental arcade, large molar crowns, M_3 agenesis, and generally robust and complex root morphology including the specialized, three-rooted M_2. This specimen is strikingly similar to Penghu 1 in most or all of these aspects (Chen et al. 2019). Chen et al. (2019) also note that the molars of the Xiahe mandible are similar to the Denisovan fossils from Altai and teeth from Xiujiayao in terms of their large size and/or surface complexity.

Tam Ngu Hao 2

Tam Ngu Hao 2 (Cobra Cave) is located in Huà Pan Province, Laos. A hominin molar (TNH2-1) recovered from a breccia block at the site was reported by Demeter et al. (2022). The reported age for this tooth, 164–131 ka, is the depositional age range measured for the fossil-bearing breccia inside the cave. The hominin tooth is an unerupted mandibular first (or possibly second) permanent molar, probably from a female individual according to a paleoproteomic examination. The crown of TNH2-1 is large and coarsely wrinkled on the occlusal surface. Its enamel-dentine junction topography shares some similarities to Neanderthals and *H. erectus*, but most closely resembles the Denisovan molars from Xiahe. Based on these morphological observations, Demeter et al. (2022) suggested that this Lao tooth belonged to Denisovans among other possibilities.

Narmada (Hathnora)

The partial hominin cranium from Hathnora in the Narmada Valley, India, was discovered from a conglomerate layer containing reworked mammalian fossils that are variously dated to between ~48 and >236 ka (Cameron et al. 2004; Patnaik et al. 2009). Most studies agree that Narmada resembles other Chibanian *Homo* (Athreya 2010; Cameron et al. 2004; Kennedy et al. 1991) rather than *H. erectus* as originally proposed (de Lumley and Sonakia 1985), and some emphasize its closer affinities with European Chibanian *Homo* such as Steinheim, or more broadly *H. heidelbergensis* (Cameron et al. 2004; Kennedy et al. 1991). On the other hand, Howell (1999) found "fundamental" similarities between the crania from Maba and Narmada and put them together to propose the Maba/Hathnora paleodeme. Although systematic morphological comparison is yet to be done, this hypothesis merits further testing given their relative geographic proximity and latitudinal similarity (see Figure 1) as well as the claimed European affinities of Maba (Pope 1992; Wu and Wu 1985).

CRANIOMETRIC VARIATION IN ARCHAIC EASTERN ASIAN *HOMO*

In order to examine cranial form variation in a large sample of Asian archaic *Homo*, we renewed the former linear measurements-based principal component analysis (PCA) (Kaifu 2017), by adding three Chibanian crania from China (Jinniushan, Xuchang, and Harbin). The sample includes 32 well-preserved crania from the Calabrian-Chibanian contexts of eastern Asia (China, Java, and Flores), Caucasus (Dmanisi), and Africa (Ethiopia, Kenya, Tanzania, and Zambia) (Table 1). Here we focus only on the fully adult specimens; subadult specimens such as Zhoukoudian Skull 3, Hualongdong 6, D2700, and KNM-ER 15000 were excluded. The inclusion of East African early *Homo* (KNM-ER 1470 and 1813) and Dmanisi *Homo* is to establish evolutionary trends through time. The African *erectus* and post-*erectus* grade *Homo* were also analyzed to compare temporal trends between the continents. Compared to other large-scaled craniometric studies (e.g., Baab 2016; Rightmire 2013), the present analysis focuses more on Asian fossils and differs in variables used.

Eight size-adjusted linear measurements were used as variables and were chosen to capture the overall cranial vault architecture while also maximizing sample size. These are maximum cranial length (glabella-opisthocranion length; GOL), porion-bregma height (PBRH), breadths across the supraorbital torus (SOTB) and the cranial vault (frontal squama [postorbital breadth; POBB], parietals [squamosal suture breadth; SQSB], and occipital [biasterionic breadth; ASB]), as well as those that largely represent breadths of the mid (biradicular breadth; BRAB) and posterior (supramastoid breadth; SMCB) cranial base. Size adjustment was done by dividing these measurements by a "size variable" for each specimen, which was defined as the geometric mean of the cranial length (GOL), the average of the six breadths (SOTB~SMCB), and height (PBRH). The PCA was conducted using the variance-covariance matrix of the eight size-adjusted linear measurements. The results are shown in Figure 4. PC1, PC2, and PC3 explain 33%, 25% and 15% of the total variation, respectively.

In PC1, specimens with a relatively narrower cranial base (BRAB, SMCB) and wider frontal squama (POBB) are loaded negatively. A relatively narrower upper face (SOTB) and a broader occipital (ASB) also contribute to this trend to a lesser extent. This PC is highly correlated with geological age (r=0.72, p<0.00001: see Figure 4A) and reflects a gross chronological trend of cranial form evolution in archaic Afro-Asian *Homo*. Regional differences between Java and China are evident for the terminal Calabrian-early Chibanian subsample (Sangiran and Zhoukoudian) in this PC, but not for the late Chibanian subsample. Specimens with higher PC2 scores tend to have narrower upper facial breadths (SOTB) relative to the mid- and posterior brain case widths (SQSB, ASB, and SMCB). This PC expresses marked regional differences within individual time slices (see Figure 4A). It is not correlated with geological age (r= -0.14), but a temporal trend is evident for the African and Javanese regional subsamples. PC3 (not shown) expresses the large within-site variation for Ngandong, but chronological and regional trends are not evident. Because of this, we do not discuss this PC below.

When PC1 and PC2 are considered together (see Figure 4B), several notable points emerge. First, the Dmanisi and African early *Homo* specimens occupy the right space, demonstrating the primitive cranial form of Calabrian *Homo* represented along the PC1 axis. Interestingly, the Zhoukoudian specimens marginally overlap with this condition, and are more positive in this axis compared to the chronologically older Calabrian individuals from East Africa (KNM-ER 3733 and 3883 or "Turkana" specimens; OH 9; Daka) and Java (Sangiran). This reflects Zhoukoudian's generally primitive cranial form, although this result may be affected by their uniquely narrow occipital bone (ASB) and the well-developed suprameatal crest that leads to a greater BRAB (Weidenreich 1943).

Second, the samples from Africa/China and Java are completely separated from each other (with one exception, Hexian, as discussed later), but at the same time each of the three regional samples show similar chronological trajectories from the upper-right corner to the lower-left corner (Sangiran➛Sambungmacan➛Ngandong in Java; Turkana *H. ergaster*➛OH9/Daka➛Kabwe in Africa; Zhoukoudian ➛late Chibanian specimens in China). However, the late Chibanian *Homo* specimens from China do not follow this trend, with the chronologically youngest Xuchang 1 exhibiting somewhat primitive cranial form compared to the geologically older Dali, Jinniushan, and Harbin. Another example that does not share such a chronological trend is the LB1 type specimen of *H. floresiensis*, which is from the Late Pleistocene but displays a cranial form similar to terminal Calabrian *H. erectus* from Sangiran, as demonstrated previously (Baab et al. 2013; Kaifu et al. 2011a).

Third, the PC scores for the African and Chinese fossils overlap extensively with some (considerable) time lag. Zhoukoudian *H. erectus* is close to Turkana *H. ergaster*, but they are ~0.8 Ma apart; Daka and OH 9 are similar to Dali and Harbin but they are >0.7 Ma apart (the Chinese fossils are younger than the Africans). Such time differences

TABLE 1. MEASUREMENTS USED FOR THE PRINCIPAL COMPONENT ANALYSIS*.

Specimen	Age (Ma)	GOL	SOTB	POBB	SQSB	ASB	BRAB	SMCB	PBRH	Data source(s)
KNM-ER1470	2.06	168	115	82	120	104	136	140	94	K17
KNM-ER1813	1.89	145	99	69	103	94	113	114	80	K17
KNM-ER3733	1.63	182	119	92	131	119	131	142	96	K17
KNM-ER3883	1.5	182	120	88	134	115	131	141	93	K17
OH9	1.25	206	*135*	100	*139*	123	135	146	*99*	R13, W91
Daka	1	180	125	95	129	116	130	139.5	101	A08
Kabwe	0.3	207	139	104	144	125	136	148	108	K17
D2280	1.77	177	*113*	86	*118*	104	132	136	*93*	R13, R17
D3444	1.77	163	104[a]	78	115[a]	104	120	132	89[a]	R13, R17, L13
D4500	1.77	169	112[a]	75	118[a]	93	132[a]	135.5	75[a]	R17, L13
Sang2	0.9	183	104	84	138	123	126	142	94	K08
Sang17	0.8	207	125	101	144	134	148	161	104	K08
Bukuran	0.85	194	113	88	139	126	133	153	98	K08
SangIX	0.85	186	111	87	132	117	126	142	93	K11b
Sm1	0.3	199	118	107	146	126	138	151	107	K08
Sm3	0.3	178	114	101	138	120	136	146	98	K08
Sm4	0.3	199	122	116	146	133	138	156	102	K08
Ngawi	0.3	187	114	101	140	127	136	147	102	K15
Ng6	0.113	221	122	108	149	128	141	155	112	K08
Ng7	0.113	192	121	106	142	124	136	147	103	K08
Ng10	0.113	202	124	110	152	127	143	159	109	K08
Ng11	0.113	203	132	114	151	128	141	160	112	K08
Ng12	0.113	201	124	107	138	126	136	151	108	K08
LB1	0.05	139	88	71	110	92	105	114	75	K11a
ZKD10	0.75	199	*119*	98	138	111	147[b]	150	106	W43
ZKD11	0.75	192	*113*	93	135	113	143[b]	145	94	W43
ZKD12	0.75	195.5	*118*	95	139	115	151[b]	147	101.5	W43
Hexian	0.4	191	114	101	146	131	139	160	97	K17
Dali	0.28	206.5	125.5	*106.4*	*149*	115	141	150.5	102.5	W&A13, L22
Jinniushan	0.26	206	136.5	116[c]	140.9	122.1	132.8	148	99.7	N21, L22,
Xuchang 1	0.115	216	143	125[c]	167	136.7	165.1	173.5	114.6	N21, L22,
Harbin	0.228	221.3	145.7	125[c]	154.6	134.4	158.8	164.1	113.9	N21

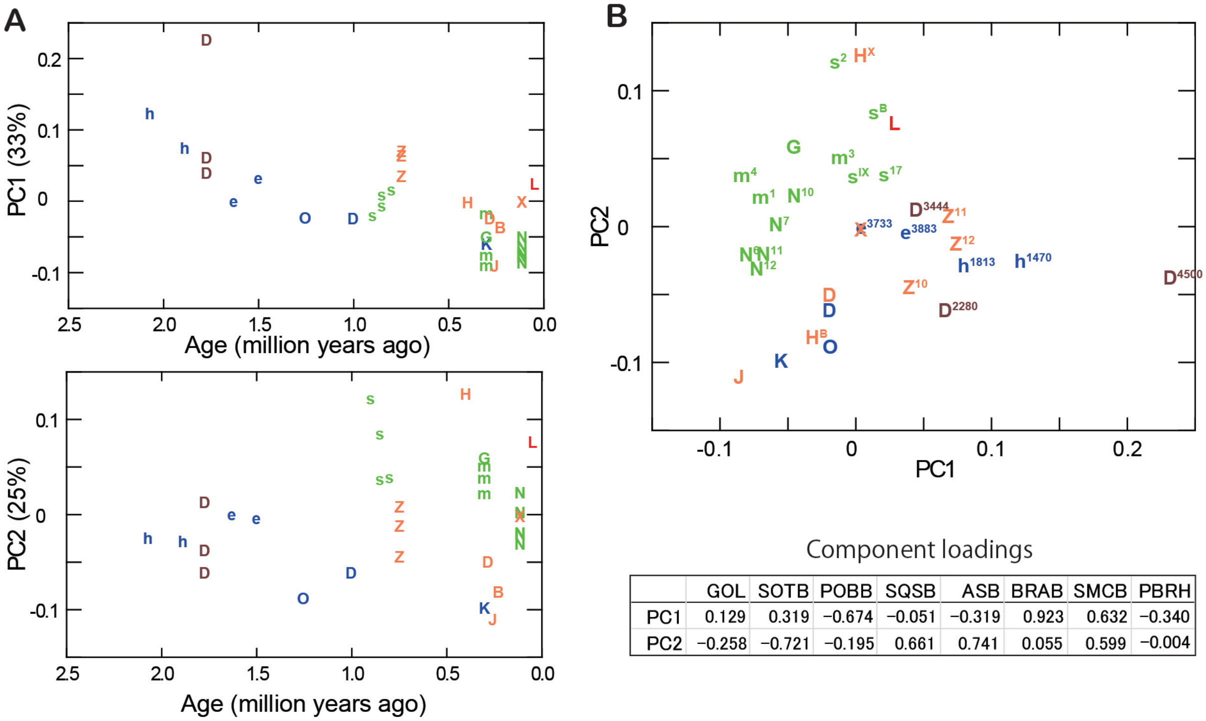
*Italic typeface indicates data obtained from a cast. Data source(s): A08=Asfaw et al. (2008), K08=Kaifu et al. (2008), K11b=Kaifu et al. (2011b), K11a=Kaifu et al. (2011a), K15=Kaifu et al. (2015c), K17=Kaifu (2017), L13=Lordkipanidze et al. (2013), L22=Liu et al. (2022), N21=Ni et al. (2021), R13=Rightmire (2013), R17=Rightmire et al. (2017), W43=Weidenreich (1943) , W91=Wood (1991), W&A13=Wu and Athreya (2013).

[a] Data obtained from published CT-based images.

[b] Regarded as equivalent to the reported biauricular breadth.

[c] Two millimeters were added to the reported minimum frontal breadth.

need to be considered in interpreting the gross cranial form similarities between the two regions. The closeness of OH 9's position with late Chibanian Africa/Chinese fossils is unexpected, given the former's unquestioned taxonomic status as *H. erectus sensu lato* (e.g., Antón 2003; Baab 2015; Rightmire 1990). OH 9 is obviously different from these post-*erectus* grade specimens, for example, in the anteroposterior development of the supraorbital torus, which cannot be captured by our metric method. Still, their gross cranial form similarities demonstrated here are noteworthy. On the other hand, the cranial shape similarities between Daka and Kabwe (and Bodo) have been pointed out by a landmark-based 3D geometric morphometric study by Baab (2016), which claims that Daka represents either an



	GOL	SOTB	POBB	SQSB	ASB	BRAB	SMCB	PBRH
PC1	0.129	0.319	−0.674	−0.051	−0.319	0.923	0.632	−0.340
PC2	−0.258	−0.721	−0.195	0.661	0.741	0.055	0.599	−0.004

Figure 4. Results of the principal component analyses based on the linear measurements. A) Time plots of PC 1 and PC2; B) Scatter plot of PC1 and PC2. Symbols: Africa (blue): D^k=Daka, e=Turkana Homo ergaster, *h=*Homo habilis sensu lato, *K=Kabwe, O=OH9; Flores (red): L=Liang Bua* Homo floresiensis; *Java (green): G=Ngawi, m=Sambungmacan, N=Ngandong, s=Sangiran; Georgia: D=Dmanisi* Homo; *China (orange): D=Dali, H^B=Harbin, J=Jinniushan, H^x=Hexian, x=Xuchang, z=Zhoukoudian. The superscripts denote the specimen numbers or names. Proposed age range is indicated for Kabwe (Grün et al. 2020; Klein 2009; Millard 2008).*

"advanced" *H. erectus* population close to the root of *Homo heidelbergensis sensu lato* or an early population of the latter.

Fourth and finally, Hexian occupies a unique position, which is remote from the main Chinese cluster and is located near the margin of the variation exhibited by the Sangiran *H. erectus*.

DISCUSSION

The present craniometric analysis examined variation in gross cranial form in a large sample of Afro-Asian *Homo* composed of balanced numbers within each chrono-regional group and excluding subadult (ZKD3, D2700, KNM-WT15000, etc.) and extensively reconstructed specimens (ZKD5, Nanjing, etc.). A major limitation is that it could not capture detailed cranial features such as the configuration of supraorbital torus and frontal curvature. However, the results were illuminating. In the sections that follow, we discuss implications of this analysis and other related evidence region by region.

JAVANESE *H. ERECTUS* AS A LOCAL EVOLVING LINEAGE

Figure 4 highlights the uniqueness of the Javanese cranial specimens relative to the Chinese, Georgian, and African fossils. Cranial form variation is continuous between the Sangiran Upper and Ngandong/Sambungmacan/Ngawi samples, supporting their evolutionary continuity and integrity as the single evolving lineage of Javanese *H. erectus*. Although the lack of Chibanian hominin fossils from mainland Southeast Asia (see Figure 1) does not allow a more rigorous test of this hypothesis, this model, which is also supported by other craniometric studies as well as detailed examinations of cranial surface features (Antón 2002, 2003; Baab and Zaim 2017; Baba et al. 2003; Kaifu et al. 2008; 2015c; Kidder and Durband 2004; Weidenreich 1943; Wolpoff 1999), is currently the best explanation from the available materials. Under such an isolated condition, *H. erectus* in Java experienced a slight brain size increase, frontal widening, and other cranial form evolution, which somewhat parallels what occurred in the continental Chibanian *Homo* (see Figure 4).

Throughout the Pleistocene, Java experienced episodic range contraction and fragmentation as glacial cycles recurred, and it was relatively isolated from the Asian mainland. During the episodes of glacial low sea levels, Java was the southernmost constituent of Sundaland, a huge peninsula extending from the present-day Malay Peninsula to Borneo (Kalimantan) and Bali, whereas it was an island during the warm interglacial epochs, as it is today (see Figure 1). The past geographic range of Javanese *H. erectus* in such a fluctuating region is unclear for now because of the lack of fossil specimens outside Java (see Figure 1). Dental morphological similarities between Sangiran *H. erectus* and the late Pleistocene *H. luzonensis* from Luzon, the Philippines (Zanolli et al. 2022), do not contradict the model that Javanese *H. erectus* had been widespread in the Sundaland. However, given the current knowledge that an insular environment occasionally or frequently offered an opportunity for dramatic evolution of archaic hominin species (Detroit et al. 2019; Morwood and Jungers 2009), there is no surprise if there existed diverse archaic hominin p-demes distributed in different parts of the Sundaland.

Presently, the fossil assemblage from Ngandong dated to ~110 ka (Rizal et al. 2020) records the last appearance date for Javanese *H. erectus*, but it does not necessarily mean that this lineage went extinct exactly at that time. It is still possible that this long-survived lineage persisted well into the Late Pleistocene, until around the time when *H. sapiens* appeared in this region, although such fossil evidence is yet to be discovered.

REGIONAL TRENDS AND EVOLUTIONARY CONTINUITY/DISCONTINUITY IN EAST ASIA

As mentioned above, the evolutionary relationship between northern Chinese *H. erectus* (Zhoukoudian p-deme) and the local late Chibanian *Homo* is a matter of debate. Many of the Zhoukoudian *H. erectus*-like cranial features are not seen in the post-300 ka East Asian *Homo*, which exhibit increased morphological diversity (Liu et al. 2022), but the reason for this remains a conundrum due to the paucity of fossil materials between 400 and 300 ka (see Figure 2). Liu et al. (2022) propose that the absence of fossils from this time period is a product of significant climatic—and, by inference, populational—instability. Specifically, MIS 11 was a characterized by significant and relatively rapid temperature fluctuations as well as overall warming in northwestern China (Shi et al. 2013; Wu et al. 2007), both of which have been linked to population movements and also increased lineage diversification (Grove 2014, Sa;toro et al. 2013). The ~335 ka Chaoxian maxilla is intriguing in that it shares a primitive premolar crown configuration with northern Chinese *H. erectus* (Zhoukoudian p-deme) and Hexian. Our craniometric analysis sheds new light on this issue.

Figure 4 displays similar patterns of regional cranial form change in Java, China, and Africa, although the Chinese case is somewhat complicated by a few outliers (Hexian and Xuchang, see below). Through time, relatively narrower cranial bases increase in frequency, as do broader frontal squama (PC1). During the Chibanian, relatively broader superior faces and narrower posterior crania (PC2) also increase in frequency. This matches the very broad general trend of encephalization in the genus *Homo* throughout the Pleistocene, particularly the Middle Pleistocene (Rightmire 2013).

Along with these overall trends, the trajectories for Africa (Turkana *H. ergaster* to Kabwe via OH 9 and Daka) and China (Zhoukoudian to Dali, Harbin, and Jinniushan) extensively overlap each other. This can be explained in several different ways. First, the transition from Zhoukoudian to the Dali/Harbin/Jinniushan conditions may reflect their evolutionary continuity, although this hypothesis is only weakly supported at present because there is no overlap in the ranges of variation exhibited by these two groups. This cannot easily be explained by the temporal gap between them, because such a distinct morphological gap is absent in Java where the temporal gap between the earlier and later *Homo* fossil records is more extensive. Second, the cranial form similarities between Daka/OH 9/Kabwe and Dali/Harbin/Jinniushan may have resulted from the dispersal of African (or western Eurasian) *Homo* (*H. heidelbergensis sensu lato*) during the Chibanian. This hypothesis does not contradict the temporal relationship, because the East African sample includes older specimens (OH 9 and Daka from the late Calabrian contexts). Although our craniometric analysis examined only gross cranial form, other researchers have repeatedly suggested general morphological similarities between the Afro-European and Chinese Chibanian cranial specimens (Rightmire 1998, 2015; Stringer 2012; Tattersall and Schwartz 2009; see also Bräuer 2008). Third, both these factors may have affected the observed similarities in combination, as variously suggested by many researchers (Athreya and Wu 2017; Etler 1996, 2006; Pope 1992; Wolpoff 1999; Wu 2014).

In summary, although this study does not solve the ongoing debate about Chinese hominin evolution in the Chibanian, the observed cranial form similarity between some of the Chinese and African fossils supports their evolutionary link. The Neanderthal-like cranial features in Maba (Pope 1992; Wu and Bruner 2016; Wu and Wu 1985; Wu et al. 2011), and in turn in Narmada (Howell, 1999), is also noteworthy in this context. We will further discuss this issue later in relation to the question of Denisovans.

UNIQUENESS OF HEXIAN

In Figure 4, Hexian was plotted very close to Sangiran *H. erectus*, but this point should be looked at with caution because they are markedly different in many characters that are not captured in this analysis. For example, they differ in glabella (anteriorly protruded in Sangiran vs. depressed in Hexian), supraorbital torus (more rounded in Hexian), frontal squama (tighter sagittal curvature in Hexian), and bregmatic eminence (present in Sangiran vs. absent in Hexian). Regardless of this issue, our craniometric examination further highlighted the morphological uniqueness of Hexian in the Chinese Chibanian fossil sample (Antón 2002; Cui and Wu 2015; Durband et al. 2005; Etler 1996; Kaifu 2017; Kidder and Durband 2004; Wolpoff 1999; Wu et al. 2006). This issue is further discussed in the following section.

WHO WERE DENISOVANS?

One of us (Kaifu 2017) previously suggested that the Ngandong/Sambungmacan/Ngawi p-deme may have been a group of southern Denisovans because they must have been along the migration path of dispersing early modern humans who reached Melanesia and Australia around 50 ka, where a higher degree of Denisovan introgression was reported among the local present-day populations (Reich et al. 2011). This view is now unlikely because recent genetic screening failed to find signals for substantial introgression from 'super-archaic' hominin admixture in the contemporary populations of Inland Southeast Asia (Teixeira et al. 2021). Genetic studies have proposed that Denisovans emerged in the mid-Chibanian as a sister group to Neanderthals (Meyer et al. 2016; Prüfer et al. 2014). Super-archaic lineages can thus be defined here as those that predate the Denisovan-Neanderthal clade. Because the current fossil evidence suggests that Ngandong/Sambungmacan/Ngawi was the terminal p-deme of the Javanese *H. erectus* lineage, Denisovan introgression to the present-day Oceanic populations probably occurred outside Java.

The robust mandible from Xiahe is currently the best candidate for Denisovan outside the Denisova Cave in Altai (Chen et al. 2019; Zhang et al. 2020). This specimen shows striking morphological similarities with another robust mandible from Penghu, although a systematic comparison between the two specimens is yet to be done. In turn, the mandibles from Penghu and Hexian share unique robust body architecture and large tooth size among the East Asian fossil sample (Chang et al. 2015; Liu et al. 2017). Furthermore, Xiahe, Penghu, and Hexian share a tendency of M3 agenesis/reduction, which is sporadically present in post ~2.0 million years ago *Homo* from Africa (Omo 75-14: early *Homo*), Georgia (D2735: Dmanisi *Homo*), China (PA 102: *H. erectus* from Lantian), Flores (LB1: *H. floresiensis*), etc. Then, can Hexian be Denisovan?

As mentioned above, Hexian is unique among the Chinese Chibanian fossils. Geographically, the site is located between Xiahe and Penghu (see Figure 1). Hexian (~400 ka) is older than the latter two (see Figure 2), but such chronology does not contradict the genetically reconstructed lineage evolution of Denisovans (which says that they branched off from the Neanderthal lineage 440–390 ka: (Prüfer et al. 2017)). The large teeth and robust mandible of Penghu and Hexian were previously interpreted as primitive features for *Homo* (Chang et al. 2015; Liu et al. 2017; Xing et al. 2014), but alternatively these may have been derived features in this lineage. In this model, the massive dentognathic morphology is not a simple evolutionary reversal because it is associated with a trend for M3 reduction/loss. Although one group of researchers has suggested that Harbin, Dali, Jinniushan, and Hualongdong formed a Denisovan clade that includes Xiahe (Ni et al. 2021), the basis of this association is weak because there is no mandible to compare for Harbin, Dali, and Jinniushan, and the mandible and teeth from Hualongdong lack specialized characters seen in Xiahe (Wu et al. 2019). Another research group proposed that the large crania from Xujiayao and Xuchang comprise a new species (*H. juluensis*), which represents a Denisovan clade that includes the fragmentary Altai Denisovan remains as well as the Xiahe 1 and Pengh 1 mandibles (Bae 2024; Wu and Bae 2025). This grouping is also not well-founded because the single existing mandible from Xujiayao (Xujiayao 14 mandibular ramus) lacks the body to compare with Xiahe 1 (see Chang et al. 2015 for a comparison between Xujiayao 14 and Penghu 1).

If we accept that Hexian belongs to the Penghu/Xiahe p-deme (Hexian/Penghu/Xiahe p-deme) that was distinct from Zhoukoudian p-deme and the Dali/Harbin/Jinniushan one, this new model also explains the strange cranial form of Xuchang 1. In Figure 4, this specimen did not follow the chronological trend displayed by other Chinese Chibanian fossils (Dali, Harbin, and Jinniushan), but was plotted in a space still remote from but closer to Hexian. Then it becomes possible that Xuchang 1 is a descendant of Hexian p-deme, which experienced substantial brain size increase during the late Chibanian (1025cc to ~1800cc). Although such a grouping cannot be directly confirmed without ancient biomolecular evidence, a recent genetic study suggests that the cranial morphology of Xuchang generally matches the reconstructed Denisovan skeletal morphology based on the DNA methylation patterns (Gokhman et al. 2019). In this scenario, a Denisovan group represented by Xiahe occupied a wide area spanning ~2000km from Tibet to Taiwan via central China (Hexian and Xuchang), or further down to northern Laos if we include the molar from Tam Ngu Hao 2 (Demeter et al. 2022).

It should be noted, however, that because genetic studies suggest that there were multiple evolving Denisovan population lineages widely dispersed in eastern Asia (Browning et al. 2018; Jacobs et al. 2019a; Massilani et al. 2020), the above scenario does not necessarily mean that other East and South Asian fossils were not Denisovans. Such a wider recognition of Denisovans becomes plausible given the above discussed fossil evidence for substantial genetic contribution from the West to the East during the Chibanian. Without ancient biomolecular evidence, the question of which fossils represent Denisovans remains difficult to confirm. Likewise, without fossil morphology, it is premature to assert the affinities and distributions of a population named from the genomic sequences at a single site.

One of us (YK) believes that the picture emerging from the combined evidence from fossil and biomolecular data is that most or all of the late Chibanian *Homo* residing in continental eastern Eurasia were Denisovans with substantial morphological variation (Peyrégne et al. 2024), and that the proposed Hexian/Penghu/Xiahe p-deme represents one of such Denisovan lineages. The other of us (SA) believes that the genomic sequence named at Denisova cave may ultimately be found in Asian fossils that have been assigned to *H. erectus*; and, that the fossils we classify as Asian *H. erectus* did not have a homogenous or singular fate. Rather, the variation we observe is the result of local population evolutionary trends that varied across the extensive landmass east of the Urals ("Asia") and included some cases of evolutionary continuity with later Pleistocene populations, and some cases of local extinction and recolonization.

MORPHOLOGICAL EVIDENCE OF DENISOVAN INTROGRESSION?

Some researchers suggest that the comparatively high frequency of 3-rooted lower molars in modern Asian-derived populations may have been a result of introgression from Denisovans, because the Xiahe mandible, a strong candidate for one of the Denisovan populations, possesses this rare feature in its second molar (Bailey et al. 2019; 2020). The presence of an almost identical 3-rooted lower second molar in Penghu 1 indicates that this may well have been a character shared by multiple individuals in eastern Asia. However, other researchers are more cautious about the above inference because Xiahe and Penghu differ from modern humans in detailed morphology. The former possess a lower *second* molar that exhibits a robust third (supernumerary) root between the lingual sides of plate-like mesial and distal roots, while in modern humans the typical condition is a 3-rooted lower *first* molar with a small third root on its distolingual aspect (Scott et al. 2020). In a similar manner, if we assume the above discussed Hexian/Penghu/Xiahe p-deme is one of the Denisovan populations based on large tooth size and a high frequency of M3 agenesis/reduction, it can be argued that they also contributed to some modern northeastern Asian populations, including a prehistoric Yayoi population in Japan, that show a comparatively high frequency of M3 agenesis (Brothwell et al. 1993; Yamada et al. 2004). Although such morphological data cannot be independent evidence of archaic introgression mainly because of unclear phenotypic signature of hybridization (Scott et al. 2020), the above observation offers useful hypotheses to be tested by future genetic studies.

DID DENISOVANS CROSS THE SEA?: FLORES AND LUZON

Among the genomes of contemporary Asia-Pacific populations, the highest levels of Denisovan introgression are found to the east of the Wallace/Huxley Lines, in Philippine Ayta Negritos, Papuan,s and Australians (Larena et al. 2021a; Reich et al. 2011; Teixeira et al. 2021). Studies of Denisovan genetic diversity demonstrated that this clade includes multiple deeply diverged branches, one of which to date has been found only in New Guinea and nearby islands (Jacobs et al. 2019a). Additionally, each of these populations carries its own proportion of DNA from different Denisovan groups, suggesting multiple introgression events occurring across different regions. These discoveries have led many geneticists to suggest that Denisovans, a presumed sister group to Neanderthals (Prüfer et al. 2014; 2017), had dispersed into some of the Wallacean and Philippine islands before 50 ka and resided there along with or nearby more primitive super-archaic hominins (Cooper and Stringer 2013; Jacobs et al. 2019a; Larena et al. 2021a; 2021b; Teixeira et al. 2021). The unidentified late Chibanian hominins on Sulawesi (Talepu) are cited as a potential candidate for such maritime Denisovan dispersals, and researchers have even suggested that some of the supposed super-archaic lineages (i.e., *H. luzonensis*, *H. floresiensis*, or both) actually represent a Denisovan group(s) (Choin et al. 2021; Larena et al. 2021a; Teixeira et al. 2021). What does the available fossil evidence inform us of regarding these issues?

H. floresiensis shows strong cranial morphological affinities with the older Javanese *H. erectus* from the terminal Calabrian contexts (Sangiran) but not with the nearly contemporaneous *H. erectus* from Ngandong, both in craniometric (see Figure 4) and detailed surface morphological characters (Kaifu et al. 2011a). This suggests that *H. floresiensis*, while specialized in many skeletal features in the isolated insular setting, retained ancestral cranial form though the Pleistocene while Javanese *H. erectus* on the Sunda Shelf experienced different cranial evolution. The deep evolutionary origin of *H. floresiensis* is also supported by the morphology of its mandible and teeth (Kaifu et al. 2011a; 2015b), as well as a series of discoveries from the So'a Basin on the same island (~0.7 Ma *H. floresiensis*-like dentognathic fragments, the occurrence of stone artifacts between ~1.0 and 0.7 Ma, absence of noticeable faunal turnover after ~1.0 Ma) (van den Bergh et al. 2016a; 2022). Therefore, *H. floresiensis* can be reasonably excluded from candidates for Denisovans.

In Luzon, there is a long gap in the archaeological/paleoanthropological record between the ~0.7 Ma unidentified hominins from Kalinga and the roughly 60 ka Late Pleistocene *H. luzonensis* fossil from Callao Cave (Detroit et al. 2019; Ingicco et al. 2018). We consider the evolutionary origin of the latter based on the morphology of the teeth. Its premolars are primitive and resemble *H. erectus* from Java. It is different from Neanderthals and modern humans in external and internal crown as well as root morphology (Detroit et al. 2019; Zanolli et al. 2022). Its posterior molars exhibit reductive trends similar to *H. sapiens*, but the M^1 internal crown and root morphology are primitive like *H. erectus*. These form the primary bases for the proposed evolutionary link between *H. erectus* and *H. luzonensis*, but primitive-looking dental features are also reported for Hexian, a possible Denisovan candidate together with Penghu and Xiahe, and possibly with Tam Ngu Hao 2 and Xuchang (Hexian/Penghu/Xiahe p-deme mentioned above).

It is worth considering whether this East Asian group could be ancestral to *H. luzonensis*. Assuming that our tooth identification for Hexian PA834 is correct (see above), the East Asian sample is characterized by a combination of large tooth size, relatively large second molar, and reductive trend of the last molar or M3 agenesis. In contrast, the Filipino specimen possesses relatively small molars with gradual, sequential posterior size reduction (M1>M2>M3) characteristic of *H. sapiens*. Although the difference in general tooth size may be explained by body size reduction on an island (Lomolino et al. 2013), the contrasting pattern of molar size proportion does not conformably fit with the hypothesized evolutionary link between the two hominin groups. Therefore, our proposed explanation for the currently available evidence is that both *H. floresiensis* and *H. luzonensis* evolved from late Calabrian early *H. erectus* populations on the ancient Sundaland. These insular species were isolated from the later—and more derived— Chibanian hominins for a substantial amount of time. Fossils are still poorly sampled from Island Southeast Asia, and no genetic information is available from either the Flores or Luzon hominins to evaluate the hypothesis of their deep roots. Under these limitations, a straightforward reading of the current fossil distribution in Figure 1 is that the Sunda Shelf and nearby islands had been the realm of *H. erectus* and its relatives throughout the Pleistocene, until *H. sapiens* appeared and dominated there around 50 ka. If this is correct, Denisovans as a sister group to Neanderthals did not cross the sea of Southeast Asia and its introgression to the present-day Australasian populations occurred in the continental areas before they occupied the islands of Wallacea and Philippines.

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DATA AVAILABILITY STATEMENT

All data used in this paper are present in the paper.

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