Sinking the "Archaic *Homo sapiens*" in eastern Asia: Establishing a Case for Hominin Diversity in the late Middle and early Late Pleistocene

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The term "archaic *Homo sapiens*" has been used to categorize Middle Pleistocene hominins since the 1960s. Its application is designed to account for morphologies that neither fit into the *Homo erectus*, *Homo neanderthalensis* (hereafter Neanderthals), nor *Homo sapiens* hypodigms (Bae, 2010). This gradistic classification is used in lieu of species designations mostly due to the high degree of variability in hominin fossils during this time which preclude them from a standardized set of criteria. While the degree of phylogenetic conservativism seen here is often employed to minimize the inflation of the human fossil record and to avoid ambiguous classifications, it is becoming more apparent that many designations in paleoanthropology are more variable than given credit and are therefore themselves gradistic in nature. This is recently realized within the group of early *Homo* species (*H. habilis* and *H. rudolfensis*) which can no longer be delineated in terms of encephalization, post-cranial proportions, or dentognathic dimensions as they once were (De Ruiter et al., 2017). This same problem is also apparent within Middle and Late Pleistocene *H. heidelbergensis* and early *Homo sapiens*. Such ambiguity has resulted in the dismissal of the former classification (now lumped with Neanderthals in western Eurasia and with the newly defined *H. bodoensis* in Africa) and a categorical expansion of the latter (Roksandic et al., 2021).

Similar to the disagreements concerning African and European post-erectine hominins, the academic climate in eastern Asian paleoanthropology embodies the taxonomic enigma known as the "Muddle in the Middle" (Roksandic et al., 2021). This paradigm reflects uncertainty in the systematic assignments and phylogenetic relationships of various hominin fossils in eastern Asia dating between approximately 400-100 ka. While the morphology of many of these fossils is distinct and, to some degree, regionally cohesive, the "taxonomic muddle" comes from commonalities shared with other Middle and Late Pleistocene taxa (*H. erectus*, Neanderthals *senso lato*, *and H. sapiens*) as well as genetic evidence supporting a Recent African Origins (RAO) model for the evolution and dispersal of modern humans (Kaifu, 2017; Lee and Hudock, 2021). Acceptance of the RAO has forced proponents of a multiregional theory for *Homo sapiens* evolution to revisit and, in some cases alter their hypothesis. Many have now adopted a

"braided stream" approach of integrating regional continuity with episodes of introgression into incoming populations of *Homo sapiens* and/or other post-erectine hominins (i.e., assimilation) (Kaifu, 2017; Lee and Hudock, 2021; Rosenberg and Wu, 2013). This explanation inevitably leads to the question, directly associated with the Muddle in the Middle, of who, or rather, what we call the population of hominins that encountered these migrants in the late Pleistocene?

The aforementioned question is at least in part dictated by whether it is answered by phylogenetic splitters or lumpers (Bae, 2010). The human fossil record in Eastern Asia has long been explained in terms of continuity through time from earlier forms (*Homo erectus*) to modern humans, with the late Middle Pleistocene fossils representing an intermediate morphology. As a result of this philosophy, many paleoanthropologists have allocated these hominins to "archaic" *Homo sapiens* (Bae, 2010; Bae, n.d.; Lee and Hudock, 2021). The splitter approach, however, sees diversity in many morphological variants and, in disagreement with the use of gradistic classifications, observes multiple species arising in the eastern Asian Middle Pleistocene. As such, proposed species designations include *Homo mabaensis, Homo daliensis, Homo longi, Homo luzonensis, Homo floresiensis,* and most recently, *Homo juluensis* (Bae, n.d.; Bae, 2010).

While the overidentification of species in paleoanthropology is a well-known point of contention, the observation of diversity over continuity highlights a clear range of variability in these hominin localities. In as much as this being true, lumping the human fossil record within this spatiotemporal facie into an overly generalized grade such as archaic *Homo sapiens*, or it's synonyms of Middle Pleistocene *Homo* and post-erectus grade *Homo*, seems inappropriate. The proposal to include these fossils with the already problematic *Homo heidelbergensis* is also unwarranted as this species designation is only loosely defined and as mentioned above, being challenged as an appropriate designation altogether (Roksandic et al., 2021).

While the purpose of this paper is not to answer questions regarding eastern Asian hominin systematics and/or phylogenetics, it will serve to review the current state of the human fossil record in this region. It will therefore update the review by Bae (2010) in which the author suggests that "until the eastern Asian evolutionary record is better known… it is better to err on the side of caution" when clarifying taxonomic issues (Bae 2010: 87). Since then, there have been new fossil discoveries and technological advances in the field that warrant a reassessment of this moment in our ancestry. Thus, I will discuss the various fossils from the region during the

late Middle and early Late Pleistocene by highlighting the recent literature associated with previously known assemblages and presenting new fossil finds. Without supporting any one interpretation over the other, I will also attempt to discuss the different ways in which these fossils have been worked into new and existing theories on the peopling of eastern Asia throughout the tail end of the Pleistocene.

A final question that requires discussion in this review concerns the potential interaction, influence, and inception of the almost morphologically invisible lineage referred to as Denisovans. To date this pseudo-taxon is defined by genomic analysis with only minor clues as to their morphology (Chen et al., 2019; Sawyer et al., 2015; Slon et al., 2017; Zhang et al., 2020; Zhang et al., 2021). With the type locality already within the margins of eastern Eurasia, these hominins have been a part of the discussion in eastern Asian phylogenetics since their inception (Ni et al., 2021). The unique dental morphology identified in Denisova cave, however, has recently taken on an even more significant role as the Xiahe hemi-mandible from the Tibetan plateau assemblage at Baishiya Karst Cave (BKC) has been tentatively identified as a Denisovan based on biochemical studies and associated genomics identified within the cave sediments (Chen et al., 2019; Zhang et al., 2020). Similarities found in the dental metrics between the BKC and the Altai Mountain fossils has ushered in new associations between Denisovans and the East Asian human fossil record with different authors associating these remains with different newly proposed species designations. This would, in effect, ascribe a long-awaited species status to the mysterious Denisovan populations.

The following review is designed to highlight the pertinent contextual and morphological data for fifteen of the most often discussed late Middle and early Late Pleistocene human fossil localities in eastern Asia (Table 1, Fig. 1). Hence, each locality will open with a discussion of the temporal designation and follow with paleoenvironmental interpretations (when available) before reviewing the specifics of the hominin assemblage. Many of these fossil localities also contain archaeological material along with other evidence pertaining to human behavior. These aspects of the human fossil record, however, fall out of the scope of this review. Instead, I focus attention on the hominin fossils as they relate to an impressive range of morphological variability throughout the region. Special attention is then given to the two most recently proposed species designations in East Asia, *Homo longi* and *Homo juluensis*.

Table 1: Eastern Asian hominin localities discussed in text

| Locality	Country	Lat/Long	Date	Dating Methods	Elements
Dali	China	34˚52'N, 109˚40'E	267-258 ka	Thermally Transferred OSL and Infrared Stimulated Luminescence	Cranium
Chaoxian	China	31˚32'55"N, 117˚51'51"E	Debated 200-160 ka or 360-310	Faunal correlation and U-Series	Partial Maxilla w/dentition, partial occipital, loose maxillary teeth
Maba	China	24˚41'N, 113˚35'E	135-129 ka or ~237 ka	U-series	Partial calotte
Jinniushan	China	40˚35'N, 122˚27'E	200-260 ka	U-series, Biostratigraphy	Partial Cranium, most of upper dentition, lots of post crania
Hualongdong	China	30˚06'34.1"N, 116˚56'54.2"E	275-331 ka	U-series	Partial Frontal, Partial Cranium, Mandible, isolated teeth, 3 partial femora
Penghu	China	Ind.	Unknown, sometime between 190 ka and 10 ka	Biostratigraphy	Right hemi-mandible w/dentition
Lingjing (Xuchang)	China	34˚04'08.6"N, 113˚40'47.5"E	125-105 ka	OSL	Cranial fragments
Xiahe (Baishiya Karst Cave)	China	35˚26'53"N, 102˚34'17"E	~160 ka	U-series	Mandible
Harbin	China	45˚45'27"N, 126˚38'27"E	309-138 ka	Biostratigraphy, U-series, OSL	Cranium
Xujiayao	China	40˚06'N, 113˚59'E	220-160 ka	Al/Be, Biostratigraphy	Cranial fragments, dentition
Panxian Dadong	China	25˚37'38"N, 104˚08'44"E	300-190 ka	U-series, OSL, ESR	4 teeth
Tam Ngu Hao	Laos	20˚12'41.5"N, 103˚24'32.3"E	164-131 ka	pIR-IRSL, U-series, ESR	Single $M_{1/2}$
Liang Bua cave/Mata Menge	Flores	08˚31'50.4"S, 120˚26'36.9"E	100-60ka /~700 ka	TL, IRSL/ $^{40}Ar/^{39}Ar$	Cranium, partial skeleton/Mandible, isolated teeth
Callao Cave	Philippines	17˚42'11.7"N, 121˚49'25.5"E	67-50 ka	U-series	Assorted dentition and postcrania
Ma U'Oi	Vietnam	20˚37'22"N, 105˚16'40"E	193-49 ka	U-series	2 teeth, occipital fragment
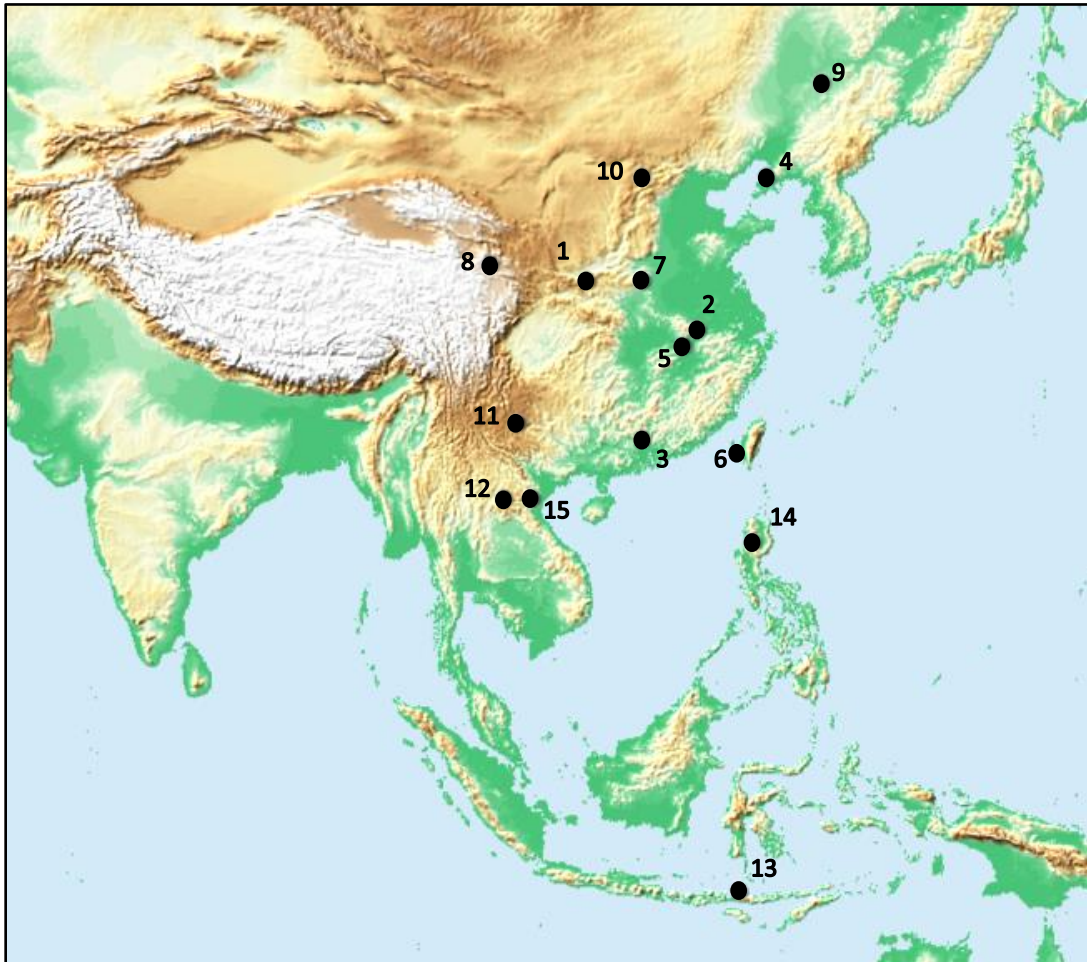
Figure 1. Map of the Eastern Asian hominin localities discussed in text. 1) Dali, 2) Chaoxian, 3) Maba, 4) Jinniushan, 5) Hualongdong, 6) Penghu, 7) Xuchang, 8) Xiahe, 9) Harbin, 10) Xujiayao, 11) Panxian Dadong, 12) Tam Ngu Hao, 13) Liang Bua, 14) Callao Cave, 15) Ma U'Oi

Maba

The Maba partial cranium was first discovered in 1958 by local farmers who were excavating fertilizer from Shizishan (Lion) Cave just southwest of Maba Village, Shaoguan Municipality, Guandong Province in southern China. The fossil originally consisted of several fragments which have been refitted to form a partial calotte (frontal and parietals) with an intact right eye orbit and nasal bones (Bae, 2010; Wu and Poirier, 1995; Xiao et al., 2014). Subsequent excavations in 1960 and 1984 yielded additional material consisting of a partial mandible and seven teeth. Analysis of these additional materials, however, has shown that they are not associated with the original cranium and rather derive from recent *H. sapiens* populations

possibly associated with neolithic material found in a different area and level of the Shizishan Cave (Xiao et al., 2014). Thus, the Maba partial cranium discovered in 1958 represents the only currently known Pleistocene hominin material at this locality.

There is currently no agreement on the exact age range of the Maba cranium. Attempts to date the fossil horizon with Uranium series methods have produced disparate results with early studies suggesting a range between 135-129 ka and later studies suggesting >237 ka (Bae, n.d.; Bae, 2010; Wu and Poirier 1995; Xiao et al., 2014). While the more recent analysis is given more credence because of the advanced methods used, authors note that the flowstone used in both of the analyses is more than 20 meters away from the fossil bearing deposit. Thus, the use of the ranges produced by these chronometric studies should be taken with caution. It is perhaps more informative then to make use of the associated fauna when considering the age of the Maba specimen which tentatively places the fossil within the Late Pleistocene (Bae, n.d.; Xiao et al., 2014).

As in the above case of poor temporal context, the paleoenvironmental context for the Maba site is still in need of refinement (Xiao et al., 2014). Bae (2010) calls attention to the surprisingly southern presence of *Palaeoloxodon namadicus* (Asian straight tusked elephant) which is typically found at higher latitudes. Xiao and colleagues (2014) reflect on the presence of *Ailuropoda* (Giant Panda) which might indicated an environment rich with Bamboo Forest. Though, the fossil record is strikingly lacking in other fauna typically indicative of this environment (i.e., the bamboo rat *Rhizyomys sinensis*). It is, of course, possible that this latter observation is due to preservation bias given the nature of micromammal remains.

Despite the contextual problems with the Shizishan Cave deposits, the Maba cranium is unique from other eastern Asian Pleistocene fossils and therefore of great interest. Primary attention is given in this respect to the shape of the preserved right eye orbit. It is unlike any other Pleistocene hominin fossil from China in exhibiting rounded instead of squared orbits and a sharp instead of rounded inferior lateral margin (Bae, n.d.; Bae, 2010; Wu and Poirier 1995). These features of the facial skeleton, especially the orbital shape, are generally absent in Middle Pleistocene fossils from eastern Asia and more strongly associated with Neanderthals. Bae (n.d.; 2010) further sees commonality between Neanderthals and the Maba specimen from robust nature of the supraorbital torii and the absence of a supraorbital notch, suggesting that "if Maba

was found in the Western Old World in all likelihood it would have been assigned to the Neanderthal hypodigm" (Bae, n.d.). Other features of the cranium draw less-specific associations. Relative to *H. erectus*, the cranial walls are thin and the frontal, while deemed flat, is noticeably elevated. Postorbital constriction is pronounced, and the maximum cranial breadth is situated only slightly above the supramastoid ridge and therefore low on the temporal bones rather than the parietals as is seen in Neanderthals and *H. sapiens* (Bae, 2010; Li et al., 2017; Wu and Poirier, 1995). Together, these characters reflect an interesting case of mosaicism which might provide evidence of introgression with Neanderthal-like hominins migrating in from the west. More data will be needed to answer this question in the future but for now the rounded eye-orbits might be considered a strong indicator of Neanderthal presence in the region.

Chaoxian

The Chaoxian hominin remains are named for their discovery at a Yinshan Hill limestone fissure deposit (potentially the remnants of a cave) in Chaoxian county, Anhui Province, eastern China. Its significance was first identified in 1981 through a geological survey of the Anhui Bureau of Geology. Subsequent investigation from IVPP researchers (Institute of Vertebrate Paleontology and Paleoanthropology) in 1982 and 1983 uncovered the single occipital and maxillary fragments and 3 isolated teeth that constitute the whole of the hominin assemblage. While associated fauna have been identified from the hominin bearing deposits (Wu and Poirier, 1995), there is no report on the paleoenvironmental or biostratigraphic context of this material. Early attempts to date some of the mammalian teeth by means of Uranium series methods produced an age range of between 200 ka and 160 ka but these have been pushed back to between 360-310 ka more recently by advanced TIMS U-series dating of speleothems within the fissure. Still, the association between the hominin material and the sampled speleothem is loose and leaves researchers with little more than a broad Middle Pleistocene correlation for the Chaoxian remains (Bae, n.d.; Bae, 2010; Wu and Poirier, 1995).

Morphological analysis is similarly limited with the Chaoxian hominin. Wu and Poirier (1995) observed moderate thickness of the occipital torus with no external occipital protuberance, and they estimate an occipital angle that "approaches that of early *Homo sapiens*" (134). It is interesting to consider the presence of a fovea which corresponds to the suprainiac fossa. This trait has been strongly associated with Neanderthal morphology in other assessments (e.g., Li et

al., 2017). In analysis of the 8 teeth (3 isolate and 5 in occlusion), however, Bailey and Liu (2010) determined that the remains were unremarkable for the Middle Pleistocene and distinctly not affiliated with Neanderthal dental morphology.

Panxian Dadong

The Panxian Dadong site is a large limestone karst cave located in the Guizhou Province of southwest China. The cave itself is only one of five interconnected karstic caverns tunneled within a 230 m-high hill at an elevation of approximately 1638 MASL (Meters Above Sea Level). The total area of the main Dadong cave chamber covers some 8000 m^2 and spans approximately 220 m long (Zhang et al., 2015). The cave site was first reported in 1990 and led to a 13-year excavation period between 1992 and 2005, yielding an abundance of archaeological materials, faunal remains, and taphonomic evidence of hominin butchery practices but only 4 hominin teeth (I^1, C, P^3, and P_3). The sedimentary sequence of the Quaternary deposits spans a depth of up to 19 meters, divided into 12 stratigraphic units. A variety of dating methods have been applied in attempts to establish the temporal sequence of the hominin bearing deposits. Uranium series has been used to date associated speleothem samples with different layers suggesting depositional sequence between 316 and 18 ka, though the association between the samples and the sediments from the excavation area has been questioned. Subsequent ESR and coupled ESR/U-series techniques were applied to mammalian teeth found at different stratigraphic levels suggesting a narrower range of approximately 300-120 ka. These dates seem also to agree with the biostratigraphic position of the associated fauna. More recently, OSL methods have been used on quartz and feldspar grains excavated from three horizons (I, V, and XII). While these dates mostly agree with the ESR results, the authors suggest a slightly older and narrower range of between 300 ka and 190 ka (Zhang et al., 2015).

The Panxian Dadong hominin remains, though limited to four teeth, are interesting in that they come from different deposits within the cave, indicative of multiple individuals and potentially different occupations. While the incisor (I^1) could not be directly associated with a particular stratum, the canine, P^3, and P_3 were excavated from different layers and thus have different associated ages within the temporal sequence (257-137 ka, 208-160 ka, 296-233 ka, respectively) (Liu et al., 2013). These dates, however, are based on the ESR sequence and therefore may be slightly older than reported. Regardless of the ESR/OSL disparity, these results suggest long

term occupation of the sight, an observation supported by an abundance of lithic artifacts and hominin altered faunal remains spanning the occupational sequence. It is also interesting to note from these studies that the occupation of the cave seems to follow glacial periods (MIS 6 and MIS 8) with breaks in the cultural sequence during warmer interglacials (MIS 7) suggesting that the cave was mostly heavily used during the cold, wet intervals. The faunal composition during these occupations is dominated by Ailuropoda (Giant Panda) and Stegodonts (Proboscidean related to elephants) typical of Oriental taxa, reflecting a mixed woodland environment with Bamboo Forest and open rocky areas with abundant grasses (Liu et al., 2013).

With a limited sample size, a thorough morphological analysis of the Panxian Dadong hominins is greatly hindered. Liu et al. (2013) provide a detailed analysis of the four teeth found within the site reporting that the morphology mostly aligns with other late Middle and Late Pleistocene fossils in Asia, though possibly some specimens showing a more derived condition. While the incisor and canine are somewhat more archaic in respect to robusticity and crown shape, the premolars seem to group, in these traits, more with other later Pleistocene hominin fossils as well as more recent *H. sapiens*. In all, the authors suggest that, while the Panxian Dadong teeth overlap with Neanderthals and *H. sapiens* in some morphological trends, they also present primitive features associated with Middle Pleistocene Asian *H. erectus*. Further, the teeth lack any discernable apomorphic traits that can directly ally them with known hominin taxa (Liu et al., 2013). Like so many other fossils from this region during the late Middle and early Late Pleistocene, the Panxian Dadong teeth represent a mosaic morphology that is more likely to be associated with a yet to be defined eastern Asian lineage.

Ma U'Oi

The Ma U'Oi cave (meaning "cave of the spirit of orang-utan") site is situated at Man Duc Village in the northeastern extremity of the Annamitic Mountain Chain and the western border of the Red-River fault zone of northern Vietnam (Bacon et al., 2004: 306). It is one of many such caves in a dense system punctuating the Tan Lac district's massive Tower Karst peaks. This particular site was first discovered through survey of a nearby cave (Chieng Xen) in 1991. It wasn't until 2001 and subsequent excavations in 2002, however, that hominin remains were identified (Bae, 2010; Bae, n.d.; Demeter et al., 2005; Bacon et al., 2006).

The total hominin assemblage at Ma U'Oi consists of three elements: 2 teeth (M_1 and M^2) and an occipital fragment. Though found during different field seasons (M_1 in 2001 and M^2/occipital in 2002), the materials were all recovered from the same stratigraphic level, suggesting that the originated from the same period of time. While most of the mammals identified from the faunal assemblage still exist throughout Vietnam today, the total composition is reminiscent of Middle and Late Pleistocene deposits. This observation was confirmed by biostratigraphic association with materials from two different sites in the region (Tham Wiman Nakin and Lang Tran) which dated the comparable remains through direct U-series analysis to ~169 ka and 80-60 ka, respectively (Demeter et al., 2005; Bacon et al., 2004; Bacon et al., 2006), though Bae (n.d.) reports a broader age range of 193-49 ka. These "diversified modern fauna", including taxa such as *Elephas*, *Rhinoceros, N. fulvescens,* and *L. sabanus* suggest a variable lowland forest environment, though the absence of *Pongo* may suggest a more open woodland (Bacon et al., 2004: 312-313).

Most of the taxonomic interpretation of the hominin teeth can be attributed to the age of the Ma U'Oi deposits and metric associations of the M^2 which fall in line with the typical range for late Middle Pleistocene hominins in eastern Asia (Table 2). Interestingly, in addition to the metrics, Demeter et al. (2005) note the lack of taurodontism and occlusal wrinkles on the molars suggesting a derived condition over *H. erectus* that is more common with *H. sapiens*. While the occipital fragment seems to have little value in taxonomic discussions, the dental observations illustrate a hominin with affinities of both earlier and later Pleistocene populations.

TABLE 2. Maxillary Molar Metrics in mm: Mesiodistal (md), Buccolingual (bl), and Crown Index (CI)

	Hualongdong	Harbin	Jinniushan	Chaoxian	Xujiayao	Ma U'Oi	*Homo luzonensis*	Denisova 4	Denisova 8
M^1 md length					13.4				
M^1 bl width					14.0				
M^1 CI					104.5				
M^2 md length	11.6	13.6	11.1	11.6	11.9	10.8	8.0	13.1	
M^2 bl width	12.7	16.6	12.3	14.1	14.2	12.7	10.5	14.7	
M^2 CI	109.5	122.1	110.8	121.6	119.3	117.6	131.25	112.2	
M^3 md length									14.3
M^3 bl width									14.65
M^3 CI									102.4

Harbin

Homo longi was named by Ji et al., in 2021 (Figure 2). The species designation is made from a single, mostly intact cranium reportedly first discovered in 1933 but kept from science until its recent donation to the Geoscience Museum of Hebei GEO University in 2018 (Ji et al., 2021).

The fossil was purportedly discovered by a local worker during the construction of the Dongjiang Bridge designed to span across the Songhua River in Harbin city, Hebei Province, China. It was subsequently hidden by its discoverer in a well before emerging again some 80 years later (Bae, n.d.). Given the unusual circumstances of the specimen's discovery, the context of the Harbin cranium is poorly understood and a point of contention regarding its designation. To address this issue, the research team performed a variety of analyses to correlate the fossil within a specific geologic/stratigraphic context and applied direct U-series dating methods to establish a geologic age. The analyses included a comparative sample of seven fossil mammals (including two human fossils) with known provenience within Songhua River deposits near Dongjiang bridge. It is worth mentioning that the Harbin area is a known fossiliferous region with more than 70 fossil species identified across well-established stratigraphic intervals. The comparative material was derived from three known stratigraphic formations, the Guxiangtun,
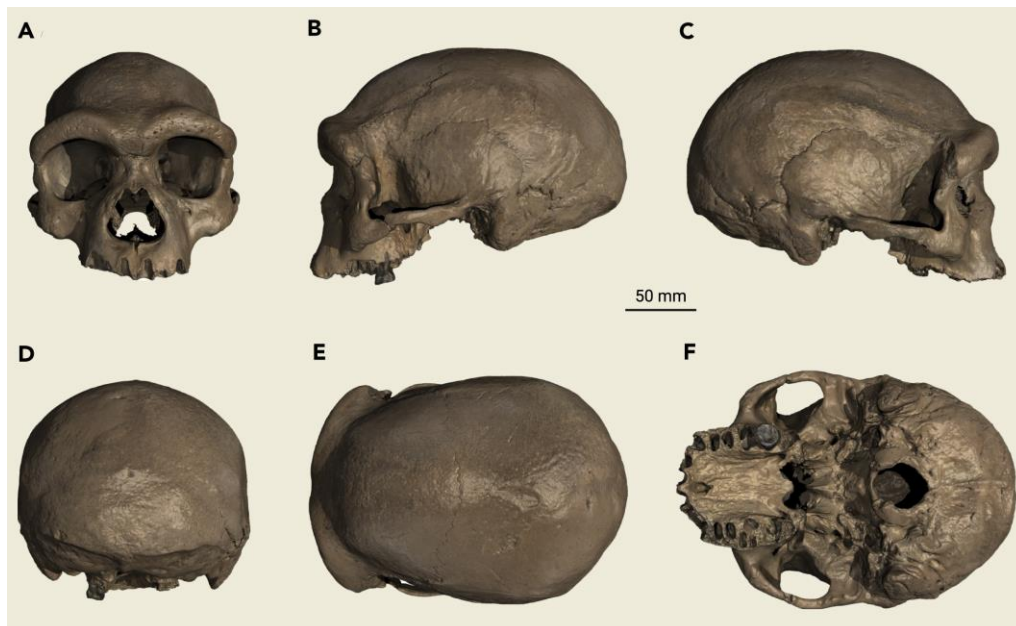

Figure 2: Harbin cranium. From Ni et al. (2021). (A) frontal, (B) lateral left side, (C) lateral right side, (D) posterior, (E) superior (F) inferior views

Harbin, and Upper Huangshan Formations, collectively dating between 309-12 ka by OSL methods (Shao et al., 2021).

The use of Rare Earth Element (REE) analysis, X-Ray Fluorescence, and Strontium isotopic analysis confirmed the geological association between the Harbin cranium and the comparative fossil material. This in turn suggested that the cranium 1) came from the Harbin area as it was reported and 2) that it came from stratigraphic formations dating between the late Middle Pleistocene and the early Holocene. The context suggested from the specimen's history of discovery is therefore deemed accurate with a likely upper age limit of 309 ka. To establish a minimum geologic age for the fossil, Uranium series methods were applied directly to the cranium. Of the ten samples taken, five exhibited evidence of Uranium leaching and another two were taken from teeth which were suggested to have experienced delayed uptake relative to the cranial samples. These seven samples were thus excluded from the analysis. The remaining three dated to 106±1 ka, 129±1 ka and 148±2 ka, capping a minimum age of ~146 ka (Shao et al., 2021). The Harbin cranium is therefore associated with a late Middle Pleistocene date ranging between 309-146 ka.

The temporal context established for the Harbin cranium is also consistent with the observed morphology. The specimen is remarkably well-preserved exhibiting a nearly complete, undistorted cranium with only minimal damage to the left zygomatic arch and post-mortem loss of all but one tooth (left M^2). It is reported as being "larger than all other known-archaic humans" recording the greatest values for maximum cranial length, nasio-occipital length, and supraorbital torus breadth within an impressive comparative sample of more than 80 Pleistocene hominin crania (Ni et al., 2021). It additionally scored the second highest values for measures of biauricular breadth, frontal chord, zygomatic breadth, and biorbital breadth solidifying the specimen as categorically robust (Table 5). Qualitatively, the Harbin cranium exhibits both archaic and derived features. It has a voluminous braincase with an estimated cranial capacity of ~1,420 cc that is well within the range of *H. sapiens* and Neanderthals. The supraorbital torus, however, is massive relative to *H. sapiens* and Neanderthals and punctuates a receding forehead sloping into a long and low cranial shape more similar to *H. erectus*. Perhaps the most surprising morphological condition of the Harbin cranium is the relatively low (albeit wide) and retracted facial skeleton that typifies *H. sapiens* facial morphology. Though this condition is seen to some degree in other eastern Asian late Middle Pleistocene fossils (e.g., Dali and Jinniushan), the Harbin condition is suggested to be derived relative to these materials and evidence supporting

the new species designation (Bae, n.d.; Ji et al., 2021; Ni et al., 2021). *H. longi*, therefore, is reported to have a mosaic morphology with a combination of features that share commonality both with penecontemporaneous Middle Pleistocene hominins (e.g., *H. erectus, H. neanderthalensis*, Dali, Jinniushan, and Dali) along with more recent *H. sapiens*.

The diagnosis offered by the Ji and colleagues (2012) raises questions regarding the phylogenetic position of *H. longi*. A metric analysis of the single M^2 (see Table 2), perhaps not surprisingly, provides robust measurements beyond that of most late Middle Pleistocene hominin fossils. This quality of robust dentition is also reported for the Xiahe hemi-mandible from Baishiya Karst Cave in the Gansu Province within the Tibetan Plateau as well as the isolated teeth associated with the little understood Denisovan population from Denisova Cave within the Altai Mountains of Siberia (Ni et al., 2021).

Interestingly, while the authors claim that the Harbin cranium is the only fossil specimen yet known to be included in the *H. longi* hypodigm, they note its shared similarities with the Jebel Irhoud, Eliye Springs, Xiahe, Dali, Jinniushan, and Hualongdong hominin fossils. The similarities seen between these fossils lead Ji et al. (2021) to conclude that, while *H. longi* is represented by a single specimen, it and the aforementioned fossils form a monophyletic clade that is a sister lineage to *Homo sapiens* (Ni et al., 2021). While the significance of this claim is considered more specifically later in this paper, it is worth discussing the hominin fossils suggested to be part of this clade as they compare to the Harbin cranium and other late Middle Pleistocene fossils. Thus, the material from Dali, Jinniushan, Hualongdong, and Xiahe, being the fossils associated with a proposed monophyletic "Harbin group" (Ni et al., 2021: 4) are considered relative to this fossil below.

Dali

The Dali hominin (Figure 3) is represented by a relatively intact cranium discovered at the southern edge of the Chinese loess plateau along the Luo River near the village of Jiefang, Dali County, Shaanxi Province, in northwestern China. It was found in 1978 within the third unit of a thirteen-layer sedimentary sequence. The fossil was discovered *in situ* positioned on top of a gravel unit made up of fluvial sediments. Subsequent excavations of the hominin unit (layer 3) resulted in a collection of 28 different faunal species ranging from mollusks to birds, fish, and an abundance of mammals. While these excavations also revealed an assemblage of archaeological

material, a review of material culture is beyond the scope of this paper and hence omitted from the discussion.

Figure 3: Dali cranium. Left, anterior view. Right: anterolateral view

The temporal sequence for the site has been established through the application of a wide array of analytical techniques and on disparate materials. Uranium series, Thermoluminescence (TL), and Electron Spin Resonance (ESR) analyses were performed on faunal teeth and shells. With the addition of chronostratigraphic correlation with central Loess Plateau deposits, these analyses provided a range of age profiles from as recent as 180 ka to more than 330 ka (Sun et al., 2015). More recently, advanced methods in Thermally Transferred Optically Stimulated Luminescence (TT-OSL) and post-Infrared Infrared Stimulated Luminescence (pIR-IRSL) have been applied to multiple fluvial and aeolian layers throughout the stratigraphic sequence. Together, these data narrow down the date range for the Dali cranium to a period between approximately 267-258 ka (Bae, n.d.; Sun et al., 2015).

In addition to environmental information gleaned from faunal analysis, palynological samples were taken from 3 sedimentary horizons within the Dali stratigraphic sequence. These sampled horizons include layers 3 (hominin layer), 5, and 6. Together with the fauna, the materials reconstruct a transitional environment from glacial cool periods dominated by steppe grassland at the time of the hominin deposition to a progressively warmer interglacial period with grassland habitats punctuated by small patches of deciduous forest shortly after (Sun et al., 2015).

The Dali cranium is mostly complete but missing the right aspect of the posterior vault (including portions of the parietal, temporal, and occipitals bones), posterior and inferior portions of the left zygomatic, the lower portion of the nasal bones, and exhibits damage to both orbital

roofs. Additionally, aspects of the facial skeleton appear to have been altered, though minimally, by post-depositional distortion (Wu and Athreya, 2013). Morphologically, it is robust with a mosaic combination of ancestral and derived characteristics. In its most outwardly apparent traits, such as the robust supraorbital torus, receding frontal, slight frontal and sagittal keeling, along with a long and low cranial shape, the Dali morphology appears to be in line with earlier eastern Asian Pleistocene hominins (i.e., *Homo erectus*) (Wu and Athreya, 2013; Athreya and Wu, 2017) as well as late Middle Pleistocene fossils such as that found at Harbin. Unsurprisingly for this geographical and temporal context, however, Dali also exhibits a variety of traits also in line with penecontemporaneous hominins from Eurasia and Africa.

While the authors agree that Dali is primarily primitive in aspects of the neurocranium (Wu and Athreya, 2013; Athreya and Wu, 2017), it is worth pointing out some of the cranial vault characteristics which illustrate continued expansion of cranial capacity at this time. In neurocranial volume, Dali appears on the lower end of the scale for this spatiotemporal facie (~1120 cc). Despite this relatively low cranial capacity, it is inferred from craniofacial measurements that the Dali hominin would have also had a relatively low body mass. Using orbit size as a proxy for body mass, it appears that the specimen reflects "considerable encephalization" (Wu and Athreya 2013: 150). The expanded brain size is also seen indirectly as it resulted in slightly arched and bossed parietals and upper expansion of the temporal squama and occipital plane. These features reflect a more globular, rounded cranium than the lower and more elongated form typical of *Homo erectus* (Wu and Athreya, 2013; Athreya and Wu, 2017).

As is the case with the Harbin, Hualongdong, and Jinniushan fossils, Dali exhibits most of its derived morphology in the facial skeleton. These features include a relatively low zygomatic which is anteriorly oriented in its medial aspect with a more inferolateral zygomatic-alveolar margin, reduced midfacial prognathism, and reduced post-orbital constriction (Athreya and Wu, 2017). Interestingly, while Wu and Athreya report on the absence of the canine fossa (a trait commonly associated with *H. sapiens*) in 2013, they report on its presence in 2017. This seems to be related to how the trait was originally defined by Rightmire (1998, 2004) and influenced by recent analysis and diagnosis of the Jebel Irhoud fossils in Morocco as early *Homo sapiens*. The latter influence confirmed that "several derived traits used to define *H. sapiens* were present as far back as 300 ka" (Athreya and Wu, 2017: 16). The combination of traits seen in the Dali

cranium are interpreted by Wu and Athreya (2013, 2017) as evidence of eastern Eurasian evolutionary continuity with episodic introgressive influence from different hominin populations in a "braided stream" network of gene flow.

Jinniushan

The Jinniushan material was discovered in 1984 outside the town of Yinkou, Liaoning Province, northeastern China (Figure 4). It was situated within an isolated karst prominence in a fissure of a collapsed limestone cave. The assemblage is impressive for its preservation and relative completeness including a cranium, 6 vertebrae, 2 ribs, a complete left patella, left ulna, left os coxa, and numerous hand and foot bones (Rosenberg and Wu, 2013; Rosenberg, Zuné, and Ruff, 2005). The total fossiliferous sequence spans approximately 12-15 meters, with the hominin materials having been excavated near the bottom from a <2 m^2 area within layer 7 (Bae 2010; Chen et al., 1994; Rosenberg and Wu, 2013). Various Uranium series and ESR dates were established from samples of associated faunal teeth providing a wide age range of ~300-200 ka (Chen et al., 1994, Rosenberg and Wu, 2013), with narrower approximations of between ~280-260 ka (Bae, 2010). These dates agree with the combination of Palearctic and Oriental fauna (*Dicerorhinus* and *Macaca*, respectively) found within the hominin deposits (Bae, 2010).

Figure 4: Jinniushan cranium. Anterior view. From Rosenberg, Zuné, & Ruff (2005).

Rosenberg and Wu (2013) report on a variety of cranial traits for the Jinniushan specimen that are differentially categorized as modern and archaic as well as those that are more like earlier Pleistocene eastern Asian hominins (*H. erectus senso stricto*). In many of these features, the Jinniushan hominin is said to resemble the Dali cranium, though, while the external measurements are similar, the thinner cranial vault leads to a slightly increased cranial capacity (Dali is at ~1,120 cc whereas Jinniushan is estimated at ~1,330 cc) (Rosenberg, Zuné, and Ruff, 2005). In its more primitive *H. erectus*-like traits, the supraorbital torus is projecting and arched over each orbit, separated from the frontal squamous by a supraorbital sulcus. While sagittal keeling is not reported (as it is for Dali), a distinct frontal keel is observed and situated within a wide but vertically oriented face. The broad interorbital distance and broad nuchal torus are suggested to be in line with other late Middle Pleistocene hominins from the region (e.g., Harbin). Some of the more gracile aspects of the cranium, however, are interpreted as evidence of early modernity in the region. These include the thin vault bones relative to Dali, a broad frontal, gabled cranial contour, and reduction of the nuchal plane. Given the similarity observed between Dali and Jinniushan, the differences in robusticity are interpreted as evidence of sexual dimorphism in the region (Rosenberg, Zuné, and Ruff, 2005).

The opportunity to study the post-cranial anatomy of Middle Pleistocene hominins is rare. Though the recent discovery of *Homo naledi* in the Rising Star cave system, South Africa has added to the sample, the Jinniushan material represents some of the only post-cranial material that falls chronologically between KNM-ET 15000 (Turkana Boy) at approximately 1.6 Ma in East Africa and Tabun 1 at ~122,000 BP in the Levant (Berger et al., 2015; Rosenberg, Zuné, and Ruff, 2005). Analysis of these fossils established the Jinniushan hominin as a female despite having a relatively robust cranium and that she stood at approximately 168 cm (~5'6") tall and weighed roughly 77 kg (~170 lbs) (Bae 2010; Rosenberg, Zuné, and Ruff, 2005; Rosenberg and Wu, 2013). The stature estimation for Jinniushan conforms to the expected environmental constraints in this region during the late Middle Pleistocene (following the principles of Bergmann's and Allen's Rules) and has also allowed for an accurate measure of encephalization. Inputting the approximated data for body mass and brain mass, the authors were able to equate an Encephalization Quotient (EQ) of 4.150 for Jinniushan (Rosenberg, Zuné, and Ruff, 2005). While this is below the estimate for Dali (EQ=5.3), Dali relied on proxy associations and was thus an admittedly "imperfect measure" (Wu and Athreya, 2013). Regardless, both specimens

exhibit encephalization scores that are higher than expected for *Homo erectus* (Rosenberg, Zuné, and Ruff, 2005, Wu and Athreya, 2013).

Hualongdong

The Hualong Cave site (Hualongdong) is located within Dongzhi County of Anhui Province, East-Central China (Bae n.d.; Wu et al., 2019, 2021). While hominin fossils were first discovered at this site in 2006 (n=2), subsequent excavations between 2014 and 2019 yielded an additional 25 fossils from cranial and post-cranial regions, representing a minimum of 16 individuals. Uranium series dates were established from three sources (associated speleothem fragments, overlaying calcitic crust, and an associated dripstone) to provide a geologic age range of ~331-275 ka. These dates were further supported by the associated faunal which, broadly similar to the well-known Hexian *H. erectus* site, situates Hualongdong distinctly in the Middle Pleistocene (Bae n.d.; Wu et al., 2019). Interestingly, the faunal assemblage was comprised of material representative of the two primary biogeographical zones, Palearctic and Oriental, established for eastern Asia. While the most abundant fauna reflects a subtropical montane Oriental Forest, the presence of Palearctic species suggests a "southward dispersal event of boreal fauna" indicative of a relatively cold or cooling mid-Pleistocene climate (Wu et al., 2019: 8).

Among the 27 hominin fossils discovered at Hualongdong, 11 represent the fragmentary remains of a single cranium, HLD 6 (Figure 5). Though fragmented, HLD 6 is undistorted and preserves necessary elements (frontal, left parietal, posterior temporal portion, maxillae, left zygomatic, palatines, left lateral sphenoid) for a nearly complete digital reconstruction through mirror-imaging of absent portions. The remains also preserve a fragmentary mandible and much of the post-canine dentition (all 8 M1s and M2s, a P_4 and a P^3 root, and the developing left M^3 crown). The developing left M^3 of HLD 6 suggests a juvenile specimen with an age-at-death of approximately 13-15 years (Wu et al., 2019; Wu et al., 2021). With nearly all elements represented in the reconstruction (lacking the occipital), HLD 6 becomes a valuable specimen for understanding hominin variation during the late Middle Pleistocene. While the juvenile status of the individual might be considered problematic for phylogenetic inference, the authors refer to previous studies on ontogenetic growth in the hominin facial skeleton that illustrate the "apparent insulation" of features under consideration during development (Wu et al., 2021: 3). Given the acceptance of facial stability in the ontogenetically younger comparative material (ATD6-69

from Gran Dolina, Sierra de Atapuerca, Spain), the authors propose that "any remaining ontogenetic growth experienced by HLD 6 would have had minimal effects" on the morphological comparison to adult specimens (3).
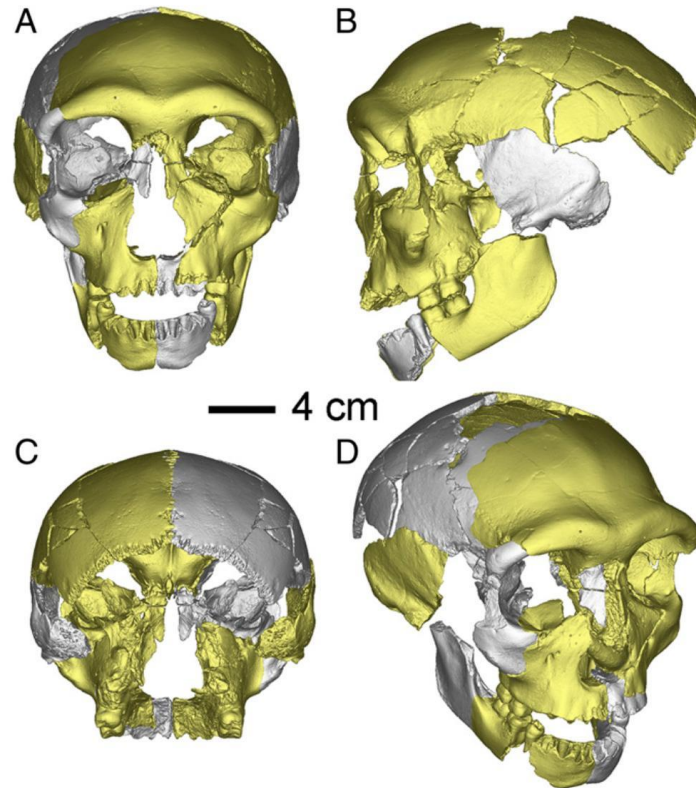

Figure 5: HLD 6 reconstruction. (A) anterior, (B) lateral left side, (C) posterior, (D) anterolateral right side views. From Wu et al. (2021).

Morphologically, Wu et al. (2021), illustrated a mix of primitive and derived features in a number of craniofacial elements including the supraorbital region, nasal region, malar region, hard palate, and paranasal sinuses. These analyses showed variable affinities with earlier *H. erectus* conditions (i.e., low and wide cranial vault, heavily constructed supraorbital torus, condition of the maxillary zygomatic process, a well-developed malar tuber, absence of the canine fossa, maxillary sulcus, and some quantitative measures such as orbit index) but much more closely allied the HLD 6 facial morphology with early *H. sapiens*. While retaining some clearly non-*H. sapiens* traits (i.e., exaggerated supraorbital torus and frontal keel), the presence of a flat face, nearly vertical mandibular symphysis, pronounced mental trigone, and overall gracile dentition (Tables 2 and 3) led the authors to claim that this specimen represents "the first

late Middle Pleistocene hominin" to reflect a dominant signal of modern facial morphology (Wu et al., 2021: 18).

Xiahe

The Baishiya Karst Cave (BKC), situated in Xiahe County, Gansu Province, China has long been a sacred site of prayer for Buddhist monks on the Tibetan Plateau (Ackerman, 2019). Known as a source of holy bones that could be ground up for medicinal use, the site has become of particular importance in recent years due to its purported association with the little understood Denisovan population of archaic humans (Ackerman, 2019; Chen et al., 2019). There is currently only one associated hominin fossil for this site (right hemi-mandible with M_1 and M_2) but subsequent investigations into the >1 km long cave system have revealed an abundance of stone artifacts and cut-marked faunal remains (Figure 6). The original context of the Xiahe mandible is difficult to establish. The fossil was first discovered by a local monk who, fortuitously, gifted the specimen to the Sixth Gung-Thang Living Buddha who then donated it to the nearby Lanzhou University for safe keeping (Ackerman, 2019). Despite the *ex situ* nature of the Xiahe mandible, tremendous effort has been put forth to analyze its temporal context from adhering carbonates, its morphological association with other hominin fossils, and, importantly, its genetic and biochemical associations with high-altitude adaptive environments and the Denisovan haplotype (Chen et al., 2019).
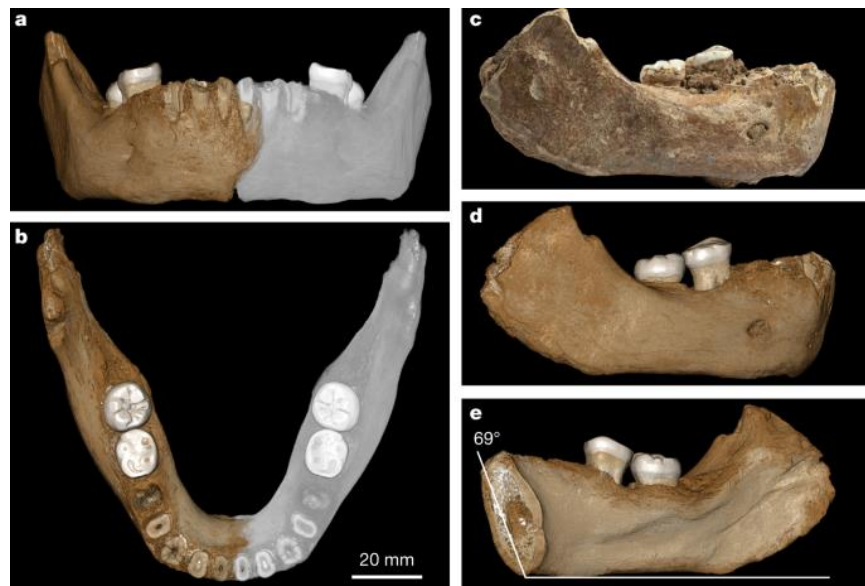

Figure 6: Xiahe mandible. (a) anterior view, (b) occlusal view, (c, d) lateral views, (e) internal view

Three subsamples of the carbonate matrix adhering to the bottom of the hemi-mandible were subjected to Uranium series analysis for age determination. While there was some expected variation in these samples, the provided dates (164.5±6.2 ka, 155±15 ka, 163±10 ka) were not statistically different and are therefore summarized as providing an age of approximately 160 ka (Chen et al., 2019). Excavations of BKC in 2018 and 2019 attempted to establish a chronostratigraphic sequence for the caves cultural and faunal deposits. These efforts identified a series of 10 layers, all of which contain archaeological and faunal materials spanning a total period between approximately 225-157 thousand years covering geologic segments from the late Middle Pleistocene to the modern era (Zhang et al., 2020). The age established for the Xiahe mandible matches the age range of layer 10 within the BKC which is suggested to have formed between 190±34 ka and 129±20 ka. The fauna associated with layers 10-7 primarily constitute large mammals such as rhinoceros, large bovids, and hyenas. Falling within Marine Isotope Stage (MIS) 6, the Xiahe hominin would have existed during the penultimate glacial period (Chen et al., 2019; Zhang et al., 2020).

With limited fossil material, a morphological assessment is inherently minimal. Most of the analysis was achieved digitally by use of micro-computed tomography. This approach allowed the researchers to virtually remove the carbonate matrix through manual segmentation, instead of physically removing the only *in situ* material that can be directly associated with the fossil. While each aspect of the mandibular morphology was assessed, key traits include an overall robust form, the lack of a distinct mental eminence (though a weakly expressed triangular mental protuberance was observed) with a receding symphyseal region, a derived dental arcade shape that is anteriorly broad and flattened (reminiscent of *H. neanderthalensis*), robust molars with metric ranges beyond that of most contemporaneous samples (Table 3), and a unique 3-rooted M_2 (Chen et al., 2019). While the morphological evidence for the Xiahe hominin is sparse, what little is available has grown in significance in recent years as advanced analytical techniques have been applied directly to the fossil as well as the BKC paleosol deposits.

Given the age and location of this find, the Xiahe fossil material has led to questions of its association with the little understood Denisovan populations first identified in the Altai Mountains of Siberia. Denisovans are understood as a robust hominin population from the late

TABLE 3. Mandibular Molar Metrics (mm): Mesiodistal (md), Buccolingual (bl), and Crown Index (CI)

	Hualongdong	Xujiayao	Tam Ngu Hao	Penghu 1	Xiahe	Denisova 2
M_1 md length	13.0	-	-	-	15.1	-
M_1 bl width	11.1	-	-	-	12.5	-
M_1 CI	85.4	-	-	-	82.8	-
M_2 md length	12.4	-	13.2	14.2	14.5	-
M_2 bl width	10.2*	-	11.3	13.4	14.1	-
M_2 CI	82.2	-	85.6	94.4	97.2	-
M_3 md length	-	14.0	-	-	-	-
M_3 bl width	-	12.3	-	-	-	-
M_3 CI	-	87.9	-	-	-	-
Deciduous						
dM_2 md length	-	-	-	-	-	10.3
dM_2 bl width	-	-	-	-	-	9.3
dM_2 CI	-	-	-	-	-	90.3

Middle to Late Pleistocene which maintain genetic affinities with modern populations from Eastern Asia and Oceania. With genomic information available from the original Denisovan material (_Denisova 3_), it became clear that these hominins harbored an adaptive allele complex (_EPAS1)_ now widely seen amongst high-altitude adapted populations from the Tibetan Plateau (e.g., Sherpas) (Chen et al., 2019; Slon et al., 2017; Zhang et al., 2021). Possibly because of this, along with the robust nature of the dental fossils found within Denisova Cave (Tables 2 and 3), many researchers have looked to the Middle Pleistocene hominins in eastern Asia (i.e., Dali, Jinniushan, and Xujiayao) as potential fossil representatives of this population (Ni et al., 2021).

To test the affinity of the Xiahe fossil with the Altai Denisovans, researchers attempted genetic sampling of the mandible. While the fossil did not preserve the needed genetic material, subsequent paleoproteomic analysis provided evidence of a genetic relationship with Denisovans (Chen et al., 2019). The analysis indicated that the specimens from BKC and Denisova Cave shared in a unique signature of amino acid polymorphisms, supporting a close relationship. These data were later supported by genomic analyses of paleosols extracted from the many cultural layers identified within the entrance chamber. While the specific _EPAS1_ allele complex

was not reported on, the authors clearly associate the mtDNA data with a long term Denisovan occupation of the cave (Chen et al., 2021; Zhang et al., 2021).

While Ni et al. (2021) suggest an affinity between the Xiahe mandible and the Harbin cranium (suggested as a sister-group), other researchers see strong association between it and the Penghu 1, Xuchang, and Xujiayao fossils (Bae, n.d.; Chen et al., 2021). While both claims reference the size of the dentition and root morphology relative to other fossil hominins, it is worth noting that the Harbin cranium lacks a mandible and mandibular dentition. Thus, a direct morphological comparison between Harbin and Xiahe becomes difficult. It therefore becomes important to recognize an alternative phylogeny from that proposed by Ni et al. (2021). This is particularly true because, while Xujiayao and Penghu 1 were excluded from the Harbin phylogenetic analysis, the authors clearly associated the Xuchang material with significantly detached clade (Ni et al., 2021).

Penghu 1

The Penghu 1 right hemi-mandible (Figure 7) was obtained from a local antiques shop in Tainan City, Taiwan. Like many vertebrate fossils in the region, it was dredged from the Penghu Channel of the Taiwan Strait some 20 km off the southwest coast of Taiwan. The specimen found its way to the antiques shop where it was purchased, cleaned of the adhering marine invertebrates, and subsequently sold (or "donated" after "financial support and encouragement") to the National Museum of Natural Science, Taichung City, Taiwan (Chang et al., 2015: supplementary 16). The specimen is nearly complete with intact but worn premolars and molars (P_1-M_2).

Given the history of the specimen, both the temporal and ecological context have been difficult to establish. Direct attempts to date the fossil were unsuccessful. Radiocarbon applications failed due to lack of preserved collagen in the bone and the uranium overprint of seawater obscured the results of laser-ablation Uranium series dating. Instead of these direct methods, the authors attempted to establish relative dates by examining faunal remains associated with the same submarine context, collectively known as the 'Penghu Fauna' (Chang et al., 2015). Assemblages of Penghu Fauna are known from a variety of different research institutions and private collections throughout Taiwan and span a wide range of time from the Middle to the Late Pleistocene. All of the mammalian species represented by this assemblage are known also from
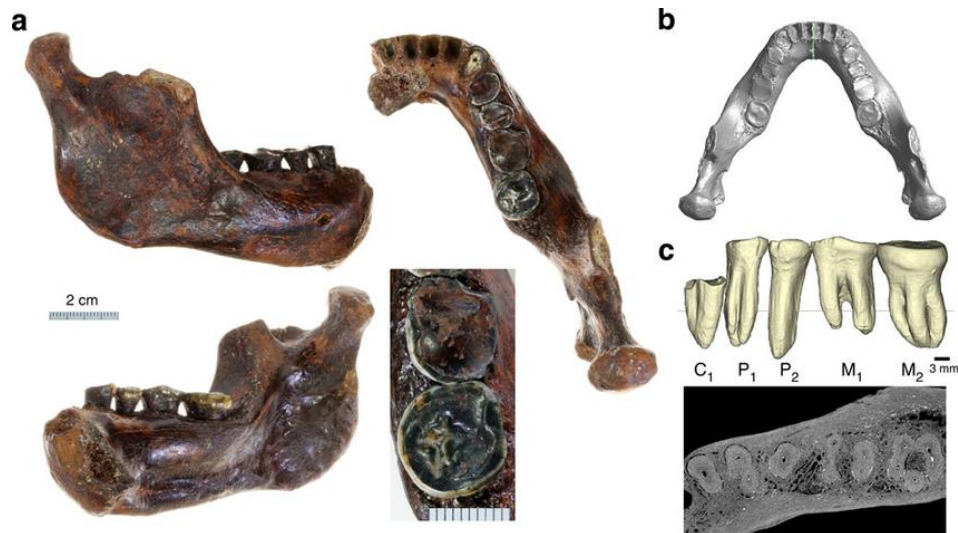
Figure 7: Penghu 1 mandible. (a) Mandible, (b) virtual reconstruction, (c) surface rendered image of the segmented mandibular dentition (upper, lingual view) and its horizontal micro-CT section at the level indicated by the dotted line. From Chang et al. (2015).

fossil localities across mainland China, suggesting that these animals reached the Strait at a time while the sea levels were lower than they are today. Drops of more than 60m in sea level, associated with glacial periods, are known to have occurred periodically throughout the Pleistocene including periods from 70-10 ka, 190-130 ka, 225 ka, 280-240 ka, 360-335 ka, and 450-425 ka. Given the high preservation of the mandible, the researchers believe that, if Penghu 1 is associated with the Penghu Fauna, it was most likely deposited in one of the more recent low-sea-level events (i.e., 70-10 ka or 190-130 ka) (Chang et al., 2015).

To correlate Penghu 1 with the faunal remains from the channel, the researchers tested the levels of Fluorine and Sodium in the respective materials allowing them to establish similarity of depositional environments for the different remains. This assessment resulted in correlations between the hominin and a variety of taxa, including the temporally sensitive *Crocuta crocuta ultima*, confirming a likely depositional period in the area between 190-10 ka (Chang et al., 2015). Despite this depositional period occurring during a glacial period, the abundance of taxa such as *Bubalus* (water buffalo) and *Elaphurus* (Père David's deer) along with two distinct turtle species (pond turtle and softshell turtle) suggest a relatively open, wet, and humid woodland with rivers, ponds, and lakes (Chang et al., 2015).

While the hominin sample is limited, the Penghu 1 mandible has garnered more attention recently as it has been associated with the Xiahe and Xujiayao fossils and, in effect, Denisovan

hominins and the recently described *Homo juluensis* (Chen et al., 2021; Bae, n.d.). The major characters of note identifiable across the mandible include a receding anterior surface (lack of a chin), a short and relatively wide dental arcade, M3 agenesis, and a corpus that is robust but maintains a relatively thin symphysis. The lack of a chin clearly distinguishes this fossil from *Homo sapiens* and situates it phylogenetically with its late Middle to Late Pleistocene designation. The thick mandibular body pushes the range of all Middle Pleistocene hominins (though Xiahe is slightly larger) but the thinner symphyseal area resembles Asian *H. erectus*. The low and relatively small mandibular ramus is associated with the more gracile facial skeleton of later Asian Middle and Late Pleistocene *Homo* (Chang et al., 2015).

Both Penghu 1 and the Xiahe mandible reflect an increasingly robust lineage for this time. This robusticity is reflected in the overall dimension of the mandibular body and ramus but also in the dental dimensions which are otherwise most closely associated with the Altai Mountain hominin remains (Tables 2 and 3). In addition to the metric similarities of Penghu and Xiahe, each specimen presents with M_3 agenesis and a unique 3-rooted M_2. While M_3 agenesis is observed in other Pleistocene *Homo* specimens (e.g., Omo 75-14, Dmanisi D2735, Lantian PA 102), the close geographic and temporal proximity of these two specimens along with the 3-rooted M_2 may support an interpretation of homology (Chang et al., 2015).

The large size of the Xiahe and Penghu dentognathic remains is unique given their temporal contexts. The more common trend in the hominin fossil record follows a reduction of this morphology throughout Pleistocene *Homo* (Chang et al., 2015). The terminal Middle Pleistocene and earliest Late Pleistocene, however, bear witness to a collection of hominin localities across eastern Asia that illustrate this unexpected increase in overall size. Significantly, in addition to an increase in dentognathic dimensions, two of these localities (Xuchang and Xujiayao) exhibit a substantial increase in cranial capacity to a level at and even above the upper limits of Neanderthals and *Homo sapiens*. It is in part because of these great deviations in size and cranial capacity that, together with the Xiahe and Penghu specimens, this assemblage is now considered as representing a new species hypodigm to be designated as *Homo juluensis* (Bae, n.d.).

Xuchang

Approximately 120 km south of the Yellow River, the late Pleistocene/Holocene Lingjing site sits in northeast Xuchang County, Henan Province, northern China. It was first discovered in the

mid-1960s with a surface collection of microblade tools and mammalian fossils. Despite this early discovery, the site was not well-researched until the small underground-spring fed ponds began to dry out in the early 2000s, exposing artifact and fossil latent strata hidden beneath. Subsequent excavations ran from 2005 to 2015 and exposed 11 cultural and fossil layers across a depth of 9 meters with an expansive excavation area spanning 551 m^2 (Li et al., 2017).

While hominin activity is identifiable throughout the entire sequence, only the lowest layer (layer 11) contained human fossil remains. The fossils were highly fragmented but preserved *in situ* without evidence of horizontal displacement suggesting contextual association. In total the hominin assemblage amounts to 46 fragments which are associated with as many as five individuals (XUC 1-XUC 5). Of these individuals, two are of note as large portions of their crania can be reconstructed. Xuchang 1 is the most complete specimen and has been reconstructed from 26 individual fragments (Figure 8). Xuchang 2 is the second most complete, comprised of 16 fragments. The remaining three individuals are each represented by a single fragment, though the authors recognize the possibility that XUC 4 (supraorbital torus fragment) could possibly derive from XUC 2. (Li et al., 2017).
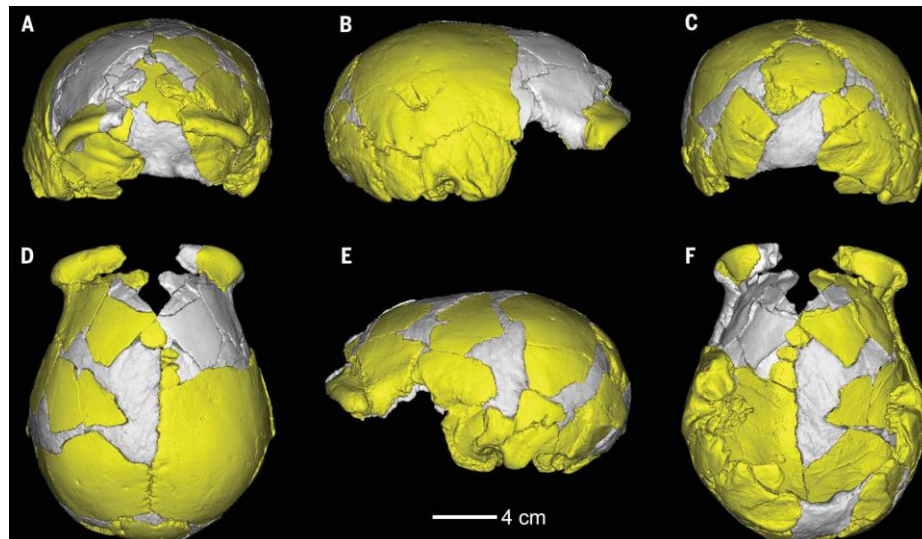

Figure 8: Reconstructed XUC 1. (A) anterior, (B) right lateral, (C) posterior, (D) superior, (E) left lateral, and (F) inferior views. From Li et al. (2017).

OSL methods were used to date the hominin bearing deposits as well as the strata lying just above (layers 9 and 10). The analyses were applied to samples of quartz and potassium-feldspar which together established an age range of ~125-105 ka for layer 11 (hominin layer) and ~100-88 ka for layers 9 and 10. As such, the Xuchang hominin fossils are associated with the last

interglacial period during Marine Isotope Stage 5 (MIS 5) (Li et al., 2017). While these dates can be corroborated to a degree by the faunal collection associated with the site, certain taxonomic compositional observations are hard to reconcile with the interpreted interglacial context (Wang et al., 2022).

As a natural spring site, it is not surprising that the Lingjing fauna is abundant and diverse. The more than 20 identified taxa are dominated by large mammals typical of the Middle Paleolithic fossil record. These taxa are typical of a temperate climate within grasslands-dominated habitats interspersed with patchy forest and marshlands along lakes and rivers. While each of the identified taxa is known to exist within the temporal range provided by the OSL dates for layers 9-11, Wang and colleagues (2022) find the biogeographic diversity to be curious for an interglacial period in this region. The site sits east of the Qinling Mountain range in an area known to have served as a corridor between Palearctic and Oriental biogeographic zones. Though the species' identified from the lower layers of the Lingjing deposit are diverse in overall habitat preference, all fall within the Chinese Palearctic classification. Some of these cold-climate taxa (*Procapra*) appear here as the southernmost distribution of their species. These findings suggest that, while in conflict with the OSL dates, the Lingjing fauna are possibly better associated with a late Middle Pleistocene glacial (MIS 6) or a Late Pleistocene glacial or stadial phase (MIS 4) (Wang et al., 2022). While this taxonomic composition warrants discussion and investigation, until contrary geochronological data appears the earlier OSL dates are the most reliable temporal indicators. The fauna thus provide insight into the dynamics of dispersal corridors and climatic influence during the early Late Pleistocene.

Morphological analysis for the Xuchang hominins is mostly limited to XUC 1 and XUC 2. While the reconstruction of these fossils provides a great deal of morphological information, neither specimen retains facial or dentognathic materials and instead mostly inform on the neurocranial anatomy. Perhaps unsurprisingly, the overall cranial morphology represents a mosaic of features that can be associated with earlier Pleistocene hominins (*H. erectus*), regionally associated late Middle Pleistocene hominins (as described in this review), as well as features reminiscent of Neanderthals and early *Homo sapiens*. These features aside, the Xuchang crania stand out as unique in their extraordinarily voluminous cranial capacities (Table 4). These metrics were achieved by manual and physical reconstruction and mirror imaging of paired elements. Through

this analysis, the authors were able to establish an endocranial volume (ECV) of approximately 1800 cc for Xuchang 1. While the ECV is not specified in the publication for Xuchang 2, it is said to smaller than XUC 1 but likely on par with the average for Late Pleistocene hominins (Li et al., 2017).

TABLE 4: Endocranial volume in cubic centimeters (cc) for applicable specimens discussed in text

Locality	Hualongdong	Harbin	Dali	Maba	Jinniushan	Xuchang	Xujiayao
Endocranial Volume	1150 cc	1420 cc	1120 cc	1300 cc	1390 cc	1800 cc	1700 cc

In overall cranial shape, the Xuchang hominins are most reminiscent of other eastern Asian Middle Pleistocene *Homo* with some aspects being similar to earlier *H. erectus* specimens. The cranial breadth is reported as the largest observed in the later Pleistocene with the widest point situated low on the temporal bones instead of on the parietals as in Neanderthals and *H. sapiens*. This temporal expansion, along with relatively short and inwardly sloped mastoid processes, produce an occipital profile markedly different from the rounded shape of Neanderthals and the laterally vertical profile of *H. sapiens* (Li et al., 2017). These features aside, a reduced nuchal torus and occipital protuberance along with a distinct suprainiac fossa and even table thickness of the inion region illustrate an occipital bone distinctly reminiscent of Neanderthals. Finally, the petrous potions of the XUC 1 and XUC 2 were preserved well-enough to assess the semicircular canals and temporal labyrinths. These phylogenetically sensitive regions have shown distinctive morphologies in Neanderthals, *H. sapiens*, and eastern Asian hominins such as the Hexian and Xujiayao populations. These features in XUC 1 and XUC 2 are most similar to the Neanderthal condition but share in this morphology with the Xujiayao 15 specimen (Trinkaus and Wu, 2017). This variety of Neanderthal traits have led Li and colleagues (2017) to believe that the Xuchang hominins, possibly along with Xujiayao may provide evidence of population interactions across Eurasia during the late Middle and early Late Pleistocene. The similarity in traits that are observed here would then reflect admixture events. This hypothesis is particularly intriguing given the association between expanded cranial capacities and introgression (Harvati and Ackermann, 2022).

Xujiayao

Xujiayao (also known as Houjiayao) is an open-air site named for its proximity to Xujiayao Village on the northwest margin of the Nihewan Basin in Yangao County, Shanxi Province, northern China (Ao et al., 2017). It was first discovered in 1974 and subsequently excavated from 1976 to 1979. The hominin material from Xujiayao is highly fragmented, yielding a total of 21 elements coming from a minimum of 10 individuals (Bae, n.d.; Wu et al., 2022; Wu and Poirier, 1995). The exposed stratigraphic sequence reaches a depth of approximately 17 meters with hominin fossil and archaeological material situated in a layer between 8 and 12 meters deep. Establishing a temporal context for Xujiayao has been contentious. The original Uranium series dates taken from associated mammalian teeth provided an estimated age of between ~125-90 ka but such assessments have been scrutinized for the susceptibility of uranium dosing associated with the open-system nature of dental and osteological remains. While carbon and paleomagnetic analyses capped the sequence within a very wide range (~500-16 ka), more recent ESL (370-260 ka) and pIR-IRSL (220-160 ka) testing has provided tighter, though not perfectly aligned groupings. Though both situated within the late Middle Pleistocene, the pIR-IRSL (post-Infrared-Infrared Stimulated Luminescence) date is better supported by recent $^{26}Al/^{10}Be$ dating (~240±50ka) and faunal analysis (Ao et al., 2017; Bae, n.d.; Tu et al., 2015).

An impressive faunal collection of approximately 5000 specimens has been extracted from the hominin bearing deposits accounting for a minimum of 21 species. As noted above, the taxonomic composition of this assemblage is in support of a 220-160 ka temporal setting and thus establishing an occupation during the MIS 6 glacial interval. The assemblage is dominated by Equids (*E. przewalski* and *E. hemionus*) and small Artiodactyls (*Spirocerus, Procapra,* and *Gazella*) all of which are indicative of temperate grassland environments and cooler conditions. There were, however, a small percentage of forest dwelling taxa that suggest a somewhat heterogenous environment. Perhaps most interesting about the faunal collection is the preponderance of hominin induced taphonomic alterations to a large percentage of the ungulate long bones suggesting a prolonged period of occupation and systematic hunting (Norton and Gao; 2008).

Besides the temporal labyrinth morphology reported on above (Trinkaus and Wu, 2017), there is very little discussion on the phylogenetic affinities of the Xujiayao cranial morphology. Wu and Poirier (1995) report on derived gracility in of the supramastoid ridge and a likely shortened face

similar to modern humans (interpreted from a less forward and downward inclination of the zygomatic process). Bae (2010) describes *H. erectus* affinities in the parietal thickness of some specimens and dimensions of the permanent maxillary teeth. An in-depth assessment of a fragmented mandibular ramus carried out by Wu and Trinkaus (2013), further recognized a handful of traits reflecting the mosaic nature of these late Middle Pleistocene remains. This assessment identified commonalities with Neanderthal and other late Pleistocene hominins in the presence of enlarged superior medial pterygoid tubercles and a possible retromolar space but also identified distinct gonial aversion along with an exceptionally wide ramus and an open mandibular foramen, contrasting Neanderthal morphology but agreeing with other eastern Asian late Middle Pleistocene hominins. It should be noted, however, that studies of mandibular morphology are thought to be less reliable for phylogenetic assessment than those pertaining to the cranium (Xiao et al., 2014).
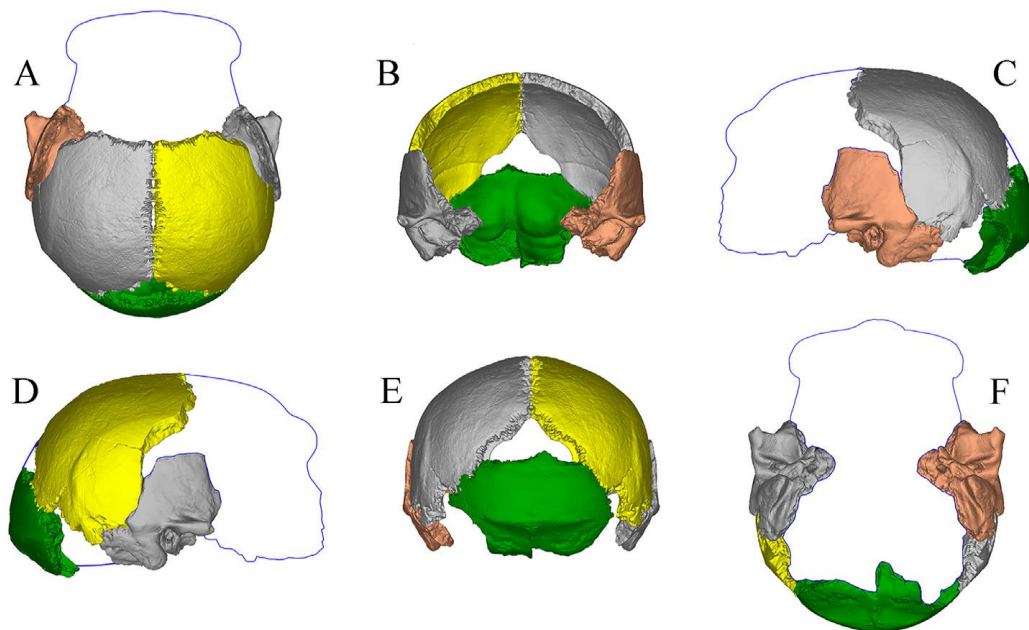

Figure 9: XJY 6 reconstruction. (A) superior, (B) anterior, (C) left lateral, (D) right lateral, (E) posterior, and (F) inferior views. From Wu et al. (2022).

The most recent attempts at understanding the Xujiayao hominins come from a cranial reconstruction from three mostly complete vault fragments (occipital, right parietal, and left temporal), designating the material as a single specimen, Xujiayao 6 (XJY 6, Figure 9). As was done with the Xuchang and Hualongdong specimens, virtual reconstruction was accompanied by mirror imaging to account for symmetry of paired bones. This reconstruction has allowed researchers to establish some common cranial metrics used in phylogenetic comparisons as well

as assess the endocranial volume for a single individual. The ectocranial measurements (Table 5) mostly reflect dimensions in the highest size range of comparative Pleistocene and modern

TABLE 5. Ectocranial Measurements in mm

Index	Hualongdong	Harbin	Dali	Maba[1]	Jinniushan	XUC 1[2]	XJY 6
Postorbital constriction	95.4	88.7	90.4	80.2	88.8	-	-
Orbit index	94.4	72.6	67	83.5	71.0	-	-
Nasal index	46	59.3	72.1	-	61.0	-	-
Upper facial index	71.4	67.1	57.5	-	62.0	-	-
Dental arcade index	81.6	93.4	93.5	-	99.0	-	-
Linear Measurements for indices							
Orbit Index							
Orbital height	40.6	41.6	34.2	38.0	36.0	-	-
Orbital breadth	-	57.3	51.0	45.5	50.7	-	-
Nasal Index							
Nasal breadth	30.0	36.2	34.9	-	31.8	-	-
Nasal height	65.2	61.0	48.4	-	52.1	-	-
Postorbital Constriction							
Minimum frontal breadth	-	116.1	105.7	98.1	109	-	-
Biorbital breadth	109.0	130.9	116.9	107.4	122.7	-	-
Upper Facial Index							
Upper facial height	79.6	76.4	64.1	-	72.5	-	-
Bimaxillary breadth	111.5	113.8	111.4	-	116.9	-	-
Dental Arcade Index							
Maxilloalveolar length	62.0	74.0	69.1	-	65.1	-	-
Maxilloalveolar breadth	76.0	79.2	73.9	-	65.5	-	-
Other linear measurements							
Frontal chord	98.2	125.1	114.9	107.9	113.5	-	-
Maximum cranial length	-	221.3	212.2	196.5	203.6	217.0	-
Maximum cranial breadth	144.0	164.1	156.4	-	144.1	173.5	175.0
Maximum frontal breadth	-	128.1	122.7	116.6	127.1	138.8	135.0
Nasio-occipital length	-	212.9	202.2	188.5	195.4	212.0	-
Supraorbital torus breadth	124.0	145.7	129	119	135.5	140.7	-
Zygomatic breadth	-	162.4	143.8	-	148.5	-	-
Biauricular breadth	-	159.1	145.8	-	139.2	161.0	-

[1] Wu and Poirier (1995) and Ni et al. (2021) present different measurements for orbital height, orbital breadth, frontal chord, and supraorbital torus breadth for the Maba cranium. The data reported for Maba here is from Ni et al. (2021).

[2] Metrics for maximum cranial breadth and biauricular breadth come from the original Li et al. (2017) publication. The rest to the Xuchang metrics come from Ni et al. (2021). Ni et al. (2021) do not report which specimen they measured. Due to its more complete nature, it is assumed here that the data come from XUC 1. Thus, while maximum cranial breadth and biauricular breadth are reported for XUC 2 in Li et al. (2017), they are not included in this table.

samples. The overall shape of the reconstructed cranium follows typical patterns for the region at this time in being large, low, and wide. The XJY 6 endocranial volume is large (~1700 cc) and most similar to the pattern seen in the Xuchang hominins though deriving from a much earlier age. This advanced cranial capacity at 220-160 ka predates all hominins of a similar endocranial volume, including the western Old-World Neanderthals and early *H. sapiens*, adding significance and phylogenetic weight to the Xujiayao hominins (Bae, n.d.; Wu et al., 2022).

Discussion

A persistent theme illustrated throughout this review reflects commonality of mosaic morphologies which incorporate traits typical of Asian *Homo erectus* (e.g., Zhoukoudian), as well as those that variably resemble Neanderthals and early *Homo sapiens*. This observation has led many authors to consider the possibility of admixture from easterly migrating late Middle Pleistocene hominin populations such as those mentioned above as well as from the poorly defined *Homo heidelbergensis* and the little understood Denisovans. In some cases, introgression events might be useful to explain certain peculiarities in overall size (Harbin) and cranial capacity (Xuchang and Xujiayao), as such events are expected to result in transgressive phenotypes exhibiting more extreme conditions than either of the parent populations (Harvati and Ackermann, 2022). In other cases, such as the circular orbits of the Maba cranium and the increased dentognathic robusticity of Penghu and Xiahe hemimandibles, alternative explanations may involve episodes of homoplasy either from similarity of environmental conditions (convergent evolution) or from morphological constraints and genetic drift (neutral evolution). Regardless the etiology of traits, the many hominin fossils found throughout eastern Asia during this period present unique morphologies with continuities which merit discussions concerning their taxonomic status.

The place of eastern Asian late Middle to early Late Pleistocene human fossils within hominin phylogenetics has become contentious in recent decades. Such discussions have led to the variable interpretation of these hominins as gradistic representatives of continuity, reflecting transitional forms between *H. erectus* and *H. sapiens* (i.e., "archaic" *Homo sapiens*, Mid-Pleistocene *Homo*, and/or post-erectus grade hominins), as well as a highly diverse and specious population including designations such as *H. mabaensis*, *H. daliensis, H. longi, H. juluensis, H. floresiensis,* and *H. luzonensis*. While it seems unlikely that either extreme version of hominin variability is entirely correct, it is clear that the variation observed in the region warrants attention and discussion beyond diagnosing these hominins as a transitional phase or lumping

them in with already ill-defined taxa such as *H. heidelbergensis*. With attention placed on the two most recent designations in China (*H. longi* and *H. juluensis*), it seems most pertinent to first establish whether the whole of the late Middle Pleistocene-early Late Pleistocene hominin fossil record illustrates one or more species that can be clearly distinguished from Neanderthals, *H. sapiens*, and *H. erectus*.

Species diversity in eastern Asia

Until recently, very few species designations have been offered for late Middle Pleistocene hominins ranging across eastern Asia. While both the Dali and Maba crania have been considered to some degree as diagnostic taxa at either the species or sub-species level, their status has varied alongside theoretical debates regarding the origins of *Homo sapiens*. Thus, these fossils are more commonly understood in the same vein as other "archaic *H. sapiens*" from the region and historically deemed as transitional between *H. erectus* and modern humans (Bae, 2010). As previously noted, however, the term "archaic *H. sapiens*", while problematic on a number of levels, specifically cannot be applied to these hominins if we are to accept a Recent African Origins (RAO) model for the evolution and dispersal of our species. If *Homo sapiens* had a specific and direct evolutionary trajectory within the African continent, then the hominins discussed here must be understood as evolving along an unrelated lineage spurring from the existent *H. erectus* populations in China and Southeast Asia. An alternative explanation would allow for the extinction of *H. erectus* in eastern Asia and their replacement by late Middle Pleistocene hominins from western Eurasia sometime before the emergence and dispersal of *H. sapiens*. If the former scenario is to be accepted, it becomes important to sort out the phylogeny of these specimens that evolved out of *H. erectus*. If the latter scenario is accepted, discussions regarding what hominin species migrated into the area are needed. Such inquiry will naturally lead to deeper investigation of Denisovan evolution and dispersal. When simplified, the question becomes one of identifying continuity from within eastern Asia or from the west. It is therefore important to consider each of the recently proposed species in light of these hypotheses.

Homo longi

Homo longi is currently defined and represented by the lone Harbin cranium. After an extensive phylogenetic analysis utilizing parsimony criteria and Bayesian tip-dating, Ji et al. (2021) suggested a unique combination of traits that warrant the new species designation (Ni et al.,

2021). The authors cite a variety of morphological features, many of which reflect the overall massive size of the skull, that they claim to "differ from all other named *Homo* species" (Ji et al., 2021: 1). Interestingly, they also concede a similarity between the Harbin cranium and the fossils from Dali, Jinniushan and Hualongdong but only suggest a close phylogenetic relationship between the four specimens. Despite this noted similarity, the authors conclude that the Harbin cranium stands alone as the only member of *Homo longi* while they suggest a separate species designation (*Homo daliensis*) for the other fossils (Ji et al., 2021).

While the Harbin specimen is massive in most dimensions relative to other fossils in the region, particularly in the supraorbital torus and maximum cranial length (though cranial length is not known for Xuchang or Xujiayao), it maintains many characteristics common in eastern Asian late Middle Pleistocene hominins (Table 6). In qualitative assessment, the cranium differs from Dali and Jinniushan primarily in its lack of a frontal or sagittal keel and a rounded occipital contour (Ji et al., 2021; Ni et al., 2021). A minimally developed occipital torus is potentially significant as well, though the gracility of this feature is also observed on the Jinniushan cranium (Rosenberg and Wu, 2013). Other features that might reflect continuity between the four hominins, such as the canine jugum and supraorbital sulcus are noticeably absent from the authors' assessment, possibly obscuring the results of their analysis. Future consideration of the relationship between these hominins will need to account for the same morphological criteria and assess the phylogenetic weight of different features.

Considered altogether, it is interesting to reflect on the preponderance of traits resembling *Homo erectus* in each of the four specimens within the so-called "Harbin group" (Ni et al., 2021: 4) that might support an anagenic transition from the former to the latter. While such a model directly contrasts with the conclusions drawn from the authors' phylogenetic analysis (from which they suggest that this clade represents a sister-lineage to *Homo sapiens*), it is difficult to overlook features such as the long, low, and wide cranial profile with the broadest cranial dimensions situated just superior the supramastoid crest of the temporal (Table 6). Additional features including a receding frontal, square orbits, pronounced supraorbital torus, reduced post-orbital constriction, and a cranial capacity ranging between approximately 1100-1400 cc can also be explained as continuity within the Harbin group and reflect an anagenic evolutionary trajectory from *H. erectus*.

TABLE 6: *Qualitative cranial traits for specimens within the H. juluensis and H. longi hypodigms*

Trait	Dali	Chaoxian	Jinniushan	Hualongdong	Xuchang	Harbin	Xujiayao
Canine fossa				Absent		Shallow	
Canine jugum	Well developed			Weakly developed			
Eye orbit shape	Quadrangular		Quadrangular	Quadrangular		Quadrangular	
Face shape				Flat			
Facial height				Large		Low	
Frontal/sagittal keel	Present		Present			Absent	
Cranial Shape	Low			Short and high	Low	Long and low	Short and high
Cranial wall thickness	Thick		Thinner than Dali		Modest		Thick
Mastoid process angle	Downward				Short and slopes inward	Forward and inward	Downward and inward
Occipital angle	Angular	Rounded	Angular			Rounded	
Occipital torus	Thick		Weak			Minimally developed	Broad
Position of maximum cranial breadth	Postero-superior margin of the temporal squama				Supramastoid	Supramastoid	
Suprainiac fossa		Small			Distinct	Absent	
Supraorbital sulcus	Present		Shallower than Dali	Shallow and broad			
Supraorbital torus form				Separated		Separated	
Supraorbital torus	Thick		Moderate	Well-developed	Modest	Massive	

The most unique quality of the Harbin cranium is its overall robusticity. This is additionally reflected in the dimensions of the single associated tooth (left M^2) which far surpass even the most robust specimens from the later Middle Pleistocene (including Denisovans). It will be interesting to see if similarly robust specimens are found in the region in the future. Given the limited sample size and the lack of morphological correlates, it is not unreasonable to consider this cranium as an anomaly pushing the morphological range of similar specimens (e.g., Dali,

Hualongdong, and Jinniushan). Possibly the biggest obstacle to overcome for designating the Harbin cranium as the type specimen for *Homo longi* is its lack of context. The location data for Harbin comes from verbal accounts and indirect associations. Such issues may stand in the way of *H. longi* becoming an accepted taxon in future paleoanthropological discussions. Despite these issues, the specimen, along with the other three it is associated with, clearly represents a distinct morphological pattern in the late Middle Pleistocene of China and should therefore be considered as representing a unique lineage separate from *H. sapiens* and other well-established *Homo* species. It seems, rather than *H. longi*, that the previous species designation of *H. daliensis* would become the classification used for these hominins. Still questionable, however, are the fossil hominins in the region that seem to deviate from the pattern observed above. Such specimens, including Xuchang and Xujiayao, are currently considered as representing an additional hominin species.

Homo juluensis

The type specimen of *Homo juluensis* comes from the Xujiayao site in northern China. Along with the Xuchang specimens, this classification is largely associated with extreme neurocranial expansion (1700-1800 cc) and, presumably, expanded dental metrics (Bae, n.d.; Bae and Wu, n.d.). The latter characteristic has led the authors to consider both the Xiahe and Penghu mandibular fragments as also belonging to this hypodigm. While most of the Xujiayao dental remains are maxillary, and thus not directly comparable, a single lower third molar appears to fall in the range of the lower molars (M_1 and M_2) described for Xiahe and Penghu (Table 3). It is worth noting, however, that both of the latter specimens present with M_3 agenesis. While this is a variable feature that is described in several hominin samples throughout the Middle Pleistocene, it is also one of the traits that is considered when comparing Xiahe and Penghu, and therefore discussed in terms of possible homology. The presence of a lower M3 in the Xujiayao sample, therefore, will call the relevance of this trait into question. In relation to the Harbin cranium, the *H. juluensis* material reflects noticeably smaller dentition (though closer in size to Denisova 4, Penghu 1, and Xiahe), but greater maximum cranial breadth, maximum frontal breadth, and cranial capacity. While both proposed species are considered robust, clearly the absolute cranial dimensions of *H. juluensis* are greater than those reported for Harbin (Tables 4 and 5). As it stands, the *Homo juluensis* hypodigm, defined by an expanding neurocranium and enlarged

dentition, includes the specimens from Xujiayao, Xuchang, Xiahe, and Penghu. As none of these remains include elements from the facial skeleton, more research will be needed to appropriately compare this species to the rest of the eastern Asian late Middle and early Late Pleistocene human fossil record. It is important to note here, however, that the hypodigm for *Homo juluensis* has yet to be published. Thus, the information offered above is tentative and awaiting published clarification.

Denisovans

Proponents of both *H. longi* and *H. juluensis* are making claims on an association with the Xiahe hemimandible and, in effect, ties to the Denisovan populations first described from the Altai Mountains, Siberia. While paleontological data suggest a Denisovan presence at Altai as far back as 250 ka, genetic studies suggest a divergence from Neanderthals closer to 640 ka (Jacobs et al., 2019; Reich et al., 2010). With little morphological data for these hominins, the most that anyone can say about their appearance is that they represent a robust population. This assessment is mostly reached by observations from dental assemblages, reflecting molar dimensions outside the typical range of *H. sapiens* and Neanderthals (Sawyer et al., 2015). Each of the East Asian proposed hypodigms is noted for the massive appearance of the fossils, though when considered with Dali, Jinniushan, and Hualongdong, the Harbin cranium is possibly better understood as an outlier within that group. While dental fossils are limited from these assemblages, the Harbin specimen includes a single *in situ* tooth (left M^2) while Xujiayao exhibits 9 teeth in total, six *in situ* within a juvenile maxilla and three isolated (presumably adult) (Ni et al., 2021; Xing et al., 2015).

The dimensions of the Harbin teeth are massive, even relative to the Denisovan material (Table 2). The largest described Denisovan dental metrics come from the Denisova 4 specimen designated as an upper $M^{2/3}$, with a mesiodistal length of 13.1 mm and a buccolingual width of 14.7 mm. These dimensions are reported to be much larger than most Neanderthal and Upper Paleolithic M^2s and M^3s (Sawyer et al., 2015). It is interesting to note the relative similarity of the mesiodistal and buccolingual measurements, resulting in a crown shape that is nearly square (CI=112.2). This same pattern is even more apparent from the Denisova 8 M^3 boasting a crown index (CI) of 102.4. In absolute dimensions, the Harbin M^2 greatly exceeds that of Denisova 4 and 8, exhibiting a mesiodistal length of 13.6 and an extreme buccolingual width of 16.6 mm

(CI=122) (Ni et al., 2021). In comparison, the upper M2 from Xujiayao (PA 1480-6) has a mesiodistal length of 11.9 and a buccolingual width of 14.2 (CI=119.3) (Xing et al., 2014). While the Harbin cranium aligns more with the mesiodistal dimension of Denisova 4, Xujiayao is more similar in buccolingual width. Interestingly, both eastern Asian hominins exhibit discernably greater buccolingual widths than mesiodistal lengths, resulting in crown dimensions that are more buccolingually rectangular in appearance than the fairly square molar form seen in the Altai assemblage. In this respect, the Harbin and Xujiayao specimens are more similar to each other than either is to the Altai Denisovans. Unfortunately, neither the Penghu nor Xiahe assemblages include maxillary dental remains. The single Denisovan mandibular tooth is classified as a deciduous M2. As might be expected from a deciduous tooth, the dimensions are relatively small (Table 3), far below all of the mandibular teeth reported on here. In the crown index, the tooth presents asymmetrically, favoring a greater mesiodistal length than buccolingual width (CI=90.3). To different degrees, this same pattern of asymmetry is seen in all other mandibular teeth in this review, though its crown index sits between Xujiayao and Penghu 1. Until additional lower dentition is found with in association with Harbin (unlikely given the absence of context), Xujiayao, Xuchang, or the Altai Denisovans or maxillary dentition is found with Penghu and/or Xiahe (also difficult given the *ex situ* context), the question of these fossil associations is likely to continue being debated.

An additional purported Denisovan tooth was recently reported from the site of Tam Ngu Hao 2 (Cobra Cave) in the Huà Pan province, northeastern Laos. It was extracted from a hard breccia/conglomerate layer from the cave entrance passage which was ascribed an age of approximately 164-131 ka by means of Uranium series and ESR dating. The tooth, a mandibular M1 or M2, is suggested to share discrete features such as an internally-positioned metaconid, low crown topography, and a slight buccal shelf with the material from Baishiya Karst Cave (Xiahe). While some of these traits are also present in Neanderthal and *H. erectus* specimens, the authors note the strong association between Xiahe and Tam Ngu Hao 2 in overall enamel-dentine junction (EDJ) shape. The association of these fossils lead the authors to conclude that the tooth is "most likely Denisovan" (Demeter et al., 2022: 6). The investigation into the internal and external structure of the Tam Ngu Hao 2 tooth considers dental traits not described in this review and therefore becomes difficult for comparison here. The overall dimensions and crown index are presented in Table 3, however, and seem to mostly deviate from the comparative material in

absolute size. While the small dimensions would be curious for Denisovans, given the emphasis on robusticity, such measures do not preclude it from the category if the qualitative traits are considered stronger evidence of homology.

Identifying any of the hominins discussed above as representative of Denisovans will have important implications for the evolutionary trajectory of eastern Asian late Middle to early Late Pleistocene hominins. Given genetic evidence supporting Denisovans as a sister group to Neanderthals, the presence of Denisovans in eastern Asia would suggest that these hominins had migrated into the region from western Eurasia (Reich et al., 2010). If we were to follow the currently understood temporal framework for the distribution of Denisovans (including *H. juluensis*), this would suggest a northern migration route into China from Siberia and surrounding regions (Figure 10). This, in turn, would suggest a likely early replacement or assimilation event in the region where *H. erectus* and/or the lineage represented by Dali, Harbin, Hualongdong, and Jinniushan thereafter disappeared.
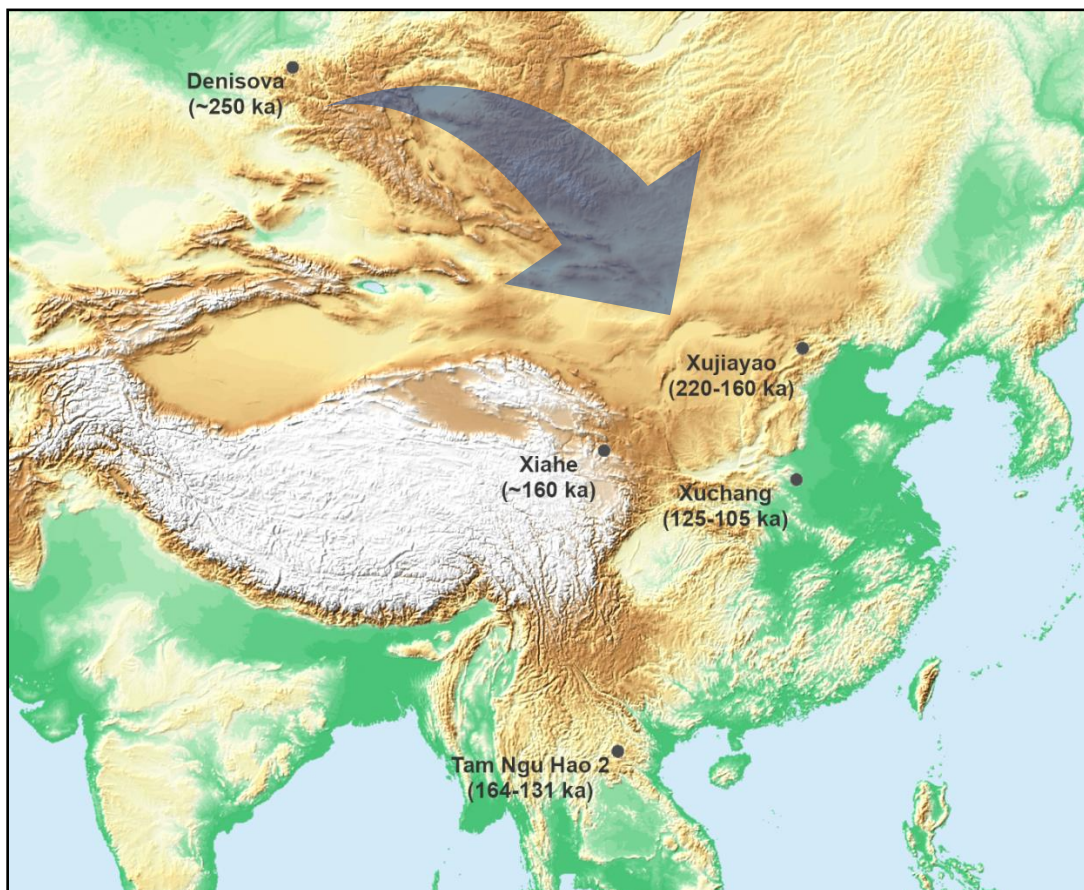

Figure 10: Distribution of Denisovans (including H. juluensis). Arrow indicates possible migration direction.

What about Southeast Asia?

Of the fossils discussed in this review, only one locality was described outside of China (Ma U'Oi). Given the preponderance of *Homo erectus* localities, there is a strong likelihood that later hominins from the timeframe discussed here inhabited the region. To be sure, there are localities that represent morphologies distinct from *H. erectus* and other such Middle Pleistocene populations. While some such assemblages, such as Thum Wiman Nakin in Thailand and Tam Ngu Hao 2 (mentioned above) in Laos are still inadequately described and/or limited in sample size, other Southeast Asian fossils are better known and constitute two proposed species, *H. floresiensis* and *H. luzonensis*. Of these, *H. floresiensis* is better established. Discovered at Liang Bua cave on the island of Flores in 2003, this species is originally represented by an impressive skeletal assemblage including a complete cranium and mandible, and many post-cranial elements (Brown et al., 2004). The specimen received much attention, positive and negative, when it was announced as a new species. Of particular interest was its diminutive size and relatively early age of between approximately 100-60 ka (Sutikna et al., 2016). Interestingly, this age range for *H. floresiensis* has been revisited in recent years as additional materials have been discovered from the So'a basin on Flores (mandibular corpus and 6 isolated teeth) *in situ* from open-air site of Mata Menge (van den Bergh et al., 2016). Corroborating the diminutive size and derived morphology observed at Liang Bua, the Mata Menge material revises the date of *H. floresiensis* to as early as ~700 ka. This date was established with highly reliable ^{40}Ar/^{39}Ar geochronological methods (van den Bergh et al., 2016). These new dates for the Flores material can also be correlated with the temporal context for hominin remains discovered on the island of Luzon in the northern range of the Philippines.

Homo luzonensis was named in 2019 from an assemblage of 13 elements (6 teeth, 1 juvenile femoral shaft, and 6 manual and pedal elements) (Détroit et al., 2019). The diagnosis of this species is similar to that of *H. floresiensis* in exhibiting notably small stature and relatively primitive manual and pedal elements. The distinction between the two purported species is mostly associated with peculiarities of the teeth such as the three-rooted maxillary premolars (Zanolli et al., 2022). The assemblage itself does not share the same deep temporal sequence as *Homo floresiensis*, only dating to approximately 67 ka (Détroit et al., 2019). Hominin activity on the island, however, is reported through taphonomic analysis of faunal remains dating to

approximately 709 ka that are indicative of hominin butchery (Zanolli et al., 2022) suggesting that the temporal range of *H. luzonensis* is on par with the material on Flores.

Assessments of these two SE Asian hominin taxa suggest that they derived from *H. erectus* during the Early to Middle Pleistocene, prior to the presence of any late Middle Pleistocene hominins discussed above. They represent a unique hominin trajectory and warrant consideration of human morphological and adaptive flexibility alongside of discussions regarding island endemism (Kaifu, 2017; van den Bergh et al., 2016; Zanolli et al., 2022). Given this uniqueness, however, they mostly fall out of the scope of this review.

Conclusion

The typical approach to classifying newly discovered fossil hominins is to assign the material to an existing species or propose a new designation. Fossils that are more likely to fall in the taxonomic doldrums are those that are fragmentary or otherwise limited in morphology and are thus shelved as 'indeterminant' until more information is gleaned (Smith, 2005). The material known throughout late Middle and early Late Pleistocene in eastern Asia is neither highly fragment nor limited in morphology for comparison. Despite this, the various fossils discussed here, with the exception of the Harbin cranium that was only recently reported on (and designated a species status) has sat without designation beyond loose gradistic categories such as archaic *Homo sapiens,* Middle Pleistocene *Homo*, or post-erectus grade hominins. The application of non-specific taxonomic terms seems to result from a combination of variability in morphology and an acceptance of a multiregional theory for the evolution of *Homo sapiens* (Bae, n.d.). The latter consideration pigeonholed these hominins as transitional forms between *Homo erectus* and *Homo sapiens* that did not warrant a distinct species designation.

With advances in paleogenomics, it has become clear that a Recent African Origins (RAO) hypothesis for *H. sapiens* evolution and dispersal is more likely than multiregional evolution. As support for the multiregional theory wanes and shifts, more attention is given to the likelihood of distinct taxa in eastern Asia which variably encountered and interbred with hominins entering the region (i.e., Neanderthals, Denisovans, and modern humans). As the braided-stream theory of eastern Asian hominin evolution continues to gain support, discussions of hominin systematics are becoming more prominent in the literature. Omitting *H. floresiensis* and *H. luzonensis* due to their unique evolutionary trajectory, this discussion is mostly focused on two newly proposed

taxa from China: *Homo longi* and *Homo juluensis*. With each of these taxa in their first year of publication, much deliberation will likely ensue. What can be sure from this review is that the place of eastern Asian hominins during this pivotal time of our evolutionary history is soon going to change. It is clear that the first step in this venture will be to sink the gradistic classification of archaic *Homo sapiens* and make a case for new Middle and Late Pleistocene hominin species in eastern Asia.

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