

Making sense of eastern Asian Late Quaternary hominin variability

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A greater degree of Late Quaternary hominin morphological variability is present in eastern Asia than previously assumed. Indeed, a number of distinct populations are present, some that now have new specific names: *Homo floresiensis*; *H. luzonensis*; *H. longi*; *H. juluensis*. With this piece, we describe the various groupings based on the current hominin fossil record of eastern Asia.

When compared to other paleontological disciplines, the field of Late Quaternary (~300,000–50,000 years BP) paleoanthropology has lagged far behind in synthesizing the degree of morphological variability in the hominin fossil record. It is now evident that morphological diversity among Late Quaternary hominin fossils from eastern Asia (East and Southeast Asia all-inclusive) is greater than we (and most researchers) expected. Indeed, there are now a number of new eastern Asian hominin taxa that have been proposed over the past several years reflecting not only a growing hominin fossil record but a greater appreciation for the degree of complexity that is present. This hominin variability is likely the result of a combination of dispersals and introgression that occurred throughout the Late Quaternary, rather than a single dispersal and complete replacement event.

During the early stages of paleoanthropology, beginning in the latter part of the 1800's, many fossils were assigned new species names. This may not be very surprising given how new the field was, how few fossils were known at the time, and importantly, how much morphological variability paleoanthropologists were aware of at the time. However, nowadays, paleoanthropologists tend to lump rather than split the Late Quaternary hominin fossils. In general, lumpers tend to emphasize similarities between fossils, focusing on intra-specific variation around a mean, while splitters emphasize differences in fossils, using these to identify different species¹. This may be partially due to efforts by scientists beginning in the 1950s, particularly from discussions resulting from the 1950 Cold Spring Harbor Symposium, to be more conservative and lump hominin fossils into broader more inclusive categories. This latter push could be related to the realization that many of the earlier proposed distinct species in fact exhibit overlapping morphologies and lack the presence of unique traits that would clearly distinguish them into separate taxa^{2,3}.

The Late Quaternary record of China may be a good example of this conservative lumping. Since the 1920s with the formal introduction of *Sinanthropus pekinensis* (later, along with *Pithecanthropus erectus*, collapsed into *Homo erectus*)⁴ and the formal designation of *Homo longi* in 2021⁵, all (>100 sites) Late Quaternary hominin fossils in China were considered to either represent *H. erectus*, a transitional

archaic version of *H. sapiens*, or modern *H. sapiens*^{5–7}. These data were then used to form the foundation of one of the primary traditional modern human origins models, “multiregional evolution”. In the multiregional model, through gene flow between populations, *H. erectus* was considered to have evolved in situ into archaic *H. sapiens* (Middle Pleistocene “non-*Homo erectus*”), which eventually evolved into modern *H. sapiens*⁸. In China, this was always interpreted to mean that modern Chinese people today could trace their ancestry directly back to at least Zhoukoudian Locality 1 *Homo erectus*, if not to the earliest appearance of hominins in China during the Early Pleistocene⁹. The other primary traditional modern human origins model, generally referred to as the “Out of Africa” or the “replacement” model posits that modern humans dispersed out of Africa and replaced all indigenous populations with no genetic contribution to living peoples¹⁰. Based on current data, it now appears that a combination of both models is the most parsimonious way to explain the origin of modern humans, where modern humans dispersed out of Africa in multiple waves and interacted with the smaller indigenous populations regularly. In other words, modern humans across Eurasia likely arose as a result of a combination of dispersals and introgression events¹¹.

Thanks largely to a growing hominin fossil record, the field of Late Quaternary eastern Asian paleoanthropology is in the midst of significant and important change that is contributing tremendously to how we view and are refining these evolutionary models (Fig. 1; Box 1^{7,12,13}). In particular, the field received a jolt two decades ago with the publication of the diminutive *Homo floresiensis* fossils from the island of Flores in Indonesia in 2004¹⁴. More recently, another diminutive species, *Homo luzonensis*, from the island of Luzon in the Philippines was added as a new hominin taxon¹⁵. In China, *Homo longi* was presented following an analysis of the Harbin fossil⁵. Fossils like Dali and Jinniushan may be tentatively included in *H. longi* as well, though we await further comparative analyses. Most recently, after a detailed study of the Xujiayao and Xuchang fossils, we have added *Homo juluensis* to these discussions¹⁶, see also ref. 13. Importantly, we have assigned the enigmatic Denisova, along with the Xiahe and Penghu fossils, to *H. juluensis* based on comparative study of the present dentognathic remains. In all likelihood, given the recent observation that the Tam Ngu Hao 2 (Laos) tooth shares traits with Denisova¹⁷, this fossil should additionally be included in *H. juluensis*. Further, the Maba (southeastern China) and Narmada (India) fossils have been grouped together in various studies, though these fossils have yet to receive a formal taxonomic name⁷. Maba and Narmada may ultimately find their way to be included in the broader *H. neanderthalensis* species, particularly given early suggestions that Maba was a Neanderthal. We await further evaluation of just what to make of the Maba and Narmada fossils. Regardless, these recent research initiatives in China, and broader eastern Asia, are showing clearly that multiple hominin lineages were present during the Late Quaternary.

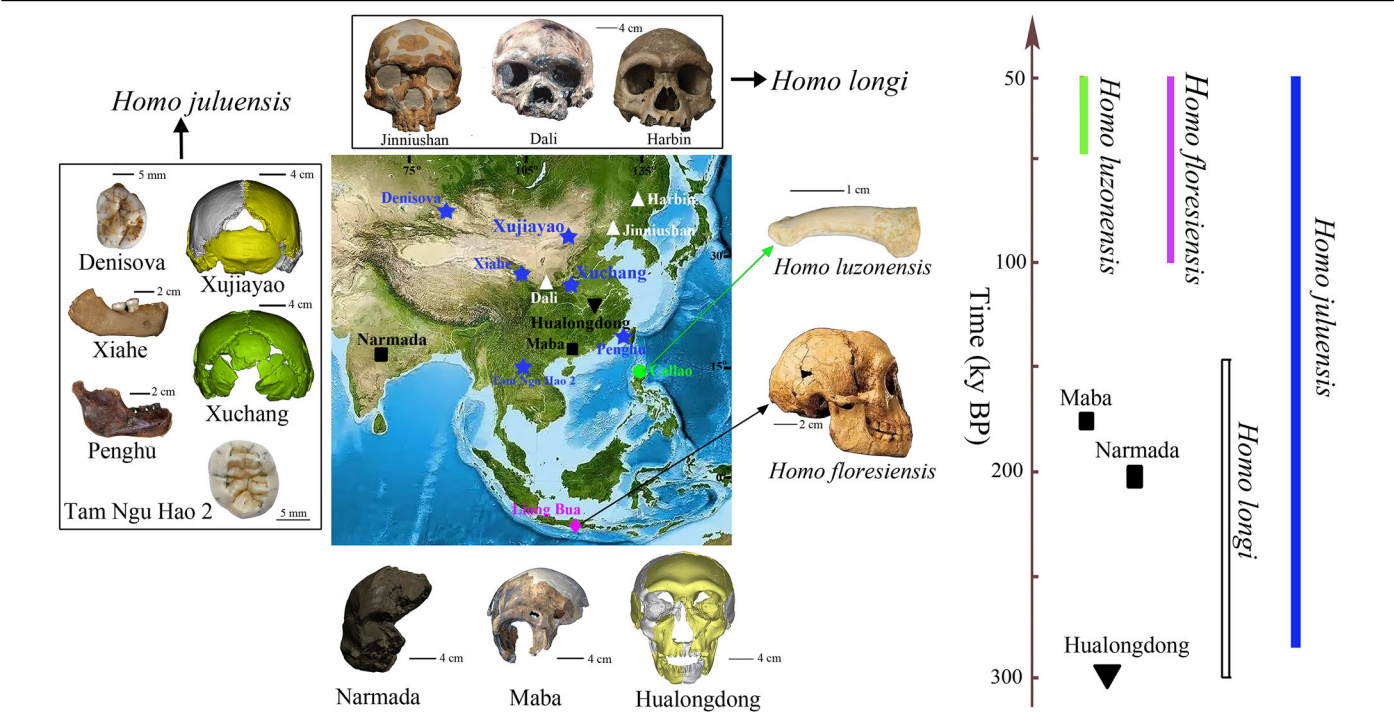


Fig. 1 | Primary Late Quaternary (~300,000--50,000 years BP) hominin taxa from eastern Asia. *Homo juluensis* (blue five-pointed stars) includes Xujiayao, Xuchang, Xiahe, Penghu, Denisova, and Tam Ngu Hao 2; *Homo longi* (white triangles) includes Harbin, Dali, and Jinniushan; *Homo floresiensis* (pink diamond) includes Liang Bua; *Homo luzonensis* (green circle) includes Callao. Although elsewhere we had tentatively grouped Hualongdong (black inverted triangle) with the *H. longi* fossils⁷, we keep it separate for now pending further ongoing investigation.

In many studies, Maba and Narmada (black squares) have been grouped together to form a separate population. It may be possible following further analyses that these latter fossils may be included in the broader *H. neanderthalensis* species or assigned a new taxonomic name altogether. The accompanying Box includes descriptive information for the type specimens and sites for the four hominin species discussed here: *H. floresiensis*; *H. luzonensis*; *H. longi*; *H. juluensis*.

Box 1. Descriptive information related to the Late Quaternary species identified in eastern Asia as presented in Fig. 1: *Homo floresiensis*; *H. luzonensis*; *H. longi*; *H. juluensis*.

Species	Type Specimen/Location	Year of Discovery	Year New Species Name Assigned	Chronometric Age	Hominin Fossils	Archeology	Paleontology	References
<i>Homo floresiensis</i>	LBI/Indonesia	2003	2004	190–50 ka	Assorted cranial, dentognathic, and postcranial remains	Assorted Late Pleistocene stone tools	Assorted Oriental faunas	14,21,22
<i>Homo luzonensis</i>	CCH6/Philippines	2007	2019	67–50 ka	Assorted cranial, dentognathic, and postcranial remains	Assorted Late Pleistocene stone tools	Assorted Oriental faunas	15,23,24
<i>Homo longi</i>	Harbin/China	1933	2021	309–138 ka	Cranium	None reported	Assorted Palearctic faunas	5,25
<i>Homo juluensis</i>	Xujiayao/China	1976–1979	2024	200–160 ka	Assorted cranial and dentognathic remains	Assorted Early Paleolithic stone tools	Assorted Palearctic faunas	13,16,26–28

It is becoming increasingly clear that the eastern Asian hominin fossils are not only increasing in number thanks to new discoveries, but that a greater degree of morphological variation is present than originally assumed or anticipated. This is likely the reason why the number of recent newly proposed Late Quaternary hominin taxa in Asia is higher ($n=4$) than Europe and Africa combined ($n=1$: *H.*

*naledi*¹⁸). Further, the increase in field and laboratory initiatives in Asia are leading to the discovery and identification of new hominin fossils that are only adding to this complexity. A good example of new hominin fossils is from the Hualongdong site in central-eastern China¹⁹. The Hualongdong fossils date to the late Middle Pleistocene (~300,000 years BP) and display a mosaic of characteristics that cannot be easily fitted into any one lineage^{19,20}. In this case, Hualongdong does not fit neatly into *H. juluensis* or *H. longi* and certainly not into *H. floresiensis* or *H. luzonensis*; a good example in fact of the intricacy of the human evolutionary record³.

Traditionally, the eastern Asian hominin fossil record and our understanding of it has lagged behind the better-known Late Quaternary records from Europe and Africa. While work continues, it is quite clear now that there are a number of distinct morphologically different hominin populations present in East and Southeast Asia that are penecontemporaneous, some that now have new specific names: *Homo floresiensis*; *H. luzonensis*; *H. longi*; *H. juluensis*, with others yet to appear. The eastern Asian hominin fossil record is an excellent example of how unilineal models of evolution, such as traditional multiregionalism, cannot adequately explain the complexity in the paleoanthropological record, particularly during the Late Quaternary^{7,16}. If anything, the eastern Asian record is prompting us to recognize just how complex human evolution is more generally and really forcing us to revise and rethink our interpretations of

various evolutionary models to better match the growing fossil record.

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Conceptualization: C.J.B., X.J.W., Investigation: C.J.B., X.J.W., Writing – original draft: C.J.B., X.J.W., Writing – review & editing: C.J.B., X.J.W., Supervision: C.J.B., X.J.W., Funding acquisition: X.J.W.

Competing interests

The authors declare no competing interests.

Additional information

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