Tracing the Origin and Migration of Humans—Significant Progress in Paleoanthropological and Paleolithic Fields Made by IVPP

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Abstract: Over the past 15 years, the Paleoanthropological and Paleolithic team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, has made significant progress in understanding modern human origins and evolution through extensive fieldwork, fossil and artifact discoveries, and cutting-edge ancient molecular analysis. The new fossil findings from Hualongdong, Xuchang, the first report on Harbin, and the reevaluations of previously found fossils like Xujiayao revealed high population diversity in East Asia during the late Middle Pleistocene, implying multiple evolutionary lineages linked to modern humans, Neanderthals, or Denisovans. Different species names were proposed for these unique fossils. Discoveries from Zhiren Cave and Fuyan Cave refreshed our knowledge of modern human emergence in China, sparking debates between the "Recent African Origin" and "Multiregional Evolution" hypothesis. Additionally, new archaeological evidence from Nwya Devu and Xiamabei highlighted human adaptations to extreme climates and technological innovations. Genomic studies further revealed complex patterns of modern human dispersal, admixture, and adaptation in China, especially in the past 40,000 years. The first mitochondrial DNA of Denisovan outside Denisova Cave was successfully extracted from the sediments on the Plateau, suggesting the long-term occupation of this population in this area.

Keywords: Modern human origins, Archaic *Homo*, Denisovan, Ancient DNA, Lithic tools

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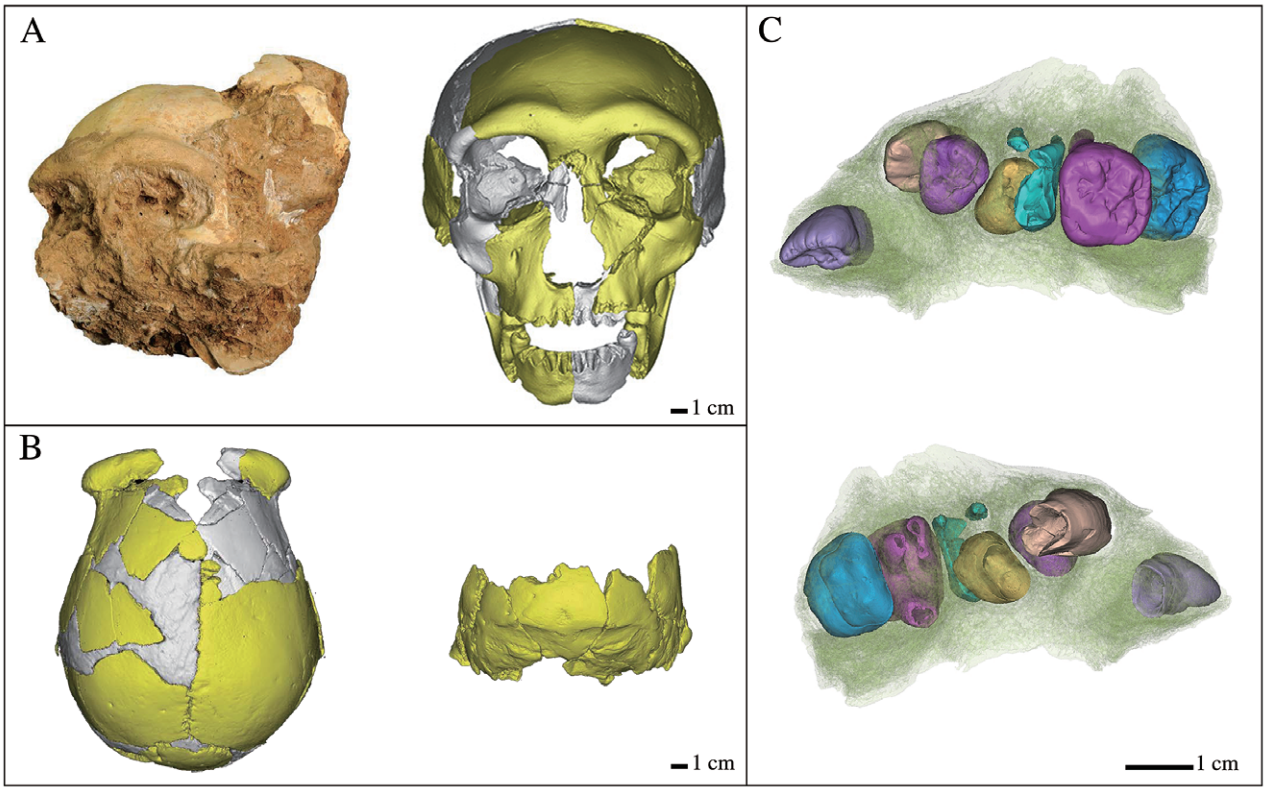
Introduction

In the past 15 years, the Paleoanthropological and Paleolithic team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, has conducted systematic field surveys and excavations in different regions and at various altitudes across the country, and a number of important human fossils and artificial remains have been uncovered. In addition, the team has also actively engaged in extensive collaborations with domestic and international scholars, developing cutting-edge techniques in extracting and analyzing trace amounts of ancient DNA from both biological samples and sediments. These efforts have led to a series of breakthroughs and significant progress in issues of universal concern, mainly including the mechanisms of modern human origins, the timing of their appearance, behavioral evolution, migration and dispersal patterns, and modes of genetic and cultural fusion.

Mechanisms of Modern Human Origins and the Timing of Its Appearance

In the mechanism of modern human origins, morphological evaluations of the cranium, mandible, teeth, and postcranial bones of East Asian late Middle or early Late Pleistocene archaic *Homo* (Hualongdong- ~300 thousand years ago or ka, Xuchang- ~125–105 ka, Xujiayao- ~224–161 ka; Figure 1), combined with the results of the studies on other contemporary hominins in China, have revealed a high population diversity and possible multi-lineages of evolutions. Among the typical characteristics, the most significant ones exhibited by the archaic *Homo* are a set of progressive features that are modern human-like (Wu *et al*., 2019; Xing *et al*., 2019). These traits mainly include a flattened and retracted face, highly-increased cranial capacity, the appearance of mental trigone, simplified dentition, and a slow and prolonged dental de-

Figure 1. The Hualongdong cranium (A), Xuchang cranium (B), and Xujiayao maxilla (C).



Graphic: Revised after Li *et al*., (2017), Wu *et al*., (2019), and Xing *et al*., (2019).

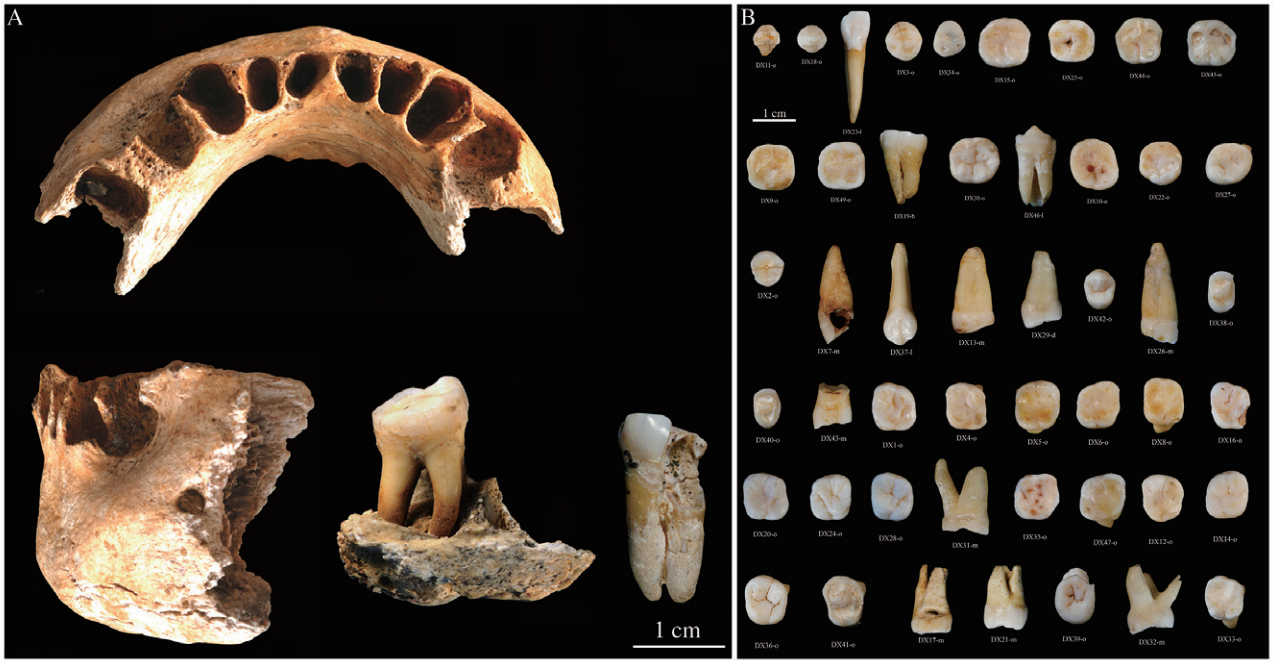
velopment and possibly others that follow the rhythm of modern humans in most aspects. It directly indicates that some of the archaic *Homo* in China had already begun evolving towards modern humans, and the key diagnostic features of modern humans had probably emerged in different regions across the world. Moreover, there is a unique group of archaic *Homo*, represented by Xujiayao and Xuchang with large cranial capacity that falls at the upper limit of variations of both Neanderthals and modern humans (Li *et al*., 2017). These hominins also display certain traits, like the structure of the labyrinth, the surface morphology of the occipital bone, and specific mandible characteristics, that are commonly found in Neanderthals. In recent few years, instead of using "archaic *Homo sapiens*" or "archaic *Homo*", different species have been proposed to name these particular groups from China. *Homo daliensis*, based on the Dali cranium, has resurfaced. Additionally, the term pre-modern human was explicitly proposed for the Hualongdong fossils. New species names such as *Homo longi*, based on the Harbin cranium, have also been formally introduced (Ni *et al*., 2021, Ji *et al*., 2021).

As for the emergence of modern humans, the discovery of the Zhiren mandible and the 47 teeth from Fuyan Cave of Daoxian, pushed the date back to ~100 ka (Liu *et al*., 2010, 2015; Figure 2). The findings and studies of these new fossils have refreshed the knowledge of modern human emergence in East Asia mainland and prompted people to reconsider the migration and dispersal patterns of modern humans across the Eurasian continent. Inevitably, the earlier appearance of modern humans in China reignites a new round of widespread discussions between proponents of the "Recent African Origin" and "Multiregional Evolution" hypothesis.

Behavioral Evolution of Modern Humans

In terms of the evolution of behaviors in modern humans, new archaeological findings continue

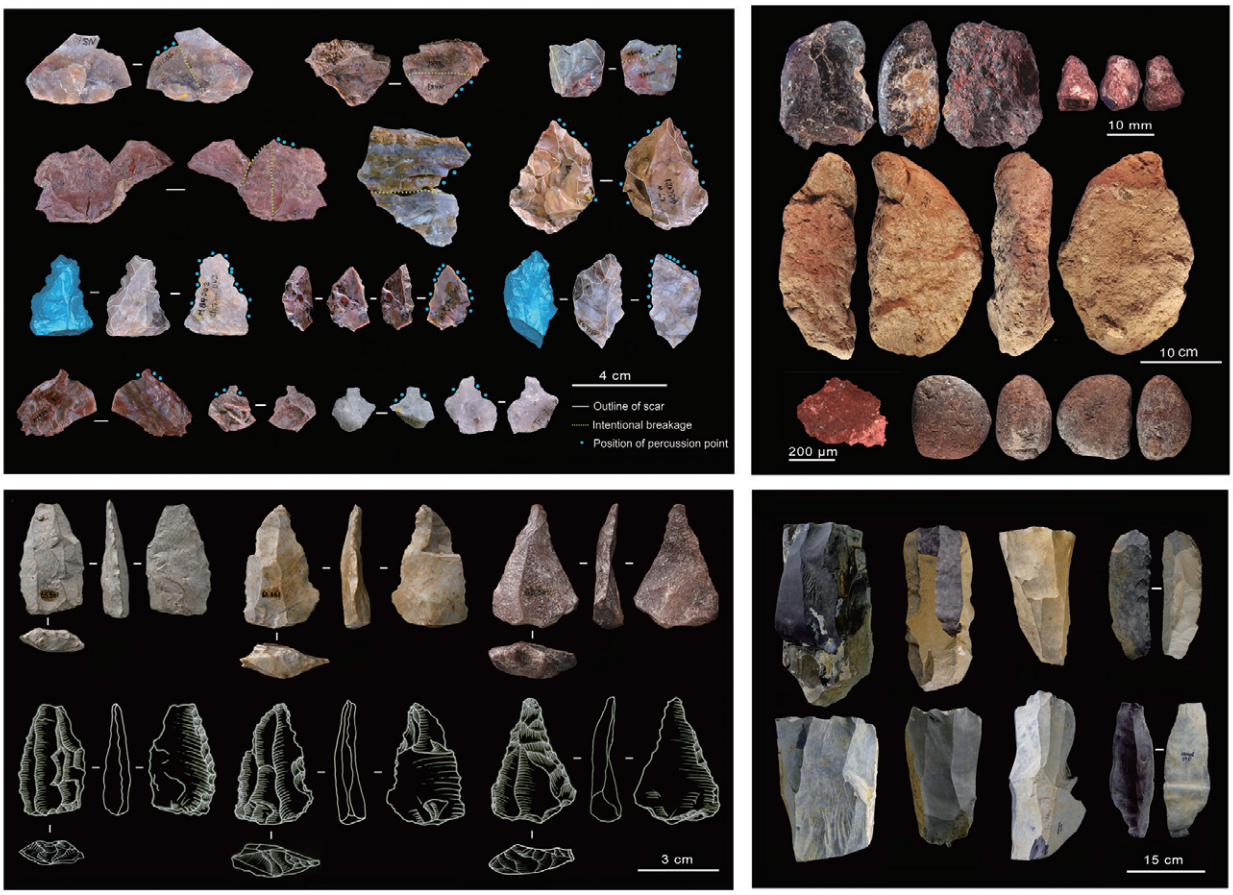
Figure 2. The Chongzuo mandible and teeth (A) and Fuyan teeth (B).



Graphic: Revised after Liu *et al*., (2010, 2015)

to challenge previous understandings (Figure 3). The discovery and research of the Nwya Devu site in Xizang Autonomous Region have extended the timeline of modern humans' presence on the Qinghai-Tibet Plateau to 40 ka, highlighting their adaptation to extreme high-altitude and low-oxygen environment (Zhang *et al*., 2018). The abundance of prismatic blade cores at Nwya Devu is nearly unique in China and resembles those in Siberia and Mongolia, and thus it is possible that early humans from Xizang and Siberia interacted. The evidence from Nwya Devu that humans were living at 4,600 m above sea level 30 ka to 40 ka provides a graphic example of how successful our species has been as a colonizing animal (Zhang and Dennell, 2018). The cultural assembly of traits at the Xiamabei site in the Nihewan basin is unique for Eastern Asia and does not correspond with those found at other archaeological site assemblages inhabited by archaic populations or to those generally associated with the expansion of *H. sapiens*. Artifacts such as pigments, ornaments, and tanged tools from the Xiamabei site reveal a complex process of cultural evolution among modern humans in East Asia, reflecting localized and mosaic patterns of cultural and technological innovation (Wang *et al*., 2022). The Shiyu site in Shanxi indicates a unique lithic assemblage and a cultural profile from 45 ka in north China, featuring a combination of technological characteristics from both the western Eurasian continent and East Asia, as well as curated ornaments and bone tools, alongside obsidian sourced from distant regions. Shiyu exhibits a set of advanced cultural behaviors, and together with the recovery of a now-lost human cranial bone, the record supports an expansion of *H. sapiens* into eastern Asia in late Late Pleistocene (Yang *et al*., 2024). These studies not only enrich our understanding of early modern humans but also provide crucial insights into the complexity of human evolution.

Figure 3. Lithic artifacts from Cenjiawan (top left), Shiyu (bottom left), Xiamabei (top right), and Nwya Devu (bottom right).



Graphic: Revised after Zhang *et al*., (2018), Wang *et al*., (2022), Ma *et al*., (2024), Yang *et al*., (2024).

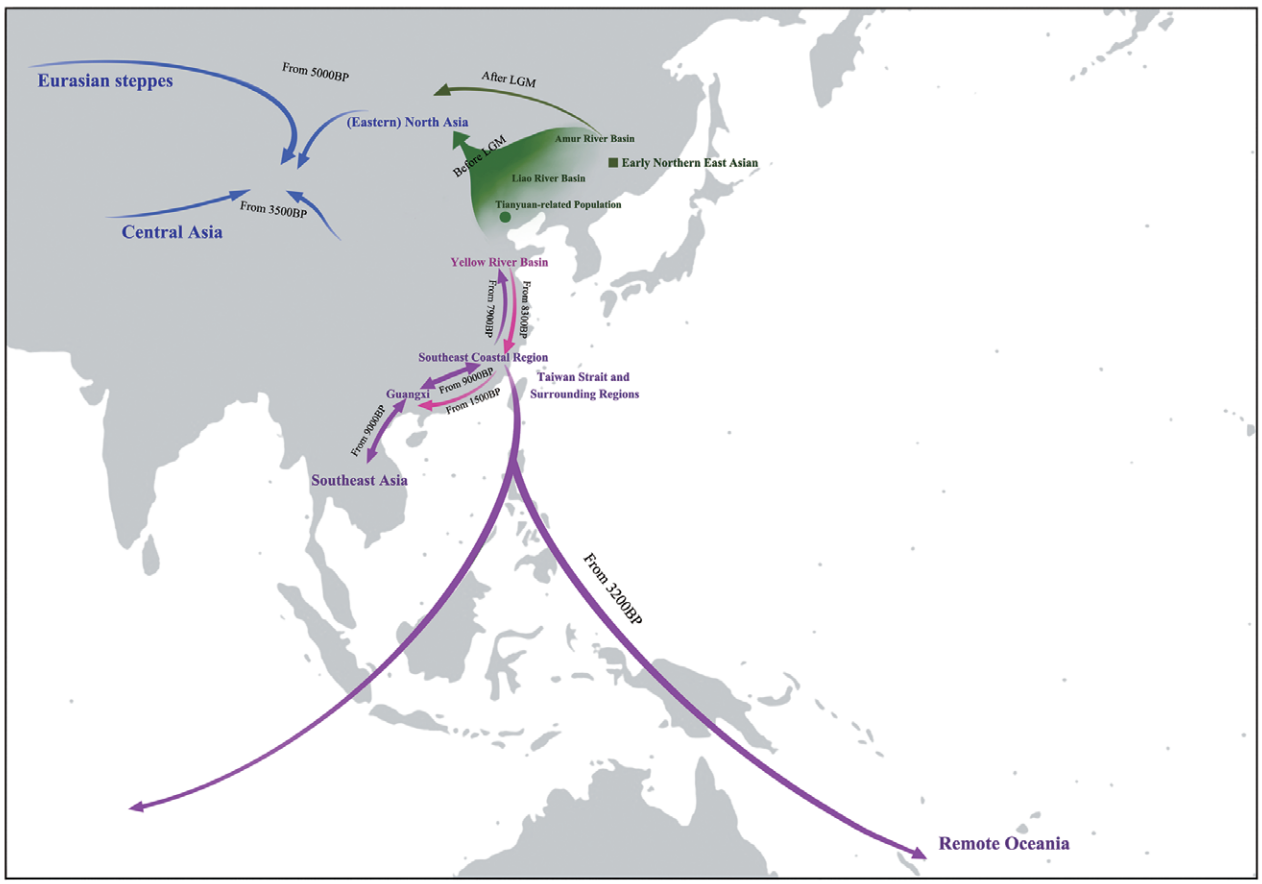
Modern Human Dispersal, Admixture, and Adaptation

Through hundreds of genomes retrieved from ancient human remains and sediments from China, ranging from 100 to 0.1 ka, FU Qiaomei and her team have uncovered the complex genetic history of human migrations, interactions and adaptive processes over the past 100,000 years in East Asia (Figure 4).

In northern East Asia, ancestry related to a 40,000-year-old individual (Tianyuan) near Beijing was widespread before the Last Glacial Maximum (LGM; ca. 26.5–19 ka) and not found after the LGM (Yang *et al.*, 2017; Mao *et al.*, 2021). Among putatively adaptive genetic variants, *EDAR V370A*, associated with thicker hair shafts and more sweat glands of East Asians, shows evidence of elevated frequency after the LGM, reflecting the influence of natural selection in low ultraviolet environments. In the Amur Region, populations show genetic patterns suggesting that they were at the forefront of interactions with Ancient North Eurasian-related populations that likely contributed to Ancient Paleo-Siberians, the closest relatives of Native American populations outside of the Americas.

In southern East Asia, sampling in Guangxi shows a deeply diverged East Asian ancestry that is not found in any present-day populations, but persisted in later Guangxi populations until at least 6,000 years ago (Wang *et al.*, 2021). In 9,000- to 6,000-year-old Guangxi populations, the ancestry was admixed with another southern ancestry sampled in Fujian, and deep Asian ancestry related to Southeast Asian Hoabinhian hunter-gatherers, showing population admixture in these regions predating the appearance of farming. Sampling in coastal China shows that by the Early Neolithic (ca. 12–9ka), northern and southern East Asian ancestries were fairly diverged and are not closely related to the deeply diverged East Asian ancestry.

Figure 4. Ancient DNA charting the migration of major modern human populations in China.



Graphic: Referred to Yang *et al.*, 2017; Mao *et al.*, 2021; Yang *et al.*, 2020; Wang *et al.*, 2021; Kumar *et al.*, 2022.

These two ancestries have profoundly impacted present-day East Asians across Asia and the Pacific. Specifically, ancestral northern and southern East Asians began shifting and mixing bi-directionally by the early Neolithic, and led up to a mixed present-day East Asian population (Yang *et al*., 2020). Austronesian speakers today like Ami and Atayal groups in Taiwan strait was demonstrated to originate from a proto-Austronesian population that derived from southern China at least 12,000 years ago.

Furthermore, ancient populations from the Qinghai-Tibet Plateau and Xinjiang Autonomous Region of China are featured with more diversified ancestries (Wang *et al*., 2023; Kumar *et al*., 2022). East Asia's first Denisovan DNA extracted out of the sediments on the Plateau indicates that Denisovans occupied the Plateau over a long period of time between 100 and 45 ka, and this group was closely related to the late Denisovans from Denisova Cave (Zhang *et al*., 2020). But for later populations living on the Plateau through the past 5,000 years, they were found to share a single origin and to show a long-term continuity, with their adaptive *EPAS1* haplotype already presented in the ancestral population by 5,100 years ago, while interactions with early populations from the Yellow River Basin and Central Asia were also highlighted. In Xinjiang, admixed ancestries related to diversified cultures were already found in Bronze Age populations, similar to present-day populations there, highlighting a certain degree of long-term population continuity in this region. Further phenotypic study shows that the majority of ancient populations sampled in Xinjiang had dark eyes (brown) and hair (black or brown), while light eyes and hair were found in several Iron Age individuals associated with the inflow and increase of Andronovo ancestry. Also, high-quality genomes of *Lactobacillus kefiranofaciens* captured from the oldest cheese unearthed in the Xiaohe Cemetery suggest that Bronze Age populations in Xiaohe had already applied Kefir grains to make the kefir cheese with their milk-producing goats related to Eurasian steppe clad, and spread their kefir production technique to inland East Asia (Liu *et al*., 2024).

Other Progresses

Significant advancements have also been made in the fields of early lithic technology and human behaviors by scientists from IVPP since 2010 (Figure 3). The discovery at the Shangchen site in Lantian, Shaanxi, which yields the oldest artifacts dated to approximately 2.12 Ma, implies that hominins had left Africa before the date suggested by the earliest evidence from Dmanisi (about 1.85 Ma). This makes it necessary to reconsider the timing of the initial dispersal of early hominids in the Old World (Zhu *et al*., 2018). Research at the Cenjiawan site in the Nihewan Basin indicates that around 1.1 million years ago, East Asian *Homo erectus* had developed prepared-core technology, establishing survival strategies and technological characteristics distinct from those in West Eurasia. This site constitutes one of the world's earliest occurrences of prepared core technologies, 0.3 Ma before the earliest record in Eurasia given in previous literature (Ma *et al*., 2024).

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