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Research Highlight

The northern dispersal of early modern humans in eastern Eurasia

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The study of the dispersal of modern humans beyond Africa is of great importance for assessing the adaptive capacities of *Homo sapiens* and for addressing why we are the only remaining hominin species on the planet today. Archaeological and genetic discussions of this process have tended to focus on the so-called "southern" route towards Arabia, South Asia, Southeast Asia, and Australasia and associated coastal and terrestrial environments [1]. More recently, increasing archaeological attention has focused on potential northern routes of human dispersal through Central Asia, Siberia, and northern China in light of new discoveries and research in this part of the world [1,2]. Technological advances and suitable preservation conditions at sites in northern Asia have increased our ability to successfully extract ancient DNA from human fossils and sediments, alongside new finds of archaeological materials, with increasingly secure dated associations in different regions. New opportunities therefore now exist to examine the northern dispersal route(s) of modern humans and their interactions with archaic hominins in northern Asia (Fig. 1a).

The fossil record of early modern humans in northern China begins by ca. 40 thousand years ago (ka) (Fig. 1c; Table S1 online), which is considerably later than its counterpart in southern China (ca. 120–80 ka) [1]. Modern human fossils from Tianyuan Cave in the Zhoukoudian area of Beijing were directly dated to 40–38 ka, and a recently revised age estimate for the Zhoukoudian Upper Cave indicates that modern humans were there by 35.1–33.5 ka and, more likely, by 38.3–35.8 ka [4]. Comparative geometric morphometric studies of these fossils suggest closer relationships with coeval groups from the European Upper Paleolithic rather than the early modern human fossils from the Levant and North Africa [5].

A few other proposed modern human fossils in northern Asia have traditionally been considered controversial or too fragmentary for morphological assessment. Fortunately, technological advances, particularly the extraction of ancient DNA, have provided greater clarity on these issues. Fu et al. [6] presented a high-quality genome sequence of a 45 ka old modern human male from Ust'-Ishim in western Siberia. This individual represents the earliest occurrence of modern humans in northern Asia. Recently, Devièse et al. [7] reconstructed the complete mitochondrial genome (mtDNA) of the Salkhit skullcap from Mongolia, indicating that this individual fell within the variation of modern human mtDNA. The skullcap was re-dated to 34.9–33.9 ka by compound-specific radiocarbon dating of hydroxyproline, placing the specimen firmly within the discussion of early modern human dispersals in northern Asia. A recently updated genome-wide dataset for the Tianyuan fossil confirmed this individual derived from a population that was ancestral to many present-day Asians and Native Americans, though postdating the divergence of Asians from Europeans [8].

Archaeological evidence of modern human dispersal in northern Asia is somewhat more difficult to firmly establish, simply because linking a specific hominin species with a particular lithic industry is contentious. However, scholars tend to correlate the wide-spread Initial Upper Paleolithic (IUP, the earliest Upper Paleolithic) or Early Upper Paleolithic in northern Asia with early modern humans because of their simultaneous occurrence in certain regions [6,7] and the appearance of macro-blade technology and ornaments (Fig. 1b). The IUP is found in several areas across northern Asia, including the Siberian Altai (e.g., the Kara Bom site), northern Mongolia (e.g., the Tolbor valley), the Transbaikal region (e.g., the Kamenka site), and northern China (e.g., Shuidonggou locality 1, Fig. 1a; Table S1 online). Technological and quantitative attribute analyses of the IUP lithic assemblages reveal a technologically coherent laminar blank production across northern Asia using a Levallois blade method. The retouched tools include both Middle and Upper Paleolithic forms. IUP sites frequently yield materials indicating symbolic behavior such as personal ornaments. Age estimates of the IUP span from ca. 50 to 35 ka, with most of the earliest occurrences coming from the Siberian Altai region (Fig. 1c; Table S1 online). The limited spatial distribution and the later emergence of the IUP in northern China, has led scholars to propose a diffusion model from Siberia to North China [9]. The archaeological, fossil, and genetic evidence of early modern humans reveal a time-transgressive pattern from west to east across northern Asia at present. This pattern suggests northern dispersal route(s) of modern humans into North China at around 45 to 35 ka, which is considerably later than the southern route(s) (ca.

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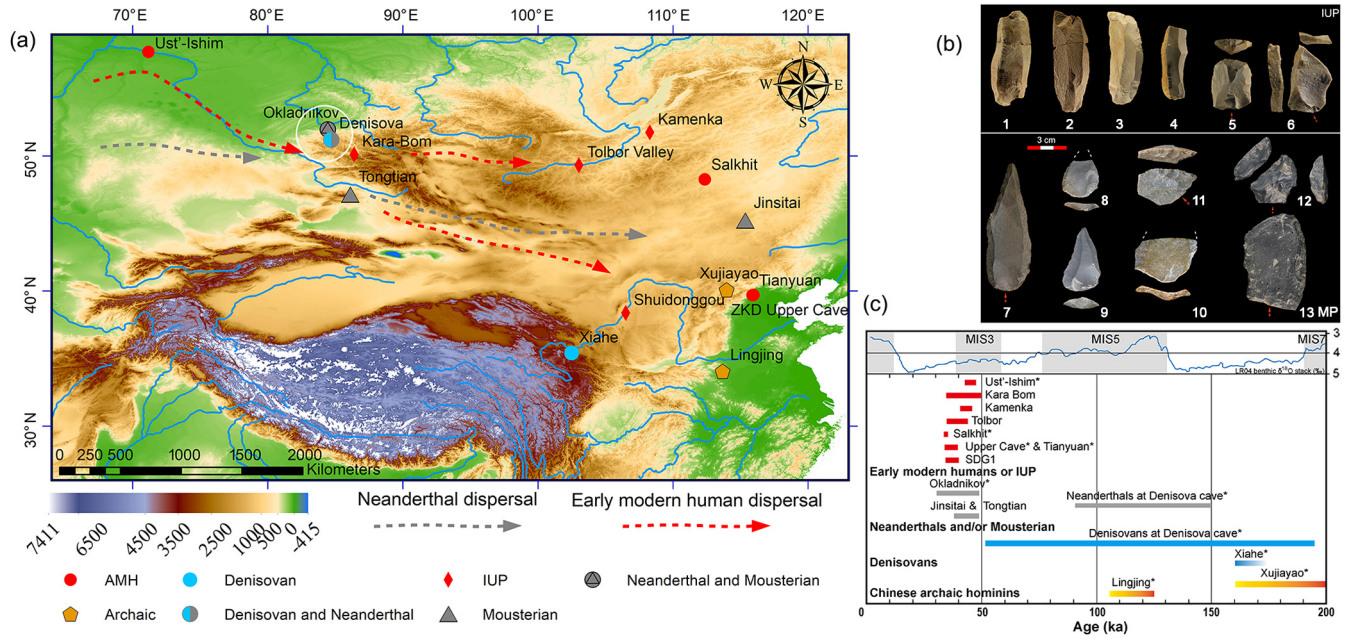

Fig. 1. Geographical location, typical lithic artifacts and chronology of the key sites mentioned in this paper. (a) Later Middle Pleistocene and Late Pleistocene fossil and archaeological sites in northern Asia and hypothetical northern routes of Neanderthal and early modern human dispersals (white circles indicate the area with Denisovan, Neanderthal, and early modern human hybridization); (b) lithic artifacts from Middle (7–13 from Jinsitai Cave, after Li et al. [3]) and Initial Upper Paleolithic sites (1–6 from Shuidonggou locality 1) (1–4, blades; 5, endscraper; 6, burin; 7–9, Levallois points; 10, Levallois flake; 11, transverse scraper; 12, deject scraper; 13, side scraper); (c) age estimates of sites mentioned in the text (* indicates sites with fossil or genetic records). For more precise potential dispersal routes plotting using GIS, see Li et al. [2].

120–60 ka) [1]. The later arrival of modern humans in northern China supports a multiple dispersal model for modern humans as suggested by Bae et al. and others [1,10]. Most importantly, complex dispersal patterns, during different periods and following different routes, enrich our understanding of the dynamics in the emergence of our species as a global one.

Along the northern dispersal route of early modern human expansions, scholars have also detected interactions with archaic hominins, in striking contrast to the southern route(s). An extraordinary example comes from Denisova Cave in the Siberian Altai. Svante Pääbo and his team working alongside their Russian colleagues, reported a "Denisovan" from the cave in 2010, and subsequent genetic research of hominin fossils and sediment has opened up a new window into the complex history of modern humans and archaic hominin groups [11,12]. The research shows that Neanderthals, Denisovans, and early modern humans had frequent genetic exchanges and, most interestingly, the traces of gene flow into early modern humans from archaic hominin groups is still measurable in contemporary populations, albeit in small proportions [13]. Denisova Cave had remained the only case example with information on this mysterious hominin until Chen and colleagues [14] identified a Denisovan fossil on the eastern edge of the Qinghai-Tibet Plateau based on paleoproteomic analysis, minimally dating to 160 ka by Uranium series dating (Fig. 1a, c; Table S1 online). This new fossil discovery, and the relatively higher proportion of Denisovan genes in present-day East and Southeast Asian populations [13], raise the possibility of finding or identifying other Denisovan specimens (probably among the archaic hominins) in China, which will enlarge our understanding of Denisovan dispersal and their relations with other hominin groups (including early modern humans).

Neanderthal fossils and genetic evidence have both been discovered in the Siberian Altai and Central Asia, but so far no typical Neanderthal fossils have been found in China, Mongolia, or the Transbaikal region, although a few morphological characteristics of some archaic hominins fossils in North China (such as the Lingjing and Xujiayao sites) were considered similar to Neanderthals of later Middle Pleistocene and early Late Pleistocene sites elsewhere [15]. Archaeological evidence for typical Middle Paleolithic assemblages, commonly associated with Neanderthals in Europe, Central Asia, and the Siberian Altai, has been lacking in China, but new discoveries at Jinsitai Cave in Inner Mongolia and at Tongtian Cave in Xinjiang, provide evidence for Mousterian toolkits in northern China at ca. 47–37 ka (Fig. 1c; Table S1 online). Li et al. [3] have suggested that the Mousterian industry in northern China may represent a Neanderthal dispersal from the Siberian Altai and Central Asia. This working hypothesis needs to be tested in the future through the discovery of new fossils or genetic findings, however. The Mousterian overlaps with the IUP in northern China, which indicates possible biological and cultural interactions of modern humans and Neanderthals in this part of the world.

New fossil, genetic and archaeological research has provided us with a complex but intriguing scenario of human dispersals and interactions in the Late Pleistocene of northern Asia. Interdisciplinary evidence tends to suggest northern dispersal(s) of early modern humans through Siberia, Central Asia, and northern China in Marine Isotope Stage 3. Interactions among various archaic hominin groups have been revealed though, not surprisingly, many questions and challenges in understanding their biological and cultural processes still remain. Indeed, little archaeological evidence has been uncovered in the vast area of northwest China, which leaves us with considerable geographic gaps along potential avenues of movement. The desertic environments in northwest China have often been considered geographic barriers for human dispersal during arid periods. However, GIS Least Cost Path models of human dispersal suggest that northwest China could have periodically acted as corridors and routes for human dispersals under wetter, interstadial conditions [2]. More systematic field survey and research are crucial for understanding the northern dispersal of modern humans. Moreover, the uneven distribution of interdisciplinary research has resulted in the difficulty in compiling systematic, comparable information between localities and regions.

There is also a remarkable scarcity of paleo environmental records associated with IUP sites in northern China more generally, making it difficult to determine the adaptations of humans moving into this part of the world compared to those of their hominin relatives.

Although scholars assume that the IUP was manufactured by early modern humans in northern Asia, cultural and biological datasets are almost always independent: sites bearing early modern human fossils often contain no archaeological materials (e.g., Ust'-Ishim, Salkhit, Tianyuan) or undiagnostic lithic assemblages (e.g., Zhoukoudian Upper Cave), while IUP sites in northern Asia have not yet yielded any fossil or genetic evidence of early modern humans. Only three early modern human specimens from northern Asia have thus far yielded useable genetic information, and the quality of the genome sequences varies due to the preservation conditions of each.

Meanwhile, no genetic data is available from southern China, where earlier modern human fossils have been discovered. This makes the study of population relationships geographically biased and incomplete. Sites with early modern human remains and archaeological materials between ca. 45 to 35 ka have mainly been dated by radiocarbon, reaching the limit of this method, thereby generating some uncertainties. Therefore, other dating methods, such as Optically Stimulated Luminescence and Uranium Series, need to be applied to get a better picture of the chronology of hominin occupations.

In sum, additional field investigations in China, particularly in the northwest of the country, are required and efforts are sorely needed to bridge paleoanthropology with other scientific disciplines, particularly molecular biology and earth sciences. By doing so, we will have an enhanced ability to answer some critical questions in human evolutionary studies including the northern dispersal of our species, examining which route(s) populations chose to move, how they interacted with archaic hominins, both biologically and culturally, and how they adapted to fluctuating regional environments.

Conflict of interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary materials

Supplementary materials to this article can be found online at https://doi.org/10.1016/j.scib.2020.06.026.

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