

PALEOENVIRONMENT. THE STONE AGE

doi:10.17746/1563-0110.2025.53.4.003-027

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The Dispersal of Denisovans and Neanderthals in China

The initial peopling of China by *H. erectus* occurred ~1.7 Ma BP, maybe even earlier. Despite climatic changes in the Pleistocene, ecological conditions for the permanent occupation of this territory by members of that taxon remained favorable, causing their continuous morphological and genetic evolution in situ along the line leading to *H. sapiens*. As a result, between 120–40 ka BP, they evolved convergently into early anatomically modern humans in this territory. A large part of the morphological variation of Late Middle to Early Upper Pleistocene hominins in China is attributable not only to the divergence of separate groups of *H. erectus* descendants, who convergently, under different ecological conditions, evolved into anatomically modern humans using various adaptive strategies, but also to the immigration of Denisovans and their assimilation of native groups. Contacts between the latter and Neanderthals in the second half of the Upper Pleistocene cannot be ruled out too.

Keywords: *H. erectus*, Denisovans (informal name of *H. s. denisovan*), *H. s. neanderthalensis*, pebble-flake, Denisovan, and Mousterian industries.

Evolution of *H. heidelbergensis*— the ancestral taxon of Denisovans and Neanderthals

The nearly three-million-year-long evolution of the genus *Homo* from its origin to evolution of anatomically modern humans followed the sapiens line, which was determined by three main factors: an open genetic system that made interbreeding and giving birth to fertile offspring possible for hominins; natural, sexual, and positive genetic selection; and the ability to subsist under the conditions of global environmental and climatic changes during the Pleistocene (Derevianko, 2019, 2022, 2025c).

Ch. Stringer (1983) and G. Rightmire (1996, 1998a, b) hypothesized that a speciation event occurred in Africa at the end of the Early Pleistocene. This hypothesis was based on the 1976 discovery

of a 640,000-year-old skull at Bodo in Middle Awash, Ethiopia. Rightmire argued that Bodo skull represented a population that was evolutionarily more advanced than *H. erectus*. This conclusion is supported by the hominin brain capacity of 1300 cm³; in addition, Bodo demonstrates many facial features characteristic of modern humans, same as the Kabwe skull (Broken Hill) (Rightmire, 1996: 32). Rightmire named the new taxon *H. heidelbergensis* and assigned to this species such fossils as Elandsfontein, Kabwe, and Ndotu from Africa; Mauer, Arago, and Petralona from Europe, tentatively Dali and Jinniushan from China (1998a, b; 2001a, b; 2004a, b; 2008).

Many anthropologists agree that a speciation event took place around 800 ka BP: *H. erectus* gave rise to a new species designated by scholars as *H. heidelbergensis*, *H. rhodesiensis*, and *H. sapiens* (Tattersall, Schwartz, 2000; Bräuer, 2001a, b; 2007,

2008; Hublin, 2001; Stringer, 2002; Foley, Lahr, 2003; and others).

Homo rhodesiensis / *H. heidelbergensis* represent a single biological species that evolved from the ancestral *H. erectus*; however, their phylogenetic histories were different: *H. rhodesiensis* stayed in Africa, where in the course of sapienization 200–150 ka BP, modern humans evolved from this ancestral taxon. *H. heidelbergensis* with the Acheulean industry migrated to Eurasia ca 800 ka BP, where they gave rise to Denisovans (informal name – *H. s. denisovan*) and Neanderthals (*H. s. neanderthalensis*). Genetic studies have shown that anatomically modern humans that migrated from Africa, Neanderthals, and Denisovans interbred with each other and produced fertile offspring. This fact indicates that the interbreeding between these taxa was intraspecific rather than interspecific, and that they belonged to an open genetic system. If at the latest stage of the almost three-million-year evolution of the genus *Homo*, the three identified taxa (in Africa, Europe, and Asia) retained an open genetic system in the chronological range of 120–40 ka BP, then the same feature should have been true for all the species identified by anthropologists in the Middle Pleistocene, and they could have also assimilated one another (Derevianko, 2019, 2022).

The split of *H. erectus* into two lineages—*H. rhodesiensis* and *H. heidelbergensis*—was a crucial event in the evolution of the genus *Homo*, marking the start of evolution of anatomically modern humans in Africa and Neanderthals and Denisovans in Eurasia. Genetic studies indicate that this occurred 812–793 ka BP (Reich et al., 2010; Meyer et al., 2012). Notably, paleogeneticists indicate different chronological periods (800–300 ka BP) when the divergence into modern humans, Neanderthals, and Denisovans occurred. Moreover, the split of an ancestral taxon into two or more taxonomic lineages means that their subsequent genetic and morphological development occurred in various places, same as the development of different lithic industries.

Only archaeological studies can clarify the issue of when this division occurred. The first split of the genus *Homo* into anatomically modern humans and Neanderthals and Denisovans occurred ca 800 ka BP, when *H. heidelbergensis* with the Acheulean arrived to Eurasia. This event marked the spread of the Acheulean lithic industry across this region, which is confirmed by the results of long-term excavations at the Gesher Benot Ya'aqov site in Israel (Goren-Inbar et al., 2018). This site, dated to the period corresponding to MIS 19 and 20, contained the oldest Acheulean industry

in Eurasia, which subsequently spread throughout Europe and a significant part of Asia following the migration of *H. heidelbergensis* to contiguous regions. The dispersal of *H. heidelbergensis* from Africa to Eurasia, and the subsequent separation of early modern humans from Neanderthals and Denisovans is evidenced by genetic findings: the first split of the genus *Homo* occurred in the chronological range of 813–793 ka BP, i.e., ca 804 ka BP (Reich et al., 2010; Meyer et al., 2012).

The second split of hominins, which also had global significance according to genetic and archaeological data, took place in the chronological range of 430–380 ka BP (Prüfer et al., 2014; Meyer et al., 2014). At that time, the taxon of *H. heidelbergensis* in the Middle East (in the Levant) divided into three branches. The population of the first branch stayed in the Middle East. Representatives of the second branch with the Acheulean industry and the Levallois primary reduction strategy migrated gradually to Europe, where they assimilated *H. antecessor*; as a result, around 200–150 ka BP, there emerged European Neanderthals and the Mousterian (Derevianko, 2024a). Humans of the third branch with the Acheulean industry and Levallois primary reduction technique expanded to the east, to Central Asia, where Denisovans emerged (Derevianko, 2019, 2022; Derevianko, Shunkov, Kozlikin, 2020). Thus, ca 400 ka BP, the second global split occurred, which led to the evolution of Neanderthals and Denisovans.

The chronological stages of separation between anatomically modern humans, Neanderthals, and Denisovans proposed by geneticists (700, 600, 500 ka BP, and others) are not supported by archaeological evidence. In the Middle Pleistocene, two events occurred that played a decisive role in the sapienization of *H. erectus*. The first event, approximately 800 ka BP, marked the divergence between anatomically modern humans and Neanderthals and Denisovans. The second, approximately 400 ka BP, marked the split between Neanderthals and Denisovans.

At the initial stage of this process, Neanderthals and Denisovans belonged to a single biological taxon. As the former dispersed across Europe and the latter across Asia, their genetic and morphological features evolved. Moreover, each taxon retained a certain common element of their ancestral genetic and morphological heritage. These two global hominin expansions took place ca 800 and 400 ka BP, which is confirmed by the spread of the Acheulean from Africa to Europe and South Asia during the first dispersal event. In the above areas, the Acheulean replaced

the Early Paleolithic pebble-flake industry. During the second dispersal, the Levallois primary reduction technique spread across Europe, South and Central Asia, and played a key role in the subsequent improvement of hominin material culture. Hence, the dates mentioned by geneticists and other researchers (1 Ma BP, 700, 600, 500, and 300 ka BP) for the possible split of hominins in the Late Early and Middle Pleistocene are not supported by archaeological findings.

Genetic and morphological development of Denisovans

The most complete Denisovan genome was derived in the course of DNA sequencing of the Denisova 3 fossil (Krause et al., 2010; Reich et al., 2010) from layer 11.2 (63 ± 6 to 55 ± 6 ka BP) at Denisova Cave (Jacobs et al., 2019: Fig. 3). The Denisova 3 fossil yielded the most complete genetic sequence, which evolved during a long period of time in the vast expanses of Central Asia and contiguous regions of the Denisovan dispersal in the Late Middle and the first half of the Upper Pleistocene. The degree of Denisovan genetic diversity was higher than that of seven Neanderthal individuals from various regions of Western and Central Europe, for whom the complete mtDNA sequences were derived, but lower than that of modern humans (Sawyer et al., 2015). It means that the Denisovan population was probably large and could have expanded across Central, East, and South Asia (Meyer et al., 2012; Prüfer et al., 2014).

The genetically and morphologically developing Denisovan taxon, after diverging from the future Neanderthals around 400 ka BP, gradually expanded over the Levant and spread to Iran (Derevianko, 2024e), and then to Central (Derevianko, 2024b, 2025a, d) and South Asia. Owing to the insufficient information on the Paleolithic of Iran (Shoae, Nasab, Petraglia, 2021; Shoae et al., 2023), no convincing evidence of Denisovan habitation in this region is available. Iran could have been the only transit region for the both processes: dispersal of Denisovans over East Asia and the initial expansion of *H. erectus* from Africa over Central and South Asia (Derevianko, 2024e). The possible dispersal of some Denisovans over the western regions of South Asia is evidenced by a small share of Denisovan genetic heritage identified in some modern populations of this region (Skoglund, Jakobsson, 2011; Bergström et al., 2021).

Denisova Cave yielded early human remains: the fossil of Denisova 2 was recovered from the

lowermost culture-bearing layer 22.1; other Denisovan fossils were found in deposits of the Main, East, and South Chambers. Furthermore, Denisovan mtDNA was recorded in the soft sediments of several cultural layers. Given the homogeneity of the Denisova Cave lithic industry, these data suggest that Denisovans inhabited the cave from 300 to 40 (30) ka BP (Derevianko, 2022).

Mitochondrial and nuclear DNA sequencing from fossils and cultural layers revealed some distinctive features in the genetic sequence of Denisovans at various stages of their habitation in Denisova Cave (Slon et al., 2017; Douka et al., 2019; Jacobs et al., 2019). On the basis of these data, geneticists inferred that two distinct populations of this taxon inhabited the cave at the early and late stages (Jacobs et al., 2025). However, this assumption is not supported by archaeological evidence. The cave was inhabited by Denisovans, who produced a homogeneous lithic industry showing clear continuity from the bottom up the whole cultural-stratigraphic sequence; hence, there is no reason to assume the existence of two different Denisovan populations. It should be borne in mind that at the initial stage of their divergence, ca 400 ka BP, Denisovans and Neanderthals constituted a morphologically and genetically single species. The morphological and genetic development of Denisovans occurred during their dispersal across Central Asia and adjacent regions, through assimilation of indigenous population (late *H. erectus*) and adaptation to various environmental conditions. Denisova 3 should be considered the haplotype of the Denisovan taxon. Thus, the Denisovan taxon evolved over a period of 300,000 years.

Denisovans occupied the vast Asian continent with diverse environmental and climatic conditions, plains and highlands, populated and unpopulated by other hominins. This inevitably led to significant variability in their morphology and some distinctions in the genetic sequence. Even the fossils from Denisova Cave cultural layers dating to the initial and terminal stages of Denisovan habitation show certain distinct features in DNA sequence. Genetic and morphological distinctions between Denisovan groups that assimilated the indigenous population (Central Asian *H. erectus*) and the Denisovan tribes that had not contacted them should have been even greater.

S.R. Browning and his colleagues proposed a new method for detecting introgression; their study showed that the East Asian population apparently interbred with two different, genetically divergent Denisovan populations (Browning et al., 2018). This suggests

a complex process of development of the Denisova 3 genome in this area. Using new methods and formerly derived results on the adaptive introgression of Denisovans with Southeast Asian populations, L. Ongaro and E. Huerta-Sánchez identified four separate Denisovan populations spread across a vast territory, with each population being adapted to its own habitat (2024). Drawing on their own data and findings of other researchers, they used the Denisovan introgression to determine the time of divergence between different populations, and concluded that two Denisovan populations, D1 and D2, participated in the introgression of the Altai Denisovans, D0. Introgression into Papuan population occurred for D2 ca 363 ka BP, and for population D1 ca 283 ka BP (Ibid.: 2614). According to another study, the estimated time of split between D2 and D0 is ~409 ka BP, and that between D1 and D0 ~222 ka BP. The Aeta Magbukún Negritos of Luzon have 25 % more Denisovan genetic heritage than the Papuans. Unlike that of the Papuans, the Denisovan heritage of the Aeta is not of Australo-Asian origin, which suggests that the Aeta underwent an additional episode of admixture with another Denisovan population, D3. L. Ongaro and E. Huerta-Sánchez came to a conclusion about the dispersal of four separate Denisovan populations in East Asia, which implies the existence of a group of various Denisovan populations, each of which adapted to its own environmental settings in a vast geographic region (Ibid.).

East Asia, during about 400–40 thousand years, was colonized not by four Denisovan populations, but rather by members of one evolving Denisovan taxon. The proposed hypothesis as to the dispersal of two or more Denisovan populations across East Asia is based on the fact that the ancestors of modern populations interbred with Denisovans at different stages of their genome evolution. The genome of Denisova 3 from layer 11.2 is also different from that of Denisova 2 from layer 22.1, as there was a gap of more than 200 thousand years between these individuals. I believe that the genetic and morphological evolution of Denisovans took place during the chronological range of 400–40 ka BP in the vast area of Central and partly Southeast Asia. Denisovans dispersed across regions with various climates, flora, and fauna, on plains and in highlands. Some groups might have experienced prolonged isolation, while others assimilated *H. erectus*. These and other factors determined some distinctions in their genome. The currently available information about the Denisovan morphology is insufficient, but I am

sure that in the future, when informative cranial and postcranial fossils of Denisovans are discovered, it will be possible to reveal significant variability in members of this taxon.

The genetic development of Denisovans was a long-lasting process. This assumption is based on the identified gene that enabled these hominins to adapt to habitation at high altitudes. This is evidenced by a Denisovan-type mandible (Xiahe) from Baishiya Cave in Gansu Province. The cave is located in the northern part of the eastern edge of the Tibetan Plateau at an altitude of 3280 m asl (Chen F.-H. et al., 2019; Zhang D. et al., 2020). The mandible was discovered in 1980 (Chen F.-H. et al., 2019); in 2018 and 2019, three test pits each measuring 2 m² were established in the cave. The cave is a karst cavity 63 m long, 8 m wide, and 5 m high (Zhang D. et al., 2020: Fig. 31). During excavations, ten lithological layers were identified; these were composed of silty sediments with numerous inclusions of angular limestone fragments accumulated in the course of desquamation of the cave walls and ceiling.

In total, 1310 lithic artifacts and 579 bone fragments of Pleistocene animals were collected. Regrettably, it is impossible to get a definite idea about the lithic industry. The article provides only a poorly legible photograph of one core and five flakes. Collections from layers 1–6 were dominated by bone fragments of small and medium-sized animals, including gazelles, marmots, and foxes. Assemblages from layers 7–10 contained bones of large animals, such as rhinoceros, auroch, and hyena (Ibid.).

The right half of the Xiahe mandible is described by researchers as having an archaic morphology, quite common among Middle Pleistocene hominins (Chen F.-H et al., 2019). The mandibular body is very robust, relatively low and thick, demonstrating a pronounced lateral prominence and a well-developed anterior marginal tubercle. Internally, the protruding alveolar prominence overhangs a marked sub-alveolar fossa. The mylohyoid line runs well below the mandibular foramen. The mental foramen is located low. The triangular mental protuberance is weakly expressed, and the symphysis is sharply inclined at an angle of 69°. The genioglossal fossa separating the upper and lower transverse tori is small (Ibid.: 410). Results of geometric morphological analysis allowed the authors to conclude that the mandible falls within the range of the Middle Pleistocene hominin sample. The outline of the dental arch is specific, being less elongated than in *H. erectus* and closer to that in hominins such as *H. neanderthalensis* and *H. sapiens*.

Dentition is the main morphological feature that links Xiahe and the fossils from Denisova Cave. Paleoproteomic analysis revealed an ancient endogenous proteome preserved in the dentin. According to the results of phylogenetic analysis, the proteome of the Xiahe jaw corresponds to the high-coverage Denisovan genome (Denisova 3). Moreover, as the researchers note, the polymorphism of one specific amino-acid also indicates a close relationship between the Xiahe individual and Denisovans (Ibid.: 409). According to the scholars, the Xiahe mandible shows the closest similarity to the Penghu 1 fossil from the Taiwan Strait as compared to other East Asian fossils dating to the same chronological period.

The Xiahe mandible was found in a carbonate interlayer. The fossil age was determined using ^{230}Th method to 164.5 ± 6.2 ka BP, which is statistically indistinguishable from the dates derived for the upper part of the carbonate interlayer— 155 ± 15 ka BP, and the lower part— 163 ± 10 ka BP (Ibid.).

In 2018 and 2019, a study was carried out to establish the possibility of DNA preservation in the cave sediments (Zhang D. et al., 2020). For this purpose, 12 soil samples and 14 bone fragments were collected from various layers of the cave. Animal DNA was detected in layers 2–4, 6, 7, and 10, and hominin mtDNA in layers 2–4 and 7. The comparative analysis of hominin mtDNA from Baishiya and Denisova caves has shown the following: mtDNA from layer 4 of Baishiya Cave falls into the mtDNA variation and forms a clade with Denisova 3 and 4; mtDNA from layers 2 and 3 of Baishiya Cave forms a clade with Denisova 3 and 4 mtDNA; mtDNA from layer 7 of Baishiya Cave is older than the fossils of Denisova 3 and 4. Noteworthy is the occurrence of mtDNA in layer 3, which is dated to the range from 46 ± 2 to 33 ± 1 ka BP, and the upper part of overlying layer 2 to 17 ± 12 ka BP. Researchers doubted that Denisovans could have survived until the emergence of anatomically modern humans in this area 40–30 ka BP (Ibid.). Chen F.-H. et al. (2019) did not exclude the possibility of Denisovans settling in this area after 40 ka BP. Important additional information about the living conditions and subsistence strategies of the Denisovans was obtained during the study of bone material from Baishiya Cave (Xia et al., 2024; Callaway, 2024).

The Xiahe fossil is extremely significant because the emergence of archaic dental morphology in Denisovans was due to their interbreeding with Central Asian *H. erectus*, while the gene allowing them to live in the high altitudes evolved during the adaptation

to new environmental conditions. Some Denisovans apparently inhabited the mountains at various altitudes over a long period of time, which led to the formation of the high-altitude adaptation gene.

The gene identified in modern Tibetans is a striking example of adaptive introgression to hypoxia, caused by the reduced partial pressure of oxygen in the air at high altitudes. Tibetans inherited this feature from Denisovans (Huerta-Sánchez et al., 2014). Acclimatization to high altitudes in lowlanders is accompanied by increased hemoglobin secretion, which leads to blood thickening, thrombus formation, and vascular occlusion, while in Tibetans hemoglobin levels are lower, which reduces the risk of cardiovascular disease. Unlike lowlanders, Tibetan women show a higher fertility rate, they do not suffer from preeclampsia during pregnancy, and their babies are of normal birth weight.

The EPAS1 gene, responsible for adaptation to high-altitude hypoxia, was transferred from indigenous Tibetan people (Denisovans) to anatomically modern humans from Africa 40–30 ka BP, when they started to expand to high-altitude regions. During the process of Denisovans assimilation, a specific variation of the EPAS1 gene developed in modern humans' genetic heritage. Comparative analysis of Tibetan and Denisovan DNA also revealed that Tibetans are genetically much closer to Denisovans than other modern human populations, and that the high-altitude adaptation mechanism of Tibetans was triggered by genes inherited from Denisovans (Ibid.).

The archaic dentition of Denisovans was a result of assimilation of a part of this taxon during the early stage of their dispersal over Central Asia with late *H. erectus*. DNA sequencing of the Denisova 3 fossil revealed certain genomic features inherited from an archaic hominin more than 1 million years old (Krause et al., 2010), which was likely obtained from *H. erectus* as a result of assimilation of these two taxa. The fact that Denisovans inherited their dentition from Asian *H. erectus* is evidenced by anthropological finds from Obi-Rakhmat (OR-1) in Uzbekistan (Grot Obi-Rakhmat, 2004). The Obi-Rakhmat Grotto is a unique site with a lithic industry showing clearly expressed blade trend and certain technical-typological features similar with the Denisovan industry of the terminal Middle Paleolithic (Derevianko, 2001, 2022).

Excavations of Obi-Rakhmat layer 16 revealed anthropological materials in association with artifacts of the Middle to Upper Paleolithic transitional type, dating to 50–60 ka BP. Individual OR-1 is represented by six separate permanent maxillary teeth and

~150 small skull fragments (Glantz, Viola, Chikisheva, 2004; Viola, Seidler, Nadden, 2004; Glantz et al., 2008; Bailey et al., 2008). Anthropological analysis of the fossils did not identify its definite taxonomic status; the individual was tentatively classified as Neanderthal (Bailey et al., 2008; Glantz et al., 2008).

OR-1 shows a number of archaic features (in particular, dentition), which distinguish it from European Neanderthals and bring it closer to Denisovans (Derevianko, 2025a). The OR-1 fossil should not be attributed to Neanderthals, because the Obi-Rakhmat Grotto stratigraphic sequence clearly shows the continuous technocomplex development from lowermost cultural layer 21 to the upper layers containing Early Upper Paleolithic industry, which matches well with the small set of typical stone tools from layer 16. The fossils from Obi-Rakhmat and Teshik-Tash belong to the same chronological period (60–50 ka BP), but the Obi-Rakhmat individual produced a Denisovan-type industry, which can be considered transitional from the Middle to Upper Paleolithic, while the Teshik-Tash Neanderthal individual produced a Mousterian industry (Okladnikov, 1949).

The process of Denisovan genome evolution implicated acquisition of positive alleles and “washing out” of negative ones; meanwhile, for a long time, they retained part of their ancestral genome, same as Neanderthals, who diverged from them 400 ka BP. Based on the data on the Neanderthal genetic heritage detected in some cultural layers, and in Denisova 5, geneticists came to the conclusion that Denisovans and Neanderthals could have alternately inhabited Denisova Cave starting from 170 ka BP, and possibly even earlier (Jacobs et al., 2019). This conclusion contradicts the continuous development of the Denisova lithic industry and a residual ancestral genetic heritage shared by Denisovans and Neanderthals (Derevianko, 2024a). In particular, the results of DNA sequencing of hominins who settled around 400 ka BP in Sima de los Huesos show that their mtDNA was Denisovan (Meyer et al., 2014), while their nuclear DNA was Neanderthal (Meyer et al., 2016).

The issue of the Denisovan material and spiritual culture is complex and multifaceted. The initial and early Upper Paleolithic industry of Denisova Cave is among the earliest in Eurasia; it is distinguished by elaborated techniques of stone working and a considerable amount of non-utilitarian items. This raises doubts that the local Upper Paleolithic was developed on an autochthonous basis. N. Zwyns, who briefly participated in fieldwork conducted by the Institute of Archaeology and Ethnography SB

RAS and examined collections of artifacts found at Paleolithic sites of the region in various years, refutes my hypothesis as to the convergent formation of the Altai Upper Paleolithic in a number of his publications (see, e.g., (Zwyns, 2012)). The scholar points to the lack of continuity between the Middle and Upper Paleolithic of Denisova Cave as the primary evidence, and also explains the emergence of the Upper Paleolithic in the Altai by migration of hominins from the west. The issue of convergent development of the Altai Upper Paleolithic on the basis of the Middle Paleolithic and the possibility of habitation of anatomically modern humans in the cave are discussed in detail in my monograph devoted to the origin of *H. s. denisovan* (Derevianko, 2022: 21–184; 431–469). Here, I will briefly dwell on this topic.

Material and spiritual culture of Denisovans

In Denisova Cave, 15 Paleolithic culture-bearing layers have been identified, spanning the period from 300 to 35 ka BP (Derevianko et al., 2003). The development of the Middle Paleolithic industry can be traced throughout the entire cultural-stratigraphic sequence: the early stage (300–160 ka BP), middle (160–120 (100) ka BP), terminal (120 (100)–60 ka BP), transitional from the Middle to Upper Paleolithic (60–55 ka BP), initial Upper Paleolithic (55–45 ka BP), and early Upper Paleolithic (45–40 (35) ka BP) (Derevianko, 2022). The continuous development of the Middle Paleolithic industry, traced in cultural layers 22–11, was marked by the growing proportion of blade flaking and the use of blades as tool blanks, along with the decrease in the number of Middle Paleolithic tools and the increase of Upper Paleolithic ones. The continuity is particularly evident between the terminal Middle and initial Upper Paleolithic. Thorough analysis of the Denisova lithic artifacts gives no grounds to doubt the reliability of the continuous development of the lithic industry from the layer corresponding to the initial occupation of the cave by Denisovans up to and including layer 11, which contains a clear and one of the earliest Upper Paleolithic industries in Eurasia (Derevianko et al., 2003; etc.).

The high level of development of the Denisovan spiritual and material culture in the Upper Paleolithic is evidenced by the variety of artifacts recovered from layer 11 of the Main, East, and South Chambers. Primary reduction was dominated by a blade-based strategy, with the Upper Paleolithic tools manufactured from laminar blanks. A large number of bone tools were recovered from this layer. Nine intact and

fragmented needles deserve special mention. Layer 11 of the Main Chamber, dating back to 40–45 ka BP, yielded an intact eyed needle 72 mm long (Fig. 1, 3–6). This is the oldest artifact of this type in the world. Its thickness at the top is a little over 1 mm, and the eye diameter is less than 1 mm. Drilling a hole of such a diameter required skilled craftsmanship. This find raises questions: what kind of work could such a thin and fragile item have been used for, and what kind of thread could have been threaded through such a small hole? Denisovans could probably have made fabric from plant fibers at that time. Further studies will provide definitive answers to these questions.

In total, 267 various personal ornaments (Fig. 1, 1, 2; 2) made of stone, bone, animal teeth, and shells were recovered from Denisova layer 11, along with Denisovan fossils, over an area of less than 100 m². The collection included fragments of mammoth tusk diadems and two fragments of a stone (chloritolite) bangle (Fig. 3), which manufacturing techniques included sawing, grinding, polishing, and drilling. A small zoomorphic figurine made of mammoth tusk dating back to 40 ka BP was the most striking (Fig. 4). The needle, fragments of diadems and bangle are among the oldest in the world. No other archaeological site dating to 45–40 ka BP, either in Africa or Eurasia, can be compared with Denisova Cave in terms of the quantity and variety of non-utilitarian items found in layer 11, which yielded the Upper Paleolithic industry and the fossils of Denisova 3 and Denisova 4 individuals, belonging to the chronological range of 63 ± 6 to 55 ± 6 ka BP (Jacobs et al., 2019; Fig. 3). Therefore, the claim about migration of hominins with such a high level of material and spiritual culture to the Altai is completely unfounded. Moreover, no evidence of such a culture has been reported from any Paleolithic site dating back to the chronological range of 55–40 ka BP, either in the Levant or in the transit area from the Middle East to the Altai.

No remains of anatomically modern humans have been found in Denisova Cave. However, genomic studies of endogenous material from the upper part of layer 11 and from layer 9 identified mtDNA of anatomically modern humans (Zavala et al., 2021). Denisovan fossils—Denisova 3 and Denisova 4—were found in layer 11.2 of the East Chamber and in the upper part of layer 11, respectively. The extraction

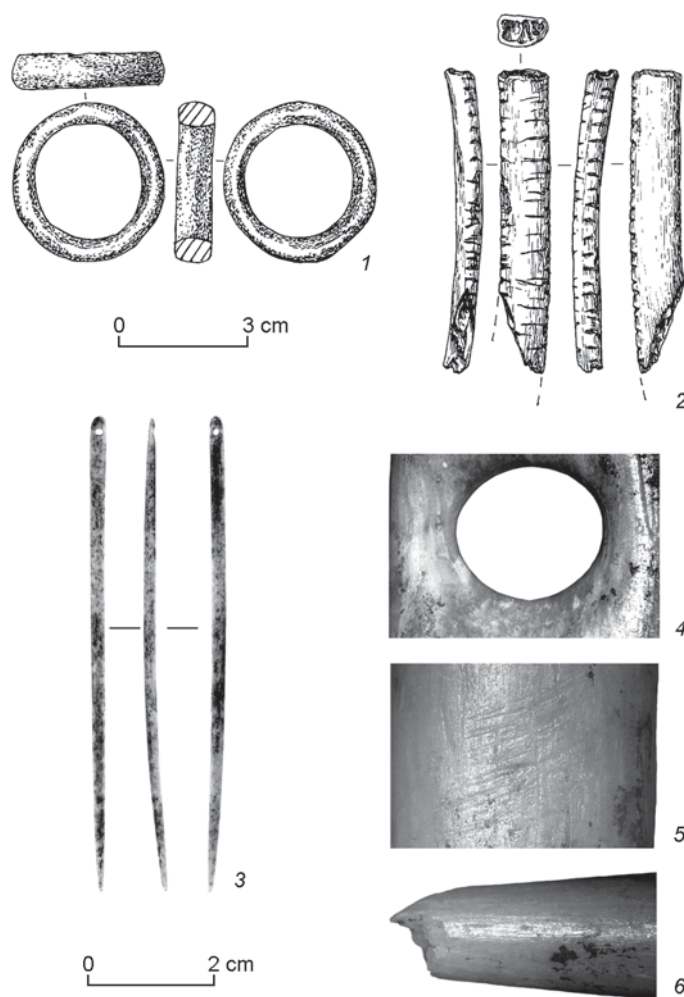


Fig. 1. Finds from East Chamber horizon 11.2 (1, 2), and Main Chamber layer 11 (3–6) at Denisova Cave.

1 – ring; 2 – blade with cut-marks; 3 – bone needle; 4–6 – macrophotographs of some parts of the needle surface at $\times 40$ magnification.

1, 2 – after (Derevianko et al., 2008); 3–6 – after (Derevianko et al., 2016).

of modern human mtDNA from layers 11 and 9 is understandable. Layer 11 covers partially preserved thin (2–3 cm) layers 10 and 9 overlain by the strata dating to the Bronze and Iron Ages and to medieval period. The base of layer 9 is dated to 38 ± 9 ka BP (Jacobs et al., 2019; Fig. 3) and attributed to the Middle Upper Paleolithic. The industry of this layer shows traces of continuity with the Denisovan lithic industry. Therefore, it cannot be ruled out that this cultural layer should also be correlated with the Denisovans. The well-stratified site of Anuy-2 (dating to 27–21 ka BP), attributed to the terminal stage of the Upper Paleolithic, was excavated 50 m downslope from the cave, on the second floodplain terrace; the site produced a lithic industry different from that of the Denisovans. There is no doubt that this site



Fig. 2. Personal ornaments made of animal teeth (1–5), tubular bone (6, 7, 10), mammoth tusk (8, 9, 11) from East Chamber horizon 11.2 at Denisova Cave (after (Kozlikin, 2017)).

1–5, 8, 11 – pendants; 6, 7, 10 – tubular beads; 9 – ring.



Fig. 3. Bangle (after (Derevianko, 2022)).

1 – external view; 2 – internal view; 3 – top view; 4 – bottom view.

was inhabited by anatomically modern humans; they visited the cave and, most likely, left behind the excretions, which could have penetrated layers 11 and 9. Layer 9 in the cave was overlain by cultural layers from the Bronze Age, Iron Age, and late medieval period. The urine and feces of the Holocene people who inhabited the cave, as well as the modern people shortly inhabiting the site of Anuy-2, could have penetrated the underlying layers.

Ust-Ishim femur (which sample was used to extract DNA and to trace the genetic sequence of anatomically modern humans (Fu et al., 2014)) was dated to $41,400 \pm 1300$ BP (OxA-25616)

and $41,400 \pm 1400$ BP (OxA-30190) 46,880 cal years.

In 2017, we surveyed the entire Ishim Valley and partly the Irtysh Valley in the presumed area where the bone was discovered. No sites older than 10,000–15,000 years were found there; moreover, the geomorphological situation precludes the existence of such sites in the area. But this is not the only reason to doubt the proposed idea about the migration of modern humans from Africa to Southern Siberia at such an early time. If we accept the date of 45 ka BP, then we must acknowledge that the Ust-Ishim bone is the earliest bone fossil of anatomically modern humans who migrated from Africa, discovered in Eurasia. The old age of the bone is questionable. It shows no signs of fossilization and has a modern appearance.

The mineralogical and chemical analyses of the fossil were carried out using a combination of physical and physicochemical techniques (thermal analysis, optical, scanning electron, and scanning probe microscopy, X-ray fluorescence analysis, gas chromatography, X-ray spectral microprobe analysis, etc.). The studied fragment of Ust-Ishim man bone shows a high degree of preservation (Silaev et al., 2017). Since the context of the fragment is unknown, its Holocene age cannot be ruled out; its old age is explained by its specific burial conditions. I contacted the researchers who determined the age of the bone with a request to re-date the bone, but unfortunately, I have never received a response.

I have every reason to assert that between 300 and 40 (35) ka BP Denisova Cave was inhabited by Denisovans, who produced one of the world's earliest Upper Paleolithic industries. This naturally raises the question: how can we explain the development of such a high-level material and spiritual culture among the Denisovans?

Denisovans migrated to the Altai ca 300 ka BP, practicing one of the earliest Middle Paleolithic industries. They had to adapt to relatively harsh climatic conditions during both warm (interglacials) and cooling (glacials) periods. The coordinates of Denisova Cave are 52° N, 84° E. The subsistence strategy of the hominins settling in more southern

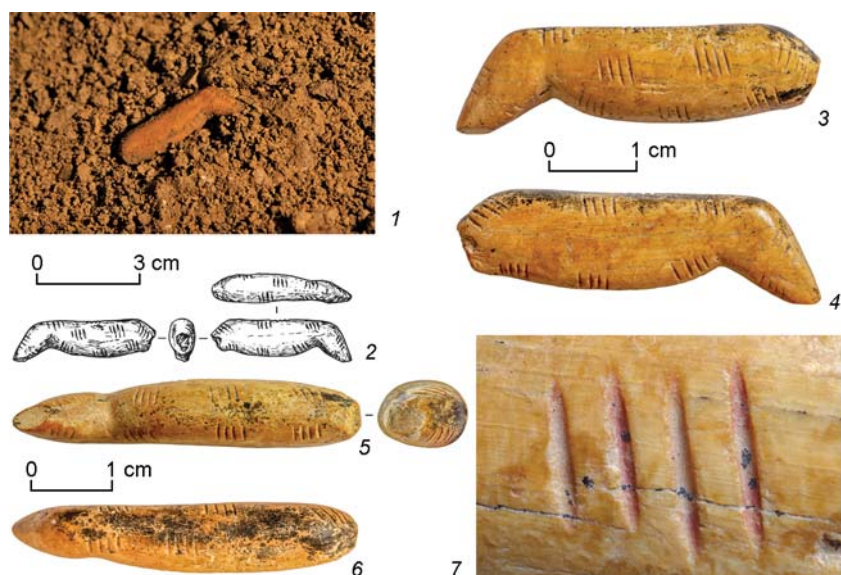


Fig. 4. Zoomorphic figurine from South Chamber layer 11 at Denisova Cave (after (Derevianko, 2022)).

1 – photo of the figurine *in situ*; 2 – trace image; 3 – right-side view; 4 – left-side view; 5 – bottom view; 6 – top view; 7 – traces of ornamental pattern and mineral pigment on figurine surface.

latitudes was based on hunting and fishing products along with vegetable foods, which played an important role in the diet throughout almost the entire year. In the Altai, nuts, berries, and roots could have replenished 5–10 % of the diet for one to two months. Denisovans obtained their food primarily by hunting medium- and large-sized ungulates. Hunting such animals required sophisticated equipment, mutual understanding and cohesion among hunting groups, as well as refined techniques and methods of chasing game. All this inevitably influenced the development of human cognitive system, the complication of social relationships, and the enhancement of communication skills. Regrettably, in the course of excavations, archaeologists usually uncover only a small amount of material remains, which makes it difficult to reconstruct the eventful, joyful, and challenging life of this remarkable taxon, whose study is just beginning.

It should also be noted that the continuity in the Denisovan industry can also be traced at other well-stratified Paleolithic sites in the Altai—Ust-Karakol, Anuy-3, Kara-Bom, and others, belonging to the Late Middle and Upper Pleistocene. Denisova Cave is not the only Southern Siberian site where Denisovans might have settled. This issue was analyzed in detail in volume VII of my series “Three Global Human Migrations in Eurasia” (Derevianko, 2025d).

Dispersal of *H. s. denisovan* over the territory of China

The dispersal of genetically and morphologically evolving Denisovans in Central Asia and the Altai, close to the modern borders of China, could have occurred 300–350 ka BP or earlier (Derevianko, 2022, 2024a, 2025a, b). A significant number of paleoanthropological finds dating back to the second half of the Middle to first half of the Upper Pleistocene have been found in China, which show the evolution of *H. erectus* towards sapienization and the convergent evolution of early modern humans on the ancestral basis of this taxon (Wu Xinzhì, 1988; Wu X., 2006; Wu X.Z., 2004; Gao X. et al., 2010; Derevianko, 2011; and others).

In the paper from the previous issue of this Journal, referring to the *H. erectus* evolution along the sapiens line in China, we noted that the collection of anthropological finds from the Late Middle to Early Upper Pleistocene included the remains of hominins whose dentition was quite specific (Derevianko, 2025c). In this regard, the Hexian fossil is of particular interest: the mandible is robust, and the preserved incisor, premolars, and molars are significantly larger than those reported from Zhoukoudian and *H. erectus* from Java.

Scholars point out that representatives of *H. erectus* populating Southeast Asia during the Pleistocene show a trend towards the decrease of teeth size and mandible robustness (Kaifu et al., 2005; Kaifu, 2006; Zanolli, 2013). The Hexian fossil deviated from the general evolutionary trend of South and East Asian *H. erectus* and, in these respect, was close to Denisovans, who inherited their archaic dentition pattern from Central Asian *H. erectus*, whose phenotypic features are not yet known to us.

The Hexian locality, unfortunately, has not been reliably dated. The first U-series dating of animal bones indicated a chronological range of 220–130 ka BP (Chen T.M., Yuan S.X., 1988). EPR-dating of animal teeth yielded an age of 160–220 ka (early uranium-uptake) and 350–250 ka (linear uranium-uptake) (Huang W. et al., 1995). According to U-series and EPR-data, the age of the hominin fossil sample is 412 ± 25 ka (Grün et al., 1998). Given the latter date is true, the Hexian fossil could be associated with the apparently earliest episode of assimilation of Denisovans and China *H. erectus* evolving towards sapienization. No stone tools were found at the Hexian site.

In Chaoxian County, 50 km southeast of the Hexian site, Chinese scientists discovered an upper jaw along with occipital bone of a hominin (Xu C. et al., 1984; Wu X.Z., Poirier, 1995). This site,

similarly to the neighboring Hexian, contained no stone tools. Using the U-series dating method for layer 2, where the fossils were deposited, the scholars obtained an age estimate of 160 to 200 ka (Chen T.M. et al., 1987). A repeated analysis of eight stalagmite carbonate samples and three bone samples from the same layer 2 determined an age older than 310 ka (Chen T.M., Yang, Wu, 1994). Wu X.Z. and E. Poirier (1995) identified the occipital bone and the maxilla as belonging to archaic *H. sapiens*, which has some apomorphic derived features as compared to *H. erectus*, but at the same time, these parts of the skull are more robust and archaic than those of modern *H. sapiens*. According to Sh.E. Bailey and Liu Wu, the dentition of the Hexian hominin is archaic and lacks the derived features identified in Neanderthals. The teeth are large, the occlusal morphology retains primitive features observed in the hominins from Chaoxian, Xujiayao, Tongzi, and some others (Bailey, Liu, 2010). The Hexian fossil also suggests the interbreeding of autochthonous Paleolithic population of China with Denisovans.

Among the sites from the Late Middle to Early Upper Pleistocene, two Xujiayao sites discovered 1 km away from the village of Xujiayao, on the border of Shanxi and Hebei provinces, attract special attention (Chia, Wei, 1976; Chia, Wei, Li, 1979; Wu Maolin, 1986; Qiu Zhonglang, 1989; Wei Qi, 2004; Keates, 2000). The sites are located on the right bank of the Liyi River, a tributary of the Sanggan River, at an altitude of 970 and 980 m above sea level. Excavations were carried out in 1974, 1976–1977, and 1979.

The Xujiayao site demonstrates a complex stratigraphic and cultural-historical sequence. Two units were identified within the 20-meter-thick exposed profile: cultural deposits occurred at a depth of 4–12 m below the modern soil (block 1); within this strata, anthropological fossils were discovered at a depth of 8–12 m (block 2) (Chia, Wei, Li, 1979). Lithological facies analysis revealed that the Nihewan Basin underwent large-scale shallowing at the time of early human habitation. The basin contained numerous lakes and streams. The climate was somewhat cooler than today: wet summers and dry, cold winters. Researchers estimated that the temperature in the site area was 4 °C lower than today (Hun et al., 2011). The landscape was shrubby forest-steppe. During rainy seasons, the water level in the lakes rose and caused floods. Cultural layers are embedded in clayey sediments with inclusions of pebbles, silt, and fine-grained sand. Cultural deposits at the sites occupy the area exceeding 5000 m².

The obtained Xujiayao dates are significantly diverse. The U-series dating of six mammal teeth produced an age estimate of 125–90 ka BP. Absolute dates for mammal bones from the cultural layer of the site range from ~125 to 104 ka BP (Chen T.M. et al., 1982; Chen T.M., Yuan, Gao, 1984). The culture-bearing deposits lie 15 m above the Blake paleomagnetic excursion (Liu C., Su, Jin, 1992), which is dated to 126–119 ka BP. The cultural layer was dated using the OSL-method to the interval from 69 ± 8 to 60 ± 8 ka BP (Nagatomo et al., 2009). The $^{26}\text{Al}/^{10}\text{Be}$ analysis yielded a date of 220–160 ka BP (Tu et al., 2015). According to ^{14}C -dates of organic materials and mammal bones, the site is older than 40 thousand years. A study of quartz samples using the $^{26}\text{Al}/^{10}\text{Be}$ method yielded a date of 240 ± 50 ka BP. The results of EPR-dating showed an average age of 260–370 ka (Ao Hong et al., 2017). Wu X.-J. and E. Trinkaus attribute the Xujiayao site to the period of MIS 5–4 (2014). Taking into account the diverse dates and faunal composition, Wu X.-J. and Ch. Bae dated the site to the Late Middle Pleistocene—between 220 and 130 or between 200 and 160 ka BP. Thus, the age of the Xujiayao site remains an open question (Wu X.-J., Bae, 2024).

During excavations at the site, Chinese scholars found a large number of Pleistocene animal bones and stone tools. Paleoanthropological finds are extremely important. Fossilized hominin bones were heavily fragmented. The first paleoanthropological find—a parietal bone—was discovered in 1976. A year later, fragments of the posterior part of the parietal bone were found. Some bones bear cutting marks; these might represent the evidence of cannibalism. A hole of 9.5 mm in diameter with signs of healing was noted on the posterior part of the parietal bone (Wei Qi, 2004). During excavations in 1974 and 1976–1979, two intact and several fragments of parietal bones, a nearly intact temporal bone, two relatively intact occipital bones, a partial and an intact mandible, a child maxilla, two upper and two lower molars were recovered.

Morphological characteristics of the anthropological remains provide information concerning their taxonomic affiliation. Initially, the Xujiayao fossils were attributed to *H. erectus*, *H. neanderthalensis*, and anatomically modern humans, because of their morphological variability and ambiguous taxonomic affiliation (Wu X.Z., Poirier, 1995; Bae, 2010; Wu X.-J., Xing, Trinkaus, 2013; Wu X.-J. et al., 2014; Wu X.-J., Trinkaus, 2014; Xing et al., 2015; and others). With the discovery of a new taxon—Denisovan—the need arose to “reevaluate the Xujiayao hominins from a global prospective” (Ao Hong et al., 2017: 62).

The most detailed description of the Xujiayao 14 mandible was provided by Wu X.-J. and E. Trinkaus (2014). According to them, the specimen has a lateral mandibular notch crest, an open mandibular foramen, a wide ramus, an asymmetric mandibular notch, an enlarged superior medial pterygoid tubercle, possibly a retromolar space, a gonial eversion, as well as an unusual depression of the triangular plane. The first two traits, according to these authors, are apparently ancestral for Late Pleistocene and recent *Homo* and normal in anatomically modern humans. The second two traits distinguish Xujiayao 14 and archaic *Homo* from anatomically modern humans. The following two characteristics are most common among Neanderthals, although the gonial eversion contrasts with Late Pleistocene Neanderthals. Thus, the researchers conclude that Xujiayao 14 stands out from Pleistocene and later *Homo* species for its mosaic morphology, which highlights regional differences throughout the Pleistocene (Ibid.: 333).

More information in terms of taxonomic affiliation was provided by nine teeth discovered at Xujiayao; these were analyzed by Xing S. and co-authors (Xing et al., 2015; Martínón-Torres et al., 2017). The dentition contained an upper central incisor, an upper canine, upper premolars 3 and 4, upper molars 1 and 2, and four isolated teeth (upper molars 1 and 3, and lower molar 3). All the scholars noted that the Xujiayao teeth were large and exhibited morphological features similar to those of Early and Middle Pleistocene hominins from Asia.

Excavations at the Zhiren and Huanglong sites yielded nine human teeth. These sites are chronologically close to Xujiayao, and the fossils found represent early modern humans (Liu W. et al., 2010a, b). Comparative analysis of the teeth from these two sites and dental materials from other sites around the world inhabited by early modern humans revealed that the Xujiayao teeth possess more primitive features, such as asymmetrical LP⁴ crowns, trapezoidal LM¹ and LM² with a narrower distal half, robust and developed root systems for LM¹ and RM³, and larger crown sizes of all teeth. These features bring the Xujiayao teeth closer to the teeth of Early and Middle Pleistocene hominins from East Asia and distinguish them from the teeth of *H. neanderthalensis* (Xing et al., 2015: 227).

M. Martínón-Torres and co-authors note that the mesiodistal and buccolingual diameters of the Xujiayao teeth fall outside the range of variation recorded in other Late Pleistocene finds, with the exception of the Denisova Cave specimen, which is also significantly larger than other specimens of its time. The researchers

believe that the lack of data about the Denisova fossils hampers proper comparative analysis of the teeth from Denisova and those from Xujiayao, but there is an undeniable connection between them (Martín-Torres et al., 2017).

A.V. Zubova and her co-authors (Zubova, Chikisheva, Shunkov, 2017) carried out a comparative analysis of the teeth; they noted distinct similarities between the Denisovan and the Xujiayao molars. Xujiayao fossils demonstrate mosaic morphology; they have significant differences from dental specimens belonging to early modern humans of China and retain an archaic component that brings them closer to the Middle Pleistocene hominins of East and South Asia (Sangiran, Zhoukoudian, Longtandong, Chaoxian). The significant similarity in the structure of the upper molars from Xujiayao and Denisova Cave suggests that the individuals belonged to the same taxon characterized by the long-term preservation of *H. erectus* features (Ibid.: 131). Similar archaic features of dentition identified in Xujiayao and Denisova fossils were recorded in anthropological finds from the Xuchang site (Xing et al., 2015; Li Z.-Y. et al., 2017).

The collection of Xujiayao fossils includes a temporal bone (Xujiayao 15), which provides important information for comparative analysis owing to the size and location of semicircular canals of the bony labyrinth of the inner ear. Wu X.-J. and co-authors compared the Xujiayao temporal bone labyrinth with that in two other fossils discovered in China, dating to the Early (Lantian 1) and Middle (Hexian) Pleistocene, as well as with the early modern human Liujiang 1 (Wu X.-J. et al., 2014). The lateral canal of Xujiayao 15 is located in the upper part of the posterior canal. The researchers compared this fossil in all respects with fossils from the Middle and Upper Pleistocene of Eurasia and noted a mosaic combination of archaic and advanced features.

The scholars have noted that the Xujiayao fossils possess morphological features typical of Denisovans and Neanderthals, which could have been inherited from *H. heidelbergensis*—their common ancestral species. After the divergence of these two taxa ca 400 ka BP, morphological and genetic evolution of Neanderthals occurred in Europe, while Denisovans evolved in Central Asia. The taxa developed new morphological features, both derivative and plesiomorphic (when interbred with *H. erectus*), as well as retained the morphological and genetic heritage of their ancestral species. Unfortunately, the amount of available fossils dating back to the Late Middle to the first half of the Upper Pleistocene is small and fragmentary, which

hampers our understanding whether the morphological Neanderthal feature established in Xujiayao 15 can be explained by the influence of *H. s. neanderthalensis* or it was a residual ancestral feature. The labyrinth of temporal bone is a good example in this regard.

This element of Xujiayao 15 has been classified as Neanderthal-type, because such a structure of the bony labyrinth is most typical of European Neanderthals. Wu X.-J. and E. Trinkaus noted that an identical temporal bone labyrinth was identified in the fossil of Obi-Rakhmat 1, which they consider Neanderthal (2014), although the other interpretation is the Denisovan (Derevianko, 2022, 2024a, 2025a, d). Notably, a similar structure of the temporal bone labyrinth has been recorded in early modern humans, for example, in the Sungir 1 individual (Razhev et al., 2024).

Some researchers argued that certain Xujiayao fossils showed Neanderthal traits. However, Wu X.-J. and E. Trinkaus believed that the occipital bones of Xujiayao 6 and 12, the temporal bone of Xujiayao 15, and the teeth from this site did not show Neanderthal morphological features (2014). At the same time, these scholars mentioned that the Xujiayao fossils exhibited more similarity to Neanderthal specimens than to *H. heidelbergensis* fossils.

The shoveling of anterior teeth, the prominence of lips, and the continuous distal trigonid crests on molars are considered the Neanderthal features (Xing et al., 2015). Along with Neanderthal traits, some morphological features that are common to *H. erectus* and anatomically modern humans have been identified (Bae, 2010; Wu X.-J. et al., 2012, 2014; Wu X.-J., Xing, Trinkaus, 2013; Wu X.-J., Trinkaus, 2014; and others).

The discoveries of Denisovans in the Altai, in Baishiya Cave (Xiahe), in Laos (Tam Ngu Hao 2) (Demeter et al., 2022), and at some other sites may indicate that Late Middle Pleistocene hominins belonged to a common ancestral stock for Denisovans, Neanderthals, and anatomically modern humans (Vincenzo, Manzi, 2023).

Wu X.-J. and Ch. Bae conducted a comprehensive analysis of maxilla XJY 1, teeth XJY 2, 13, and 16, nine parietal fragments XJY, posterior skull XJY 6, occipital bone XJY 12, and mandible XJY 14, and inferred that the Xujiayao fossils were morphologically unusual. They identified five key distinguishing features: 1) very large cranial capacity (1700 cm³) combined with low and wide shape; 2) unusual, Neanderthal-like bi-level nasal floor, temporal bone labyrinth, and thin occipital torus; 3) relatively large teeth that display a mosaic of primitive and advanced features; 4) slow pattern of dental growth and development state that is more in line

with modern humans than earlier hominins; 5) mosaic combination of archaic and modern features of the mandible and temporal bone (Wu X.-J., Bae, 2024).

Noteworthy is a well-preserved skull dated to ca 150 ka BP, discovered in 1933 near Harbin in northern China during the construction of a bridge across the Songhua (Sungari) River (Ni Xijun et al., 2021). The exact location of the fossil discovery is unknown, but the strontium isotope composition identified therein falls within the range of values characteristic of local Middle Pleistocene to Early Holocene deposits. The earliest age of ca 146 ka was determined for the skull using the U-series method (Ibid.: 1).

The overall size, robustness, thick and well-developed supraorbital ridge, large mastoid process, and prominent temporal lines of the Harbin skull led Chinese anthropologists to identify a male individual approximately 50 years old. The researchers argued that the braincase, with a capacity of 1420 cm³, displayed a number of ancestral features. Its supraorbital ridge, base, and palate are very wide. In the lateral view, the braincase is long and low, with a sloping frontal bone and a uniformly rounded parietal region. The occiput is neither angular with a pronounced transverse ridge, as in *H. erectus* and *H. heidelbergensis/rhodesiensis*, nor prominent with a suprainiac depression as in Neanderthals. The maximal breadth is in the supramastoid region, below which a well-developed mastoid slopes downwards and inwards. The squamous suture differs in shape from that of *H. erectus* fossils, and there is no upper parietal expansion typical of modern humans (Ibid.: 2).

The scholars pointed to surprising combination of both archaic and *H. sapiens* features in the Harbin skull, and the cranial capacity was unusually large for the Late Middle Pleistocene skulls found in China. Overall, the scientists concluded that the Harbin skull possessed a distinctive set of traits and likely represented a distinct species of *Homo*, differing from other species of Middle and Late Pleistocene humans, including *H. sapiens*, *H. neanderthalensis*, and *H. heidelbergensis/rhodesiensis*. Large overall dimensions distinguish the Harbin skull from all other fossils, but in its shape and proportions it is similar to other large skulls belonging to the species of late archaic *Homo* (Ibid.).

The facial region of the Harbin skull is considerably wide, but low. The shape of the zygomaticomaxillary region is similar to that of *H. sapiens* and *H. antecessor* and is close to the Middle Pleistocene fossils from Dali and Jinniushan. The facial region is moderately prognathous, as in early modern humans. According

to the researchers, the combination of features makes the Harbin skull more similar to the skulls of early *H. sapiens*, such as Jebel Irhoud 1 and Eliye Springs, than to those of younger representatives of this lineage (Ibid.).

The researchers mention large square orbits, a marked supraorbital torus indicating deep eyes. A large and wide pyriform aperture suggests a large, bulbous nose. An expanded perinasal region and a relatively protruding midface correspond to flat, short cheek regions, similar to those of modern humans. Large incisor and canine sockets indicate that this individual likely had quite large anterior teeth and a broad mouth.

The most striking feature of the Harbin find is the morphology and large size of M² (mesiodistal length 13.6 mm, buccolingual width 16.6 mm). Among the Late Pleistocene fossils, it is closest to the permanent molars from Denisova Cave (Denisova 4: M^{2/3}, mesiodistal length 13.1 mm, buccolingual width 14.7 mm; Denisova 8: M³, mesiodistal length 14.3 mm, buccolingual width 14.65 mm) (Ibid.). Ni Xijun and his co-authors note that although nothing is known about the mandible of the Harbin individual, phylogenetic analysis indicates the possibility of combining the Harbin skull and the Xiahe mandible into a single sister group. The scholars suggest a phylogenetic relationship between the Harbin skull and the Xiahe mandible, which belongs to the Denisovan lineage (Ni Xijun et al., 2021: 5).

The mandible Penghu 1, which bears strong resemblance to that of Denisovan, is the “easternmost” fossil discovered in China. It was together with animal bones in a fishing net raised from a depth of 60–120 m at a distance of 25 km from the west coast of Taiwan (Chang et al., 2015). Penghu 1 belonged to hominins who inhabited this region, which may have been part of the landmass during the periods of low sea levels 190–130 and 70–10 ka BP.

The mandible Penghu 1 shows mosaic morphology: a small condyle, a low and thick corpus, and a relatively thin symphysis. Researchers also note the extremely large size of the anterior teeth and the unusual morphology of the root of M², which correlate this fossil with Hexian remains.

Researchers have proposed three possible taxonomic classifications for Penghu 1. First, such archaic morphology could have been characteristic of the earliest *H. erectus*, which initially settled in Southeast Asia; Early and Middle Pleistocene *H. erectus* in Java (Sangiran and other) had a thinner jaw structure and smaller molars (Kaifu, 2006;

Zanolli, 2013). This hypothesis, according to the researchers, could be correct in the case of dispersal of two *H. erectus* species or demes with a more primitive and derived dentition in Southeast Asia, which is unlikely. Second, the archaic morphology could be associated with hominins with the Acheulean industry who migrated from Africa to China and who possessed a thick dentition. To my mind, this theory is not supported by either anthropological or archaeological evidence. In China, bifacial industry emerged convergently around 1 Ma BP (Derevianko, 2014, 2019). Third, hominins of Penghu 1 type evolved from a local population of *H. erectus* with a more gracile jaw, but this assumption contradicts the general trend towards sapienization of *H. erectus*. At present, researchers have no doubt that the archaic dentition of Penghu 1 exhibits the closest similarity to that of Denisovans.

The processes of Denisovan assimilation and acculturation with the indigenous populations of China are evidenced by the archaeological materials from both the northern and southern regions. Since 1991, excavations have been underway in Panxian Dadong Cave in Guizhou Province, where artifacts associated with the Levallois primary reduction strategy were recovered (Huang et al., 2015), along with anthropological materials including teeth showing morphological similarity to the finds from Xujiayao and Xuchang, and hence, to the fossils from Denisova Cave. According to researchers, these remains belonged to a hominin of the transitional type from Paleoanthropes to Neanderthals (Liu W., Si, 1997; Miller-Antonio et al., 2004; Liu W. et al., 2013).

The morphological features of the dental fossils from Panxian Dadong Cave, traces of the Levallois reduction strategy, and the availability of Acheulean biface-type tools in the lithic industry, along with the age of the finds in the range of 150–300 ka suggest that this cave site was inhabited by Denisovans or by individuals of the Denisovan and indigenous people mixed ancestry.

In 1972 and 1983, four hominin teeth were recovered from Yanhuidong Cave, Tongzi County, southern China (Wu M., Wang, Zhang, 1975; Wu M., 1984). The age of the finds was estimated to 172–240 ka. The morphological features of the Tongzi teeth differ from those of classic *H. erectus* and are close to the Xujiayao and Panxian Dadong specimens. The researchers attributed them to archaic *H. sapiens* and archaic *Homo* (Wu X.Z., Poirier, 1995; Wu X.-J. et al., 2012; Li Z.-Y. et al., 2017). Xing Song and co-authors analyzed the dental finds from Tongzi,

Xujiayao, and Panxian Dadong and proposed to separate the remains of representatives of “non-erectus” East Asian hominins from other Middle Pleistocene anthropological fossils (Xing et al., 2019a).

Anthropological finds from the territory of China, dating back to the Late Middle Pleistocene, demonstrate both undoubted *H. sapiens* traits and plesiomorphic ancestral morphological features. The mosaic morphology is due to two main reasons: divergence in the course of dispersal of individual groups of late *H. erectus* evolving towards sapienization, and assimilation with Denisovans. Mosaic craniofacial and dental morphology in hominins expanding to China in the Late Pleistocene produce a complex picture of diversity, which leads to the conclusion as to the coexistence of several hominin species in this territory (Liu W. et al., 2013; Xing et al., 2015, 2019a, b; Li Z.-Y. et al., 2017; Chen F.-H. et al., 2019). These might have included late archaic *H. sapiens*, early unknown humans, Denisovans, and one more unknown group (Xing et al., 2015; Li Z.-Y. et al., 2017; Chen F.-H. et al., 2019).

I believe that during the Late Middle Pleistocene, China could have only be colonized by *H. erectus* evolving towards sapienization and the Denisovans migrating there in small groups from Central Asia and the Altai Mountains. Fossils from this period display an archaic dentition typical of Denisovans; this is most evident in the Xujiayao, Penghu 1, and Harbin fossils (along with certain traits characteristic of modern humans, such as shovel-shaped incisors, which are particularly common among modern Chinese populations). Cranial and postcranial remains of Denisovans, which will be discovered in future, will allow for reconstruction of more complete picture of the interactions between Denisovans and the indigenous populations of China during the Late Middle Pleistocene and the first half of the Upper Pleistocene. In my opinion, Denisovan skull might be most similar to the Harbin find.

Possibility of expansion of *H. s. neanderthalensis* over the territory of China

F. Weidenreich hypothesized the evolution of modern humans in China on the ancestral basis of *H. erectus* through a convergent process; he suggested that *H. s. neanderthalensis* could have been a transitional form (1947), which idea implied the dispersal of representatives of this taxon over the region. The Maba

skull found in Guangdong Province was regarded as the evidence supporting this hypothesis. Having reconstructed the skull, Woo R.K., like many other researchers after him, noted certain features of the Zhoukoudian *H. erectus* and Neanderthals in the Maba morphology (Woo, Peng, 1959). In classifying Maba as a Neanderthal, researchers paid special attention to the similarity of its facial morphology to Neanderthal specimens (Wu X.Z., 1988). G. Pope noted that the Maba skull with its rounded eye sockets and “saddle-shaped” nose is unique among Chinese fossils. From his point of view, the above-mentioned and other traits, identified by physical anthropologists during the study of this find, fully correlate with Neanderthals (Pope, 1992). This fossil is usually dated to the chronological range of 135–129 ka BP (Yuan, Chen, Gao, 1986). There are also older dates for the Maba skull, corresponding to MIS 7–6 (Gao B., Shen, Qui, 2007; Shen et al., 2014). Many researchers expressed doubts concerning the feasibility of attributing the Maba fossil to Neanderthals (Howell, 1999; Wolpoff, 1999).

Some experts in the physical anthropology compared the Jinniushan skull with the Petralona specimen, identified certain similar morphological features, classified both fossils as Neanderthals, and attributed them, along with other finds, with Dali in particular, to a single category (Hublin, 2013; Ao Hong et al., 2017). Researchers also noted that the suprainiac fossa of Xuchang 2 and the semicircular canal morphology in the Xuchang 1 and 2 skulls exhibited close parallels to those of Neanderthals (Li Z.-Y. et al., 2017). Certain Neanderthal features were also recorded at some other China fossils associated with the terminal Middle to the first half of the Upper Pleistocene.

Genetic findings provide support for the hypothesized dispersal of Neanderthals in East Asia. DNA sequencing of the human populations nowadays has shown that the proportion of the Neanderthal genetic heritage in East Asians is much higher than in Europeans (Meyer et al., 2012; Wall et al., 2013). There are also other arguments in favor of the hypothesis as to the Neanderthal migration to China.

A seemingly convincing piece of evidence supporting the above assumption can be provided by the archaeological materials recovered from Jinsitai Cave, located in Inner Mongolia, 20 km from the Sino-Mongolian border (Li F. et al., 2018). The cave with an area of approximately 120 m² is located at an altitude of 1401 m asl. Excavations of the cave began in 2000–2001 (Wang et al., 2010). In 2012–2013, the studies were resumed (Li F. et al., 2018). According to Li Feng and his co-authors, the methodological

level of 2000–2001 excavations was low, so I will consider the data of 2012–2013. The excavations revealed nine lithological layers. The deposits contained yellow-brown gravels, clayey silt, clay, and silty sand with granite breccia. The lowermost layer 9 was archaeologically sterile. Overlying layers 8 and 7 contained Paleolithic artifacts. The researchers dated layer 8 to a chronological range of 47,034–43,720 cal BP, and layer 7 to 44,289–42,306 cal BP. The overlying layers were attributed to the Late Paleolithic, Neolithic, and Bronze Age.

A total of 720 lithic artifacts were recovered from the lower layers: 231 spec. in layer 7 and 489 spec. in layer 8. The researchers analyzed 228 spec. from layer 7 and 433 spec. from layer 8 (Ibid.: 79). The hominins used mainly volcanic rocks (basalt, andesite, and tuff) and quartz crystals in the manufacture of lithic tools. The cores were dominated by discoid varieties demonstrating radial flaking and by multi-platform cores for flake blank removals. The researchers noted the absence of blade production evidence at the site. Layer 8 yielded a Levallois core with traces of recurrent reduction. The Levallois technique in layers 7 and 8 was represented by points ($n=3$), blades ($n=2$), flakes ($n=6$) with faceted and chapeau-de-gendarme platforms, and débordant flakes. The tool-kit included side-scrapers of various types ($n=30$), notched and denticulate tools. The set of Upper Paleolithic tools comprised three end-scrapers from layer 8 and one burin from layer 7. Judging by the signs of primary flaking, the toolkit typology, and the working techniques, the researchers attributed the Jinsitai Cave industry to the late stage of the Mousterian Middle Paleolithic.

A logical question arises: who were the bearers of this industry? The scholars inferred that the Jinsitai industry was a result of the dispersal of Neanderthal populations (?) or was borrowed from the inhabitants of the Altai (Siberia), which was previously populated by hominins producing similar lithic artifacts (Ibid.: 82). The researchers noted that this hypothesis would remain purely preliminary until some diagnostic human fossils were found or DNA was extracted (Ibid.).

Unfortunately, the publication by Li Feng and colleagues (2018) contain few photographs of stone tools, which makes it impossible to determine the specifics of the cave lithic industry.

Undisputed Neanderthal fossils, associated with the Sibiryachikha Mousterian industry, in the area close to Jinsitai Cave, were recorded only at two cave sites in the Altai Mountains: Okladnikov and Chagyrskaya caves (Derevianko, Markin, 1992; Derevianko et al.,

2018). Finds from Chagyrskaya Cave are dated to 60–45 ka BP, and those from Okladnikov Cave to 45–40 (37) ka BP. Levallois flaking was not recorded in Chagyrskaya Cave, while the evidence of its use, as well as Levallois points with faceted platforms, were noted in Okladnikov Cave. However, the occurrence of these artifacts is due to the contacts between the Chagyrskaya Neanderthals and Denisovans (Derevianko, 2024c, d).

No other sites with the Sibiryachikha Mousterian industry of the Chagyrskaya type dating to 60–40 ka BP are known in Southern Siberia and Mongolia. Sites of that type could support the hypothesis as to the migration of Chagyrskaya Neanderthals from the Altai Mountains to northeastern China. In Denisova Cave, the period of 55–45 ka BP is represented by an Early Upper Paleolithic industry. Unlike the Sibiryachikha industry of Okladnikov and Chagyrskaya caves, the Jinsitai industry exhibits the Levallois technology. The Jinsitai industry differs from the Mousterian technocomplex of European Neanderthals, too. Based on the scarce data available, given the occurrences of the Levallois reduction components, Levallois points, blades, and flakes, the Jinsitai industry is closer to the Denisovan.

In Central Asia, there is one known locality with Neanderthal remains and Mousterian industry—Teshik-Tash Cave in Uzbekistan. It is dated to 60–50 ka BP. The Teshik-Tash lithic industry also differs from that at Jinsitai. Thus, there is no basis for assuming a Neanderthal migration from the Altai Mountains and Central Asia to China. The Jinsitai industry should be considered a local variant of the Denisovan Upper Paleolithic. R. Dennell, reviewing the finds from Jinsitai Cave, concluded that, given the possible interbreeding between Neanderthals, Denisovans, and anatomically modern humans, the cave inhabitants (either in part or in whole) can be classified as Denisovans (2020: 299).

The hypothesis that the Jinniushan, Dali, Maba, and other fossils chronologically attributed to the Late Middle Pleistocene belonged to Neanderthals is supported by neither anthropological nor archaeological evidence. Morphologically and genetically, European Neanderthals emerged primarily in Western Europe not earlier than 200–150 ka BP (Derevianko, 2024a). They produced the Mousterian industry, which, despite its great variability, was characterized, according to the above-mentioned researchers, by distinctive primary reduction techniques, a tool kit (tool blanks were mainly flakes), and manufacturing techniques. So far, no Neanderthal fossils and sites with Mousterian

industry older than 100 thousand years have been found anywhere along the possible migration route from Western Europe to China (neither in Eastern Europe, nor in the Caucasus and Central Asia); hence, these hominins could not have appeared in the territory of China in the Late Middle Pleistocene (Derevianko, 2024a, d).

The question arises: how can the Neanderthal morphological features of the Jinniushan, Dali, Maba, and some other fossils from China dating back to the Late Middle Pleistocene be explained? Some morphological traits interpreted as Neanderthal are common to hominins of Africa and Eurasia, which suggests a common evolutionary development of all hominins towards sapienization. At the same time, researchers mention certain morphological features of *H. heidelbergensis* in Chinese hominins. C. Groves (1994) attributed the Dali and Jinniushan fossils to *H. heidelbergensis*. Moreover, not all experts in physical anthropology identify Neanderthal traits in the Dali, Maba, and Jinniushan fossils. In my opinion, Neanderthals did not disperse in China, but taken into account the currently available materials, this issue should be considered open.

Discussion

Only 15 years have passed since the discovery of *H. s. denisovan*. We still know very little about the morphology of this taxon: in Denisova Cave, only three teeth and several small, morphologically indeterminate bones including skull fragments were found (Viola et al., 2019). Besides Denisova Cave, Denisovan-type fossils have been found in Tibet (Xiahe mandible fragments) (Chen F.-H. et al., 2019), in the Taiwan Strait (Penghu) (Chang et al., 2015), and Laos (Tam Ngu Hao) (Demeter et al., 2022). Thus, the possibilities of discovery of similar morphological features in fossils found in contiguous regions, including China, are extremely limited.

Studies of Denisovans as a biological species are just beginning. Comparative analysis of fossils from adjacent regions is hampered not only by the paucity of anthropological material but also because of the fact that after diverging from Neanderthals, ca 400 ka BP, some part of the ancestral *H. heidelbergensis* taxon (future Denisovans) expanded through Iran into the western regions of South and Central Asia and other adjacent territories, where the genetic and morphological development of Denisovans occurred. In the course of migration, hominins had to adapt to

a wide range of environmental and climatic conditions on plains, lowlands, highlands, and mountain basins—from the cold northern regions to the humid and warmer subtropics and tropics. In some regions, Denisovans encountered indigenous populations of *H. erectus*, while in others, such as Uzbekistan and Turkmenistan, where no sites with Early Paleolithic pebble-flake industry have yet been found, they were likely pioneers (Derevianko, 2024b, 2025a). In the areas populated by *H. erectus*, the migrants (future Denisovans) assimilated the indigenous populations, which resulted in the acquisition of archaic dentition and other features of *H. erectus*. In the areas where the migrants did not meet indigenous peoples, morphological development proceeded differently. Because of settling in the highlands, future Denisovans acquired a gene responsible for adaptation to hypoxia (Huerta-Sánchez et al., 2014). Consequently, in the chronological range of 400–40 (35) ka BP, Denisovans developed a mosaic morphology and certain specificity in the genome in the course of expansion into the areas with various environmental settings, assimilation the indigenous population, and natural and sexual selection.

Denisovan fossils were found in the Main, East, and South Chambers of Denisova Cave. Denisovan mtDNA was also extracted from the soil of several culture-bearing layers. Taking this into account, along with the homogeneity of the Denisovan industry, it can be concluded that Denisovans inhabited the cave for approximately 250,000 years. Extraction and sequencing of mitochondrial and nuclear DNA from fossils and culture-bearing sediments of the cave, as well as mtDNA from several modern populations in East Asia, revealed that the genetic sequence of Denisovans at various stages of their evolution showed certain differences from the basic genome of Denisova 3 individual.

In China, the Middle Pleistocene (in contrast to Early Pleistocene) is represented by a considerable number of fossils demonstrating mosaic combination of plesiomorphic and apomorphic morphological features—Zhoukoudian, Dali, Jinniushan, Maba, Xuchang, Xiahe (Baishiya), Panxian Dadong, Xujiayao, Huanglong, Tongzi, Penghu 1, etc.

All researchers studying paleoanthropological finds from the Late Middle to Early Upper Pleistocene noted the variability of their morphology, which has led to the emergence of different scenarios of phylogenetic history of these hominins, including their contribution to the evolution of modern humans. Moreover, with the introduction of new factual material and research methods, anthropologists often reasonably change

their viewpoints about the taxonomic affiliation of a particular fossil.

Some Chinese experts in physical anthropology believe that the fossils dating to the Middle and Early Upper Pleistocene, despite their mosaic morphology, belonged to a single ancestral lineage, the long evolutionary development of which resulted in the development of anatomically modern humans, and that the Late Middle Pleistocene fossils of Dali and Huanglong are the latest transitional form between the Asian taxa of *H. erectus* and *H. sapiens* (Wu X., Athreya, 2013; Wu X.-J. et al., 2019; and others). I also adhere to this point of view (Derevianko, 2011, 2025c).

There is also an alternative point of view. A new species, *Homo longi*, a sister species to *H. sapiens*, was identified on the basis of the Harbin fossil (Ni Xijun et al., 2021; Ji et al., 2021). Wu X.-J. and Ch. Bae tentatively assigned the Dali and Jinniushan fossils to this taxon. After studying the Xujiayao and Xuchang fossils, they identified a new species, which they proposed to give the informal name of *Homo juluensis* ‘big-headed man’. One of the reasons was their cranial capacity: in Xujiayao 6 (XJY 6) it was ~ 1700 cm³, and in the Xuchang 1 ca 1800 cm³ (Wu X.-J. et al., 2022). The researchers assigned the fossils of Penghu 1, Xiahe, and Denisovans, as well as Tam Ngu Hao 2 (Laos), to this taxon (Bae, Wu, 2024; Wu X.-J., Bae, 2024).

The identification of new taxa of *H. longi* and *H. juluensis* at this stage of Chinese fossil research is hardly justified. Most importantly, paleoanthropological finds in this area contain no hominin remains that could have been the ancestral basis for the evolution of these new taxa, nor is it possible to trace their subsequent phylogenetic history.

This article was already submitted for publication when *Science* published in the September issue an article by X. Feng et al., which clarified the origin of *Homo longi* and Denisovans (Feng et al., 2025).

Three skulls from the site of Yunxian provide valuable information on the morphology of hominins in the Late Early Pleistocene. These fossils have been analyzed by many experts in physical anthropology, and all scholars, taking into account certain variability in their morphology, have classified them as a *H. erectus* taxon. Other anthropologists have proposed to classify these fossils as a subspecies of *H. erectus yunxianensis* (Li Tanguan et al., 1994, 1996; and others). Studying Yunxian skulls and comparing them with other Pleistocene paleoanthropological finds from Africa and Europe have led Chinese and French researchers to the

conclusion that certain morphological features of the Yunxian finds do not provide sufficient grounds for classifying Yunxian man as a separate subspecies, different to *H. erectus* (Le site..., 2008).

I won't address all the controversial issues from the paper by X. Feng and his co-authors, but will focus only on the main problem outlined in the title: "The Phylogenetic Position of the Yunxian Cranium Elucidates the Origin of *Homo longi* and the Denisovans".

Feng and his colleagues restored and reconstructed the damaged skull of Yunxian 2. Morphometric and phylogenetic analysis showed the following: 1) the Yunxian fossil belonged to an early member of the Asian *longi* clade, which included Denisovans and was the main part of the sister group to the *H. sapiens* clade; 2) the *H. sapiens* clade, as the *H. longi* clade, had deep roots extending beyond the Middle Pleistocene (Feng et al., 2025: 1320). The researchers dated the origin of the *H. longi* clade to 1.2 Ma BP. They argued that the emergence of the *H. sapiens* clade was estimated to be 1.02 Ma BP; the divergence between the *longi* and *sapiens* clades occurred 1.32 Ma BP; the monophyletic clade of Neanderthals diverged from the first two (*longi* and *sapiens*) 1.38 Ma BP (Ibid.: 1323).

Most anthropologists attribute all the Early and Middle Pleistocene fossils found in China to the *H. erectus* evolutionary lineage. In my view, the evidence provided by Feng et al. in favor of the assumption that the *H. longi* clade emerged in China about 1.2 Ma BP was unconvincing. Moreover, Chinese anthropologists, following F. Weidenreich, substantiated the hypothesis as to the convergent evolution of *H. sapiens* in China on the ancestral basis of *H. erectus* (Derevianko, 2025c).

The mosaic morphology of hominins in the Late Middle Pleistocene is explained by two main factors. Noteworthy is the complexity of terminal stage of the convergent evolution of anatomically modern humans on the ancestral basis of *H. erectus* along the sapiens line. These humans spread across the vast territory of China with diverse landscapes: plains, foothills, and mountains of moderate and high elevation. Separate human groups lived in isolation in various environmental settings for a long time; this excluded the exchange of subsistence innovations and genes. Noteworthy is also the paucity of finds dating to the time range from 400 to 40 ka BP and the lack of reliable dates for the available fossils.

The expansion of Denisovans to China in the Late Middle Pleistocene and the first half of the Upper

Pleistocene had a significant effect on the mosaic morphology of hominins in China. At present, we can hardly reconstruct the interrelations between the early modern humans and Denisovans. Members of these taxa populated contiguous regions and undoubtedly competed for hunting grounds and lithological resources, which situation contributed to the development of hostile relations. However, since the population groups settling in adjacent regions were small and had an open genetic system, it is entirely possible that their relationships involved the exchange of innovations. The exchange and abduction of women, which led to assimilation processes, cannot be ruled out.

Noteworthy is another specific feature of the interrelations between representatives of these taxa. There is no doubt that during the Late Middle to Early Upper Pleistocene Denisovans and hominins in China interbred and assimilated; however, both populations retained their own mentality, which was reflected in material and spiritual culture. Unlike Denisovans, Chinese hominins largely retained their pebble-flake industry, as it was effective for their subsistence in local environmental conditions.

In the Altai Mountains, Denisovans and Neanderthals settled in the adjacent territories for 20,000 years, sharing hunting grounds, meeting, and interbreeding. In Denisova Cave, the fossil of Denisova 11 was discovered. This female specimen was the daughter of a Denisovan father and a Neanderthal mother (Slon et al., 2018). However, each of the taxa under discussion retained their lithic industries, which considerably differed from each other. The Chagyrskaya Neanderthals rarely used bone in tool manufacturing; no personal ornaments were recovered from their culture-bearing layers. Members of different taxa contacted, interbred, but their material and spiritual cultures remained unchanged.

In my opinion, the identification of new taxa of *H. juluensis* and *H. longi* in China lacks a convincing evidence base. The findings of anthropological and genetic studies do not support the idea that Denisovans originated in China. The established scientific view is that Denisovans and Neanderthals shared a common ancestor and diverged genetically and morphologically ca 400 ka BP. The Denisovan material culture contradicts the hypothesis as to their origin in China. The Denisovan lithic industry was based on the Levallois and blade reduction techniques, followed the Acheulo-Yabrudian industry of the Levant, and was fundamentally different from the pebble-flake industry of hominins in China.

The Denisovan taxon originated in Africa. Three stages can be distinguished in the process of genetic and morphological development of Denisovans. First, *H. heidelbergensis* expanded from Africa to Eurasia approximately 800 ka BP, which marked the genetic split of a single ancestral taxon *H. erectus* into anatomically modern humans (who were developed in Africa 200–150 ka BP), and Neanderthals and Denisovans (who originated in Eurasia). Second, ca 400 ka BP, a part of the late *H. heidelbergensis* expanded from the Near East (Levant) to Europe, and the other part moved to Asia, which led to the genetic and morphological divergence of Neanderthals and Denisovans. Third, 400–40 (30) ka BP, the Denisovan taxon underwent genetic and morphological evolution during its dispersal over the eastern regions of Asia and adaptation to changing environmental and climatic conditions, as well as assimilation of the indigenous population (*H. erectus*).

The study of Denisovans as a new biological taxon is just beginning, in contrast to Neanderthals, who have been studied for over 150 years. I am sure that future archaeological and physical anthropological research will provide many new, perhaps unexpected, results. Undoubtedly, Denisovans settled over a vast territory of eastern Asia. During their dispersal, they developed morphologically and genetically and were able to create a unique material and spiritual culture, one of the oldest in Eurasia.

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