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Origin of Neanderthals. Neanderthals of the Altai: Myth or Reality?*

Some 3 mln years ago, the genus Homo originated from australopithecines in Africa. In the Pleistocene, in the course of subsequent evolutionary processes such as natural selection, hybridization, and adaptation to changing environments, in the 200–100 ka BP interval, anatomically modern humans emerged in Africa, H. sapiens neanderthalensis in Europe, and H. sapiens denisovan in Central and Northern Asia. The origin of these taxa has been discussed in various publications and at many symposia. In the course of debates, several hypotheses were advanced—African Eve, multiregional evolution, evolution with hybridization, etc. All of them proceed from the assumption that the earliest anatomically modern humans originated in Africa. The main disagreement between the experts concerns the role of native Eurasians in the origin of H. sapiens sapiens following the migration of anatomically modern humans from Africa to Eurasia. In several publications of mine, a scenario of the phylogenetic history of the genus Homo, somewhat different from the currently discussed hypotheses, was proposed. The analysis of the genetic legacy of anatomically modern humans, H. sapiens neanderthalensis, and H. sapiens denisovan has shown that those hominins were able to hybridize and that the hybrids were fertile. This means that hybridization and assimilation proceeded not between separate species but within a single species, whose populations were open genetic systems. Consequently, if, at the final stage of the phylogenetic history of Homo, 200–100 ka BP, three taxa capable of hybridization emerged on various continents in the process of a long evolution, then all previous Early and Middle Pleistocene taxa in Africa, Europe, and Asia, established by the analysis of fossils, had likewise open genetic systems. This means that over a nearly 3 mln year long evolution of the genus Homo, resulting in progressive sapienization, three key factors—natural selection, hybridization, and adaptation to changing environments of the Pleistocene—have shaped both morphology and genetics of that genus. The article addresses the origin of a single basal species in Africa, ancestral to all anatomically modern humans, their spread to Eurasia, and role in the origin of H. sapiens neanderthalensis in Europe.

Keywords: *H. erectus, H. rhodesiensis (heidelbergensis), H. antecessor, H. sapiens sapiens, H. sapiens neanderthalensis, H. sapiens denisovan, Acheulean, Mousterian, Denisovan Middle Paleolithic industry.*

Introduction

More than 150 years have passed since the discovery of human fossils in the Neanderthal Valley in Germany; on the basis of the derived data, the Neanderthal taxon was identified, and studies of *Homo sapiens neanderthalensis* have been carried out since that time. The origin and the material and spiritual culture of representatives of this species have been discussed in dozens of books and hundreds of papers.

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I became interested in Neanderthals back in my student years. For me, they were real explorers who, owing to their small numbers, could settle in comfortable environmental conditions; there were enough such zones in the Pleistocene. Neanderthals occupied not only the most favorable areas between the 40th parallel north and 40th parallel south, but also far to the north. In the process of adaptation to more severe climatic conditions and thanks to hunting large animals, including predators, using spears mainly in close combat, Neanderthals developed a special morphology: short stature, wide chest, special facial structure, robust bones, and others.

In 2005, in one of my papers, I wrote about my special attitude toward Neanderthals, who bravely explored northern latitudes (Derevianko, 2005: 107). I think that if a European Neanderthal had visited a fashionable barber and put on a business suit, he probably wouldn't have managed to direct an orchestra, but would have enjoyed Vivaldi's music for sure. Dear colleagues, please do not offend Neanderthals. They are among our ancestors! After many years, I have only become more convinced in this opinion.

In the Altai, researchers from the Institute of Archaeology and Ethnography of the SB RAS have been conducting studies for more than 40 years. In total, ten caves and eleven open-air sites have been and are still studied there. The established Paleolithic sites are multilayered, with long stratigraphic sequences. Archaeologists, physical anthropologists, geneticists, geochronologists, geologists, biologists, paleogeographers, paleontologists and other experts, not only from Russia, but also from other countries, take part in field and laboratory works. Extensive archaeological and paleontological collections have been recovered, while anthropological remains are unfortunately rare. Particularly important results were achieved in the studies of Denisova Cave; the archaeological works in the cave are still going on.

The abundant archaeological material is quite clearly subdivided into the Middle and Upper Paleolithic collections. Previously, researchers involved in the study of the Altai Paleolithic attributed the entire Middle Paleolithic industry to Mousterian and correlated it with Neanderthals; the Upper Paleolithic industry was associated with *H. sapiens*. And this subdivision was reasonable; in the last century, scholars knew only two taxa existing in the terminal Middle and Upper Pleistocene: *H. sapiens neanderthalensis* and *H. sapiens sapiens*. In 1984, a cave was discovered, named in honor of the outstanding researcher of the Paleolithic of Asia, Academician A.P. Okladnikov. It revealed a Mousterian industry, which differed significantly from the Middle Paleolithic industry at other sites, including Denisova Cave (Derevianko, Markin, 1992). Chronologically, this lithic industry is close to the terminal stage of the Middle Paleolithic of the Altai, but in all technical and typological characteristics these industries differed from one another. The question arose: what two populations with the different industries could have inhabited the Altai?

The collaboration with the outstanding geneticist and a Nobel Prize winner Svante Pääbo and his team from the Max Planck Institute for Evolutionary Anthropology in Leipzig has provided the answer. In 2007, in the course of joint research, it was established that Okladnikov Cave was inhabited by Neanderthals with the Mousterian industry (Krause et al., 2007), and Denisova Cave, by representatives of a new taxon—*H.s. denisovan*, which was revealed by the data of DNA sequencing from small bone (Denisova 3), rather than through the analysis of anthropological fossils (Krause et al., 2010; Reich et al., 2010).

In 2007, anthropological remains of Neanderthals and Mousterian industry were discovered in Chagyrskaya Cave, same as in Okladnikov Cave (Derevianko, Markin, Kolobova et al., 2018). The studies have shown that this group of Neanderthals, called Chagyrskaya, migrated to Altai ca 60 ka BP and lived next to the Denisovans for more than 20 thousand years. The Neanderthals and the Denisovans used the same areas for foraging, but at the same time retained their mentality. The Chagyrskaya Neanderthals produced the almost unchanged Mousterian-like Micoquian industry. Their archaeological materials do not contain tools made of bone or non-utilitarian ornaments. At the same time, Denisovan industries of the period of 60–55 ka BP evidence the transition from the Middle to Upper Paleolithic, and those of 55 (50)–45 ka BP reveal the initial Upper Paleolithic, one of the earliest and brightest in Eurasia (Derevianko, Shunkov, Agadjanian et al., 2003; Derevianko, 2019, 2022; Derevianko, Shunkov, Kozlikin, 2020; and others). The Denisovans and the Chagyrskaya Neanderthals could meet and interbreed with each other: in Denisova Cave, fossils of a hybrid (Denisova 11) were discovered, whose father was a Denisovan and mother was a Neanderthal.

Identification of the Altai Neanderthals in Denisova Cave on the basis of genetic studies (Prüfer et al., 2014) is highly questionable, unlike the Chagyrskaya Neanderthals, whose dispersal in the

Altai ca 60 ka BP is well confirmed by anthropological finds from the Okladnikov and Chagyrskaya caves, the data of DNA sequencing, and the recovered Mousterian industry. The sequencing of soil samples from the cultural layers of Denisova Cave suggests the possible dispersal of Neanderthals in the Altai earlier than 175 ka BP and the alternate habitation of the Altai Neanderthals and Denisovans in the cave (Douka et al., 2019; Jacobs et al., 2019; Zavala et al., 2021). However, this assumption is not confirmed by the archaeological evidence. The entire cultural-stratigraphic sequence in Denisova Cave, from the lowest layer 22 to layer 11 inclusive, contains a homogeneous Denisovan industry, showing a clear continuity in the industry development from the early Middle to the initial Upper Paleolithic. The appearance and long-term habitation of Neanderthals in Denisova Cave would certainly have been confirmed in the cultural layers—the Mousterian industry would have been uncovered; however, it has not been found in the stratigraphic sequence. Any possibility of migration of Neanderthals from Europe to the Altai earlier than 175 ka BP is excluded, since Neanderthals morphologically and genetically developed into a separate taxon in the chronological interval of 200–150 ka BP, i.e. the possibility of their appearance in the Altai earlier than 175 ka BP is very doubtful. Moreover, no sites with Mousterian industry or remains of Neanderthals older than 100 thousand years have been found in the transit territory from Europe to the Altai.

Neanderthals populated a vast territory—from Spain to Eastern Siberia; they often lived in small groups in various climatic and environmental conditions, with various types of vegetation, fauna, availability of water resources, and stone raw materials for the manufacture of tools, which factors determined the variability of their morphology and social relations. Many researchers have repeatedly discussed this in various publications (McCown, Keith, 1939; Endo, Kimura, 1970; Vandermeersch, 1981, 1989; Trinkaus, 1983, 1987, 1989, 1991; Churchill, 1998; Voisin, 2007). The original explanation for the morphologic variability of Neanderthals was proposed by J.-L. Voisin (2006): as Neanderthals moved from west to east, the range of changes in their morphological features expanded, and their morphology became more and more blurred in the context of this taxon. But where and when did its morphological and genetic development take place?

Evolution of the ancestral taxon of anatomically modern humans, Neanderthals, and Denisovans

The genus *Homo* evolved in Africa ca 3.0–2.8 Ma BP on the ancestral basis of Australopithecines. At the earliest stage of anthropogenesis, three species are identified: *H. rudolfensis, H. habilis, H. ergaster/erectus*, which had open genetic systems; they could interbreed and produce fertile offspring (Derevianko, 2020, 2022; etc.). About 1.75 Ma BP, *H. ergaster/erectus* began to settle in Eurasia. In Africa, early *Homo* continued to evolve along the sapient line and to develop the pebble-flake industry. In Africa, about 1.75 Ma BP, hominins developed bifacially worked stone tools (axes), which formed the basis for the new industry—Acheulean (Beyene et al., 2013, 2015). It is very likely that in the time range of 1.75–1.4 Ma BP Africa was inhabited by two taxa: *H. habilis* with the Oldowan industry and *H. erectus* with the Acheulean industry, and a genetic drift may have occurred between them.

The smallest number of anthropological fossils found in Africa falls within the time range of 1.5–0.6 Ma BP. At the site of Nariokotome III, located on the western shore of Lake Turkana, cranial and postcranial remains of a juvenile aged ca 12 years were found (Brown et al., 1985). The age of the fossils is 1.6 million years. After the discovery of this uniquely informative fossil, a small amount of anthropological evidence was discovered on the continent.

A series of anthropological remains from the Olduvai Gorge indicates the further evolutionary development of *H. erectus* to sapient features: OH 9 (Rightmire, 1990); OH 12 (Leakey, Clarke, Leakey, 1971; Holloway, 1973; Antón, 2004); OH 22 (Rightmire, 1980), and others. The oldest fossil, OH 9, includes fragments of supraorbital structures and cranial vault. Analysis of the fossil, 1.25 million years old, discovered in the upper part of Bed II (Leakey, Clarke, Leakey, 1971) has shown the cranial capacity of the individual to be approx. 1076 cm^3 (Holloway, 1973). Fossil OH 12—the posterior part of a small skull (700–800 cm^3) (Holloway, 1973) and several fragments of facial bones (Antón, 2004)—were found on the surface of Bed IV (Leakey, Clarke, Leakey, 1971).

Some of the most informative materials—a well-preserved skull with the vault (BOU-VP-2166), three separate femurs and a proximal part of the tibia—were discovered during excavations in the middle reaches of the Awash River (Ethiopia) in the Bouri Formation, in the Dakanihylo, or Daka, member, aged 1042 ± ± 0.009 million years (Asfaw et al., 2002). The cranium capacity was 995 cm^3. The vault and supraorbital parts showed traces of peri-mortem injury in the form of scraping. The skull discovered at Bouri is of great importance for the phylogeny understanding. B. Asfaw and his co-authors made an important conclusion: in terms of metric indicators, the Daka skull is close to both African and Asian specimens of *H. erectus*; this implies the lack of any reasons to subdivide Asian and African *H. erectus* into different species (Ibid.). The metric and morphological features of the Daka skull indicate that Asian and African *H. erectus* belonged to a single biological species.

Chronologically close to the hominin fossils from Dakanihylo are the early human bones discovered in the Danakil Formation in the Afar Valley, near the village of Buya (Eritrea). These are a cranium with preserved facial parts, roots of molars and premolars, two incisors, and a fragment of the pelvic bone (Abbate et al., 1998). Based on the age estimations derived from paleontological findings, paleomagnetic dating, and measurements of the tephra layer decay, the finds are close to the upper part of the Jaramillo Subchron (~1 million years) (Bigazzi et al., 2004). The cranium capacity is in the range of 750–800 cm^3. According to S. Anton, in some morphological features, this skull differs from the Daka fossils. As E. Abbate and co-authors note, Buya skull shows a number of transitional features to modern humans. Other researchers have classified these fossils as late *H. erectus* (Macchiarelli et al., 2004).

In tropical Africa, several other human fossils dating to the range of 0.9–0.6 Ma BP were found. The Olorgesailie site (Kenya) revealed the frontal and left temporal bones and nine fragments of a hominin cranial vault (KNM-OL 45500) (Potts et al., 2004). The age of these finds is 0.97–0.90 million years. According to the researchers, the hominin was short in stature and had a small skull; the frontal bone is not wide. The thickness of the supraorbital torus and the overall size of the temporal bone are close to the corresponding parameters of the skull of an adult hominin of the Lower and Middle Pleistocene. R. Potts and his co-authors compared the Olorgesailie finds with other fossils representing the *H. erectus* lineage (KNM-ER 3733, KNM-ER 3883, and KNM-WT 15000 from Turkana in Kenya; OH 9 and OH 12 from Olduvai in Tanzania; Daka and Bodo from Ethiopia; Buya from Eritrea; Ndutu from Tanzania; D 2280 and D 2282 from Dmanisi in Georgia; Ceprano from Italy; Atapuerca from Spain; Zhoukoudian from China; Sangiran and Ngandung from Java; Kabwe from Zambia, and Saldanha from South Africa), and came to the conclusion that all of them, despite the large differences in chronological affiliation and significant distance from one another, can be combined into one polytypic species *H. erectus*. Several other anthropological fossils have been discovered in southern and eastern Africa.

In 1996–1998, P.G. Rightmire put forward a hypothesis that a speciation event occurred in Africa or Europe during the Middle Pleistocene or slightly earlier. The hypothesis was based on the discovery of a 640 thousand years old skull in the Bodo area, on the middle Awash, Ethiopia, in 1976. "The Bodo cranium", wrote P.G. Rightmire, "cannot be excluded from a population that is advanced anatomically in comparison to *H. erectus*" (1996: 32). This observation seems to be correct given the brain size of this individual, as well as the presence of many facial features in common with Kabwe (Broken Hill), typical of more modern hominins. The researcher also noted the similarity of this skull to those of *H. erectus/ergaster*, which was expressed in the excessively wide and robust base of the facial part, thickened bones of the cranial vault, the low, archaic skull, a flat face, and a prominent torus. The Bodo skull is 1300 cm^3. Rightmire defined this fossil as *H. heidelbergensis*, together with other anthropological finds made in Africa—Elandsfontein, Kabwe, Ndutu, in Europe—Mauer, Arago, Petralona, and in China—possibly Dali and Jinniushan (1988).

In his later works, Rightmire examined the further evolutionary development of the species *H. heidelbergensis* along the Neanderthaloid and sapient lines. In the terminal Middle Pleistocene, *H. neanderthalensis* and *H. sapiens* developed from Heidelberg man. The researcher regarded the finds from Florisbad, Laetoli, and Jebel Irhoud as a confirmation of the hypothesis on emergence of the first anatomically modern humans in Africa. Apparently, modern humans evolved in the process of anagenetic speciation (finds from the Klasies River in South Africa; Skhul, Kafzeh in Israel) during the terminal Middle Pleistocene (Rightmire, 2001a, b; 2009a, b; and etc.).

Many anthropologists support the hypothesis as to a speciation event that occurred in the terminal Early to early Middle Pleistocene: *H. erectus* sensu lato gave rise to a new species, designated differently: *H. heidelbergensis*, *H. rhodesiensis*, *H. sapiens*

(Rightmire, 1996; 1998a, b; 2004, 2008, 2009a, b; 2013, 2015; Tattersall, Schwartz, 2000; Bräuer, 2001a, b; 2007; Hublin, 2001; Stringer, 2002; Foley, Lahr, 2003; and others).

This species is a matter of debate between physical anthropologists. Initially, C. Stringer attributed early archaic hominins, European pre-Neanderthals, and, possibly, some archaic East Africans to this species (2002). Later, he came to the conclusion that *H. heidelbergensis* was the ancestral form of *H. sapiens*, Neanderthals, and Denisovans (Stringer, 2012). R. Foley classifies the available Middle Pleistocene anthropological remains into three species: *H. heidelbergensis, H. halmei*, and *H. sapiens* (2001). S. McBrearty and A. Brooks reject the species name *H. heidelbergensis* and propose *H. rhodesiensis* instead, considering the taxon *H. heidelbergensis* as specifically European (2000). Some anthropologists admit the possibility of evolution of *H. heidelbergensis* in the territory of China (Elter, 2010). J.-J. Hublin also believes that in relation to materials from Africa it is preferable to use the species name *H. rhodesiensis* (2001). In his opinion, the name *H. heidelbergensis* should be used only to designate populations that evolutionarily preceded the first pre-Neanderthal and Neanderthal hominins as two separate species: *H. heidelbergensis* and *H. neanderthalensis* (Hublin, 1998).

An original approach to the phylogeny of Middle Pleistocene hominins was proposed by G. Manzi (2011). In accordance with the trinomial nomenclature and the International Code of Zoological Classification, he classified all the available Middle Pleistocene hominins from Africa and Eurasia into four subspecies: 1) *Homo heidelbergensis heidelbergensis*—jaw from Mauer, Arago, Bodo, Ceprano and, possibly, Petralona; 2) *Homo heidelbergensis steinheimensis*—fossils from Atapuerca (SH). This subspecies was ancestral to *H. neanderthalensis*; 3) *Homo heidelbergensis/rhodesiensis*—Kabwe and possibly all African anthropological finds dating back to the late Middle Pleistocene, including the group of "archaic" *H. sapiens*; 4) *Homo heidelbergensis daliensis*—a selection of "non-erectus" specimens in which the Dali fossil was the typical model. To this subspecies Manzi attributed fossils from Denisova Cave as well.

The discussion about the taxonomic affinity of *H. rhodesiensis / heidelbergensis* has continued since the moment when the existence of this taxon was established. Moreover, researchers are most interested in *H. heidelbergensis*, while *H. rhodesiensis* remains "in the shadows". Interesting data have been provided by M. Roksandic et al. (2022). Their search in the Web of Science citation database yielded 274 direct citations to *H. heidelbergensis* and only 17 to *H. rhodesiensis*.

Roksandic and her colleagues propose to abandon the identification of the taxon *H. heidelbergensis* sensu stricto, since "supporting this argument is the recent consensus that the Sima de los Huesos hominins should be considered as early members of the Neanderthal lineage… As such, there is no need to introduce another species with the same morphology" (Ibid.: 22). No less radical is the proposal of these researchers to abandon the taxon *H. rhodesiensis*. In their opinion, "there are two primary reasons for this: (1) the taxon is poorly defined and variably understood and used; and (2) the taxon name is associated with sociopolitical baggage that our scientific community is trying to dissociate itself from" (Ibid.). Instead of *H. heidelbergensis* and *H. rhodesiensis*, the researchers introduce a new taxonomic unit—the Middle Pleistocene hominin species *H. bodoensis*, which is the direct ancestor of *H. sapiens*, from their point of view. The name *bodoensis* is associated with the fossil Bodo 1 (Ethiopia).

S. Athreya and A. Hopkins, when considering the problem of hominin taxonomy, pay great attention to the systematics and designation of *H. heidelbergensis*. They consider the discussion about the names of the identified members of the group and the definition of the term *H. heidelbergensis* itself to be premature, until sufficient information is gained to give a name to the new species, and propose to direct efforts on discussions of the issues of human evolution (Athreya, Hopkins, 2021: 18).

There are also other viewpoints on classification of these taxa. Some researchers changed their minds with the emergence of new data. This diversity of judgments can be explained by the fact that Middle Pleistocene fossils show both common and distinctive morphological features; in addition, scholars often differ in their assessment of the marker significance of individual morphological traits, when comparing anthropological materials. From my point of view, regardless of the differences in environmental and climatic conditions during early human dispersal, and certain morphological differences between hominins, their anatomical and genetic evolution continued toward sapienization. Hominins developed similar derived features, and most importantly, they maintained open genetic systems, which enabled interbreeding and producing fertile offspring.

H. rhodesiensis and H. heidelbergensis belonged to a single biological species that evolved in Africa 900–800 ka BP. This taxon split into two parts 800 ka BP, and each played its role in human phylogeny. 800 ka BP, there was a major event in the evolution of the genus *Homo*. One part of this taxon (*H. rhodesiensis*) stayed in Africa; it formed the ancestral basis for early modern humans, which evolved in the course of further evolutionary development, natural selection, genetic drift, and adaptation to changing climatic conditions 200–150 ka BP. The other part (*H. heidelbergensis*) with the Acheulean industry migrated to the Near East 800 ka BP. The site of Gesher Benot Ya'aqov (Goren-Inbar et al., 2018) provides the evidence of this migration. Subsequently, Neanderthals evolved in Europe 200–150 ka BP on the ancestral basis of *H. heidelbergensis* during assimilation with *H. antecessor*. The assimilation of *H. heidelbergensis* with the late *H. erectus* in Central Asia led to the formation of the Denisovans. This scenario for human evolution in the Middle Pleistocene is confirmed by genetic studies. According to some data, the divergence of DNA sequence between modern Africans, on the one hand, and Denisovans and Neanderthals, on the other, took place 804 ka BP (Reich et al., 2010). According to other data, the divergence of DNA sequence between modern humans from Denisovans with Neanderthals occurred in the chronological range of 812–793 ka BP (Meyer et al., 2012).

Homo heidelbergensis in the Near East and the origin of anatomically modern humans and Palestinian Neanderthals

The earliest site providing evidence for the migration of *H. heidelbergensis* to the Near East is Gesher Benot Ya'aqov in Israel. This is a unique site that reveals a stratigraphic sequence accumulated during ca 50 (100) thousand years. Studies undertaken at this site have been discussed in many publications, and the summarizing monograph appeared in 2018 (see (Goren-Inbar et al., 2018)). The early stage of deposition of its cultural horizons dates back to ca 0.78 Ma BP; in general, the site belongs to the period corresponding to MIS 20–18 (Feibel, 2004). This locality has yielded numerous artifacts related to the Acheulean industry.

Populations of *H. heidelbergensis*, which species had evolved in Africa, migrated to the Levant where they probably met the autochthonous population—late *H. erectus*. Since both the newcomers and the indigenous population had open genetic systems, their interbreeding resulted in producing fertile offspring. This determined the differences in the processes of further evolution of *H. rhodesiensis* in Africa and *H. heidelbergensis* in Eurasia. The former gradually evolved into *H. sapiens*, without mixing with other taxa (owing to their absence). The dispersal of *H. rhodesiensis* over the African continent with various ecology created the conditions for variability in both human morphology and lithic industry. This appears to have been the key reason for some differences in the morphology of early modern humans and their industry in the northeastern, southern, eastern, and western parts of the continent (Ragsdale et al., 2023). But most importantly, the evolution into *H. sapiens* occurred only in one species, *H. rhodesiensis*, without mixing with other taxa.

In the Levant, the further evolution of *H. heidelbergensis* occurred with their assimilation with the indigenous population, the late *H. erectus*. As a result of such hybridization, in the Near East, unlike in Africa, the evolution into *H. sapiens* followed a different path. The diffusion of the techno-typological complex of newcomers and the indigenous population can also be recognized in the development of lithic industry. As a result, the Gesher-Benot Ya'aqov industry acquired many features that distinguished it from the African Acheulean industry.

Excavations undertaken in the Levant produced sparse anthropological finds, and my hypothesis about the further evolution of *H. heidelbergensis* in the Near East certainly needs to be confirmed by new archaeological, anthropological, and genetic evidence. The key anthropological remains of the Middle Paleolithic were discovered in Israel, but unfortunately these are few in number, and not all of them have reliable dates. As early as 1925, in Mugharet el-Zuttiyeh Cave, a frontal, a right zygomatic, and a partially preserved sphenoid bones were found. These paleoanthropological fossils are referred to in the literature as the remains of the Zuttiyeh hominin. Sadly, the absolute age of these remains, recovered from the Acheulo-Yabrudian cultural horizon, has not yet been established. Some researchers dated them to early period (500–200 ka BP). However, recently, their age has been estimated as 150–110 thousand years (Bar-Yosef, 1988) or >122 thousand years (Millard, 2008).

Early in the study of the Zuttiyeh man, anthropologists noted its morphological proximity to Neanderthals. A. Hrdlicka found that these remains revealed common features with the Asian Early

Pleistocene skull EI from Zhoukoudian, which he identified as a Neanderthal (1929). T. McCown and A. Keith recognized the remarkable similarity of the Zuttiyeh fossil with Tabun C1, as well as with Skhul 5 cranium (1939). F. Weidenreich also pointed to the closeness of the Zuttyieh to Skhul 5, which he considered a "progressive Neanderthal", an intermediate link between more primitive forms and modern humans (1943). Fossils from Mugharet el-Zuttiyeh Cave were attributed to a common ancestor of Western Asian Late Pleistocene hominins such as Amud, Tabun, Shanidar, Skhul, and Qafzeh (Smith, Falsetti, Donnelly, 1989; Trinkaus, 1989; Simmons, Falsetti, Smith, 1991). Researchers noted that these fossils showed the mixture of features from various groups, and represented a prototype of a single species (Frayer et al., 1993; Sohn, Wolpoff, 1993; Arensburg, Belfer-Cohen, 1998). S. Sohn and M. Wolpoff, using a metric analysis, showed that Zuttiyeh morphology is closest to that of the Near Eastern Neanderthals, and reveals certain similarities to the Zhoukoudian hominins (1993). G. Rightmire believed that the Zuttiyeh frontal bone links this specimen with both early Neanderthals and the direct ancestors of humans from Skhul and Qafzeh (2001a). The occurrence of Acheulo-Yabrudian artifacts (350–300 ka BP) in Mugharet el-Zuttiyeh Cave makes it possible to associate the Zuttiyeh hominin with an archaic population that used to inhabit Africa, i.e. with the taxon that includes individuals from Bodo, Elandsfontein, Broken Hill, Eyasi, Ndutu (Rightmire, 2009a). G. Bräuer associated the Zuttiyeh man with early archaic *H. sapiens* (2008).

There are different hypotheses concerning the taxonomic affinity of the above fossils; however, the experts always point to the mosaic combination of morphological features typical of Neanderthals and anatomically modern humans. This argues in favor of my hypothesis that in the Middle Pleistocene, the single biological taxon, *H. heidelbergensis*, split into two related subspecies: anatomically modern humans and Palestinian Neanderthals (Derevianko, 2020). The finds from Mugharet el-Zuttiyeh Cave illustrate one of these transitional stages.

In one of the latest papers addressing this issue, S.E. Freidline and her colleagues presented the results of their study, carried out using three-dimensional geometric morphometry and multivariate statistical analysis, to determine the morphological correspondence of Zuttiyeh remains to a specific Pleistocene group: *H. erectus* sensu lato, *H. heidelbergensis* sensu lato, *H. neanderthalensis*, transitional *H. sapiens*, early *H. sapiens*, and Upper Paleolithic *H. sapiens*. The use of new methods provided data about the traits that are difficult to measure using traditional anthropometry. Ultimately, the researchers proposed four hypotheses on the evolution of the Zuttiyeh hominins, based on the results of morphology analysis of the Zuttiyeh and other fossils and taking into account the opinions of other experts (Freidline et al., 2012: 237–238). In terms of time, Zuttiyeh fossils coincide with the Amudian industry.

The researchers conclude that the Zuttiyeh hominin is morphologically similar to Near Eastern Neanderthals (Shanidar V), Middle Pleistocene hominins (Arago XXI), and Near Eastern early modern humans (Skhul V). As noted by Freidline and co-authors, the results of the study do not provide an unambiguous taxonomic attribution of the Zuttiyeh remains, but their morphology is suggestive of a population ancestral to both Neanderthals and modern humans, or a population that existed immediately after the split of these two species (Ibid.).

In my opinion, the Zuttiyeh fossil, like several other paleoanthropological finds, provides the evidence for the split of a single biological taxon of *H. heidelbergensis* that took place in the Levant during the Middle Pleistocene. The morphology of all fossils discovered in this area reveals a mosaic combination of various *H. sapiens* and *H. neanderthalensis* features. This mosaic pattern is explained by the dispersal of different hominin populations in the adjacent areas and settling in the same caves, which frequently resulted in assimilation. A similar process took place in Western Europe, where about ten different Middle Pleistocene species of hominins have been identified.

Layer E of Tabun Cave yielded a femoral diaphysis and a worn lower molar, which were attributed by E. Trinkaus to archaic people (1995). These fossils also exhibit a mosaic combination of morphological features.

More informative paleoanthropological evidence comes from Qesem Cave (Hershkovitz et al., 2011). Excavations produced a large number of lithics related to the Amudian industry; researchers of the cave suggested the local origin of the artifacts and no relation to the complexes in Africa or Europe (Barkai, Gopher, Shimelmitz, 2005; Gopher et al., 2005). Both maxillary and mandibular teeth were found. I. Hershkovits and his co-authors proposed three hypotheses to explain the morphology of teeth from Qesem Cave.

The first hypothesis: the cave dwellers belonged to the local archaic *Homo* population inhabiting

Southwest Asia 400–200 ka BP; their teeth, despite some plesiomorphism, indicate a greater degree of their affinity with the populations of Skhul and Qafzeh than with Neanderthals (Hershkovitz et al., 2011).

The second hypothesis: the evolution of *H. neanderthalensis* in Southwest Asia was as long as that in Europe, where the Neanderthal evolutionary lineage goes back to the Middle Pleistocene. The authors believe that the remains of the archaic modern humans from Skhul and Qafzeh are younger than those from Qesem Cave, but they are older than most Neanderthal fossils from the Levant. The cultural layers in the cave fall within the time range of 400–200 ka BP.

The third hypothesis: as compared to the maxillary teeth, the mandibular ones were located in lower horizons and were smaller in size. These did not show any plesiomorphic traits characteristic of younger maxillary dentition. Both chronological and morphological differences between the teeth may reflect interpopulation differences at the species level and point to the replacement of human population in the region.

In my view, the difference in the teeth sizes does not suggest an interpopulation difference at the species level, but rather the possible alternate occupation of the cave by representatives of two subspecies that evolved on the ancestral basis of *H. heidelbergensis*.

One of the latest anthropological finds is the left half of a maxilla from Misliya Cave, which dates back to 194–177 ka BP (Hershkovitz et al., 2018). The fossil retains most of the alveolar and zygomatic processes, part of the palate and nasal base, as well as a complete left dentition—starting with the first incisor (represented by a broken root) and ending with the third molar (Ibid.: 456).

The study of this fossil has led to some important conclusions.

1. The incomplete maxilla of Misliya 1 does not show any derived skeletal or dental features of Neanderthals (Ibid.: 458–459).

2. The comparison of the Misliya 1 dentition with maxillary and mandibular teeth from Qesem Cave revealed a number of differences. In particular, the Qesem incisor I^2 shows a prominent lingual cusp, more pronounced than that in the Misliya specimen. Qesem canine C1 is distinguished by its more distinct shovel-shape, the presence of a prominent lingual cusp and a mesial ridge. These morphological features distinguish the anterior teeth of Qesem from those of Misliya 1, and are most common of Neanderthals.

3. In most dental features, Misliya 1 resembles the younger *H. sapiens* fossils from the Levant, such as Skhul and Qafzeh, and differs from them in the degree of hypocone reduction.

4. Misliya 1 provides the oldest evidence of migration of members of the *H. sapiens* clade out of Africa.

I cannot agree with the latter conclusion. The earliest fossils, with the morphological features sometimes defined as "modern", come from Northeast Africa (Jebel Irhoud) and are aged to ca 300 thousand years (Hublin et al., 2017; Richter et al., 2017). But these fossils can only very tentatively be attributed to modern humans. Researchers of Misliya Cave compare its early Middle Paleolithic industry with the Middle Stone Age technocomplexes of the Maghreb (Jebel Irhoud), East Africa (Gademotta and Kulkuletti Formations in Ethiopia, and Kapthurin Formation in Kenya). However, the Misliya industries show a very distant resemblance to those of the Middle Stone Age of East and Northeast Africa, and even under the greatest assumption, they reveal no signs of continuity with the Jebel Irhoud industry.

According to the generally accepted view among archaeologists, physical anthropologists, and geneticists, modern humans evolved in Africa in the time range of 200–100 ka BP. Hence, the anthropological and archaeological finds from Misliya Cave cannot be considered as evidence of the migration of modern people to the Levant 194–177 ka BP. In my opinion, given the fossils from Misliya Cave can be associated with modern humans, it can be assumed that the taxon they represent evolved directly in the Levant, and the younger fossils from Skhul and Qafzeh should be considered a continuation of this *H. sapiens* evolutionary lineage.

One more inference by Hershkovitz and his co-authors, based on the results of an analysis of teeth from Qesem Cave (2011), is noteworthy: these fossils may have belonged either to a Neanderthal, or a modern human individual, or a hominin ancestral for both species. This conclusion suggests that the fossils from Misliya are younger than those from Qesem, and belong to the next stage of the evolution of *H. heidelbergensis* in the Levant toward the modern human lineage. The parietal bone and mandible, dated to the period of 120–140 ka BP, from Nesher Ramla (Hershkovitz et al., 2021) are among the finds that are difficult for taxonomical identification. The parietal bone shows morphological similarities to Asian *H. erectus*, and the mandible, to Neanderthals.

Thus, the sparse anthropological materials from the Levant, presumably dating back to 350–150 ka BP, do not provide reliable grounds for identification of any particular taxon: they show a combination of plesiomorphic and modern traits. These fossils represent the final phase of split of the ancestral taxon of *H. heidelbergensis* into two taxa—early modern humans and Palestinian Neanderthals.

In the Levant, during the late Middle to early Upper Pleistocene, phylogenetic history developed differently from the rest of Eurasia and Africa. The final split of *H. heidelbergensis* in the Levant occurred ca 250–100 ka BP. The younger paleoanthropological materials from the Levant, dating to the chronological range of MIS 5 and 4, are debatable. Some researchers believe that all the fossils belonged to a single population close to the anatomically modern humans (Arensburg, Belfer-Cohen, 1998; Kramer, Crummett, Wolpoff, 2001; and others); others attribute skeletal remains from Tabun, Amud, and Kebara to Neanderthals, and those from Skhul and Qafzeh to early *H. sapiens* (Tchernov, 1992; Jelinek, 1992; Vandermeersch, 1992, 1997; Stringer, 1992, 1998; and others).

Tabun Cave was presumably inhabited in the chronological range of 140–110 ka BP by hominins that slightly differed from one another in morphological type. Some inhabitants (Tabun II) were people of the anatomically modern type, similar to those whose bone remains were discovered in Skhul and Qafzeh Caves; while others (Tabun I) showed many plesiomorphic features along with *H. sapiens* traits and belonged to the Palestinian Neanderthals. This inference is of fundamental importance. Modern humans and Neanderthals lived in Tabun Cave during the period corresponding to the late MIS 6 to MIS 5. Consequently, Neanderthals did not migrate to the Levant from Western Europe (Stringer et al., 1989; Shea, 2001, 2003; and others), but evolved simultaneously with modern humans from the common ancestral base—*H. heidelbergensis*. Notably, the taxonomic affinity of fossils from Tabun Cave has often been the subject of debate, probably because of the morphological similarity between the finds. In addition, some scholars believe that modern humans, whose remains were found in Skhul and Qafzeh, and the Neanderthal individual Tabun I belong to the same chronological period (Grün et al., 2005; Ronen, Gisis, Tchernikov, 2011). This inference also supports the hypothesis as to the simultaneous dispersal of early modern humans and Neanderthals in the Levant.

Human bone remains found in Skhul and Qafzeh caves undoubtedly belong, according to many anthropologists, to the modern anthropological type. Skhul Cave yielded bone remains of ten individuals of various ages: eight men and two women. The cranial and postcranial morphology of these people is mosaic. Therefore, it is understandable that until recently some experts have associated these fossils with modern humans and Neanderthals. The former could have migrated to the Levant from Africa (Andrews, 1984), and the latter, from Europe (Vandermeersch, 1981).

Taking into account differences in the stratigraphic position of the remains, the Skhul hominins were suggested to be subdivided into two groups in accordance with the chronology: an earlier one (III, VI–X) and a younger one (I, IV, V) (McCown, Keith, 1939). This point of view was supported by A. Ronen (1976). According to D. Kaufman (2002), the recognition of these two groups does not necessarily imply that there was a long chronological gap between them.

The Skhul hominins demonstrate the anthropological characteristics typical of *H. sapiens*, such as a tall stature (173–179 cm), very low orbits, and large facial width (Zubov, 2004). At the same time, these hominins show many features similar to those of Neanderthals.

Skhul V is the best preserved skeleton in the sample. This was a tall, gracile built man 30–40 years old, with a cranial capacity of 1518 cm^3, skull with a high vault, low orbitals, and a rather high and wide face (Ibid.). The metric and non-metric traits of the supraorbital area in Skhul V link this individual to Mladeč 5 and Brno I, showing the morphological features characteristic of both Neanderthals and modern humans. The zygomatic region is typical of *H. sapiens*; the angle between the frontal and temporal processes, which equals 115°, also falls within the modern range. The shape of the frontal process links Skhul V to Oberkassel 1 and Broken Hill, whereas the comparative analysis of the angles defining neurocranial shape reveals affinities with Amud, Broken Hill, and Ngandong XI. In a number of parameters, the Skhul V mandible is similar to those of Amud, Le Moustier 1 and 2, Oberkassel 1 and 2, and other Neanderthal specimens.

The cranial and postcranial skeleton of Skhul V retained many Neanderthal features. Moreover, in particular individuals, the combination of evolutionarily derived and ancestral features was expressed differently in the facial and cerebral parts of the skull and postcranial skeleton. As noted by S.V. Vasiliev (2006), the statistical analytical data confirm that the evolution of the facial skeleton occurred faster than that of the braincase. In phylogenesis, metric traits changed faster than structural (descriptive) characteristics (Zubov, 2004: 163).

Qafzeh Cave revealed a larger cemetery than that found in Skhul Cave. It contained the remains of 15 modern hominins (Ronen, 2012). For these fossils, a TL-date of 92 ± 5 ka BP was generated on burnt flint. Direct dating of teeth through the ESR analysis provided more reliable estimates: 100 ± 10 and 120 ± 8 ka BP (Grün, Stringer, 1991).

The best preserved remains of Qafzeh 9 represent a woman aged ca 20 years. Next to her, a child (Qafzeh 10) was buried, suggesting that this was a double burial. The female skull is characterized by a high cranial vault, a gentle slope of the frontal bone, a relatively weak supraorbital relief, a strongly protruding, distinct chin; a rounded occiput without a chignon or bend; modern structure of the zygomatic region, a canine fossa, thin cranial walls, and a cranial capacity of 1554 cm^3 (Zubov, 2004: 348). The well-preserved skull of Qafzeh 6 also shows features typical of anatomically modern humans. Individuals from Qafzeh Cave demonstrate more *H. sapiens* traits than hominins from Skhul.

Excavations at Ras el-Kelb Cave, in the homonymous mountain range, revealed a Middle Paleolithic industry of the Tabun C type, including flakes detached from discoid cores; side-scrapers of various types, notched-denticulate pieces, and a few Levallois points and blades (Copeland, 1978). The layer containing these artifacts yielded three human teeth. One tooth belonging to a young man 16–20 years old was identified as a large premolar with a combination of *H. sapiens* and Neanderthal traits (Vallois, 1962). The other two teeth, an upper second molar from an individual ca 23 years old and an upper second deciduous molar, demonstrated more modern features than those of Neanderthals.

In the Levant, both *H. sapiens* and Palestinian Neanderthals developed. Western European Neanderthals of the period 120–50 ka BP were polymorphic in structural features of skull and postcranial skeleton. The Levantine Neanderthals differed from them in a greater number of apomorphic features and similarity to *H. sapiens*. In Western Asia, burials of Neanderthals were found in the caves of Amud, Kebara (Israel), Shanidar (Iraq), and Dederiyeh (Syria).

Above is a brief description of morphology of the female specimen from Tabun Cave (Tabun I). She had a height of 154 cm, cranial capacity of 1271 cm^3, low skull, sloping forehead, prominent supraorbital torus, and almost no mental protuberance. The ascending mandibular ramus is wide and robust, with a high and wide coronoid process and a shallow notch. These and other features suggest the definition of Tabun I skull as the closest to Neanderthal among all anthropological finds from Mount Carmel. Other fragmentary human fossils from Tabun Cave also demonstrate Neanderthal traits.

Amud Cave yielded the remains of several individuals, which included the skeleton of a young male (Amud I) buried according to a special rite. Morphological characteristics of other finds from this cave are indeterminate because of their fragmentation.

The skeleton of Amud I, discovered and analyzed by H. Suzuki and F. Takai, is morphologically more developed than those of Tabun I and Shanidar I, although it has some common features with them. In terms of cranial morphology and supraorbital torus size, Amud I resembles Skhul IV. Apart from the Neanderthal morphology, researchers noted significant differences between this individual and classic European Neanderthals (Suzuki, 1970; Takai, 1970).

The Amud I male skeleton was described by many anthropologists. Experts compared the taxonomic status of this individual with other finds from Africa and Europe and identified both plesiomorphic and apomorphic traits. The Amud I individual was about 180 cm tall, had a gracile skeleton and a cranial capacity of 1740–1800 cm^3. According to descriptive characteristics, his supraorbital region shows Neanderthaloid features (a low glabella and a virtual absence of supraglabellar groove) (Vasiliev, 2006: 150–151). In a number of metric parameters, Amud I shows similarities with the skeletal remains of Shanidar I, Skhul IV, Arago XXI, and Tabun I. Amud I shows a zygomatic notch, which is not typical of Neanderthals, and no bulging at the base of the frontal process of the maxilla. Metric parameters and indices of the zygo-maxillary region link the Amud I find with Oberkassel 1, Sungir 1, Fish Hoek, and Skhul V. In terms of trigonometry of the facial skeleton, it is similar to Skhul V, Florisbad, Sungir 1, and Gibraltar 1. The mandible shows sapient features in a number of parameters (even the mental protuberance can be recognized). S.V. Vasiliev notes a number of other traits that bring Amud I closer to both Neanderthals and *H. sapiens*. According to G. Bräuer scale, this specimen can be attributed to the "late archaic *H. sapiens*" (1984).

Descriptions of the Amud I skeleton made by other anthropologists suggest that both the cranium and the postcranial skeleton combine features typical of classic Western European Neanderthals and of early anatomically modern humans in Africa. The postcranial skeleton of Amud I appears to be unusual for European Neanderthals. This individual is significantly taller and has long lower and upper limbs, which brings it closer to the male individuals from Skhul and Qafzeh. One cannot but agree with the B. Arensburg and A. Belfer-Cohen arguing that the morphology of Amud I individual rather contradicts the proposed attribution of these fossils to the Neanderthal type, and indicates a divergence from this category (1998).

Based on the fact that no remains of anatomically modern humans younger than 80 (75)–40 ka BP have yet been found in the Levant, some researchers come to the conclusion that modern humans were replaced by Neanderthals migrating from southern Europe to this region. This conclusion is questionable. The replacement of modern humans by European Neanderthals should have entailed changes in the technical and typological complex of stone tools, because the European Mousterian that falls within this time range was significantly different from the late Middle Paleolithic of the Levant. The Tabun I and Tabun II fossils suggest that as early as about 100 ka BP, the Levant was inhabited by Palestinian Neanderthals and modern humans, who occupied the same caves. J. Schwartz and I. Tattersall classified the fossils from Qafzeh Cave into two groups: they identified anthropological individuals Qafzeh 1, 2, 9, and 11 as *H. sapiens*, and others not, because they definitely did not belong to this species (2005b). Consequently, this cave could have been alternately inhabited by groups of anatomically modern humans and Palestinian Neanderthals.

The examination of the anthropological finds of the Middle and Upper Pleistocene from the Levant and analysis of their morphological features revealed the need to clarify the previously formulated hypotheses: as to the regional origin of Neanderthals (Trinkaus, 1983), the existence of a single population close to anatomically modern humans (Kramer, Crummett, Wolpoff, 2001), and the attribution of Tabun I, skeletal remains from Amud and Kebara to Neanderthals, and those from Skhul and Qafzeh, to early *H. sapiens* (Tchernov, 1992; Jelinek, 1992; Vandermeersch, 1992, 1997; Stringer, 1992, 1998; and others). At present, many researchers support the idea of two parallel evolutionary lineages represented by modern humans and Palestinian Neanderthals (Rak, 1986, 1990; Arensburg, Belfer-Cohen, 1998; and others), but propose different chronological estimations for the dispersal of each of those populations in the Levant. The scarce anthropological materials discovered in Israel indicate that further evolutionary development of *H. heidelbergensis* continued in this region. This led to the development of early modern humans (Skhul, Qafzeh) and Palestinian Neanderthals (Amud, Kebara and, possibly, Tabun Cave, alternately inhabited by early modern humans and Neanderthals) (Derevianko, 2019, 2020, 2022).

More recently, J.M. Bermúdez de Castro and M. Martinón-Torres published an article in which, based on the study of Middle Pleistocene fossils from Africa and Eurasia, they came to the conclusion that the search for the ancestors of anatomically modern humans should be carried out not only in Africa, but also in Southwest Asia, especially in the Levant (2022: 91).

The thorough analysis of the evolutionary development of *H. heidelbergensis* in the Levant was necessary because this taxon played a major role in the origins of Neanderthals and Denisovans. Some representatives of this taxon, which was at the stage of the divergence process, at different periods migrated to Europe and East Asia, where Neanderthals and Denisovans evolved.

Homo heidelbergensis in Europe and development of the Neanderthal taxon

About 700 (600) ka BP, some groups of the *H. heidelbergensis* population with the Acheulean industry migrated to Europe, where they met with the indigenous population—representatives of the late form of *H. erectus* with the pebble-flake industry*. The earliest anthropological materials in this area have been recovered from Sima del Elefante in Atapuerca: layer TE 9C yielded a fragment of the hominin mandible with several teeth, and a separate lower second premolar of the same individual aged 1.3–1.1 million years (Carbonell et al., 2008: 465).

Anthropological fossils (from four to six individuals, according to various sources) found by Spanish researchers in Atapuerca at the site of Gran Dolina (level TD 6 – Aurora) date back to a slightly younger period (800–900 ka BP). Fossils from TD 6 include 85 fragmented cranial and postcranial bones (Bermúdez de Castro, Nicolás, 1997).

On the basis of the analysis of these finds, the researchers attributed them to a new species, *H. antecessor*. J.M. Bermúdez de Castro and his co-

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*For more details, see: (Derevianko, 2019: 437–470).

authors concluded that *H. antecessor* was the ancestor of *H. heidelbergensis*, which later became the ancestor of Neanderthals, anatomically modern humans, and Denisovans (J.M. Bermúdez de Castro et al., 2008, 2017a–c; 2019; Martinón-Torres et al., 2019).

The recognition of a new species, *H. antecessor*, based on the mandible from Sima del Elefante and fossils from horizon TD 6 at Gran Dolina, separated by a chronological gap of ca 300–400 thousand years, which, according to Spanish researchers, is the ancestor of *H. neanderthalensis, H. sapiens*, and *H. denisovan*, from our point of view, seems premature. Many anthropologists express doubts about the validity of such a conclusion. One can only agree with the identification of a late form of *H. erectus* and its designation as *H. antecessor*.

Homo heidelbergensis with the Acheulean industry migrated from the Near East to Europe, where he met with *H. antecessor* (indigenous population), a descendant of *H. erectus* with the pebble-flake industry. Both the newcomers and the aboriginal populations had an open genetic system, and over the course of 500 thousand years of their common settlement in the vast European continent, as a result of the assimilation of these two taxa, natural selection, genetic drift, and adaptation to changing environmental conditions, a new taxon of *H.s. neanderthalensis* originated.

In the period of 700–200 ka BP, about ten species of hominins have been identified, retaining important morphological information. These species demonstrate a mosaic pattern of morphological characteristics, indicating the complexity of the evolutionary process. Notably, all discovered fossils, on the basis of which the anthropologists identified species, are subspecies. Each species must have an ancestral form, which gives rise to a new taxon. New taxa were formed mainly as a result of assimilation of the indigenous population with the newcomers—*H. heidelbergensis*; mixed offspring were born, in which further hybridization occurred, leading to morphological mosaic pattern in the descendants, who in turn preserved the open genetic system.

In Europe, archaeologists have identified several industries existing in the chronological range of 700–200 ka BP: pebble-flake, Acheulean, small-sized tools, and others, which showed great variability. The mosaic pattern of morphology in hominins and the variability of their industries are explained by the complexity of the processes that took place in Europe in the Middle Pleistocene in connection with the evolution of a new taxon—*H.s. neanderthalensis* and the Mousterian industry. Difficulties in understanding the phylogeny are associated with the fact that there are rather few anthropological remains aged to the range of 700–200 ka BP, and they were found mainly in Western Europe. Moreover, these finds are fragmented and their chronological affiliation is problematic.

Let's discuss some of the most significant and oldest fossils. *H. heidelbergensis* emerged in Africa, but was named after the place where the mandible of this species was first found—in a quarry located by a place called Mauer, near Heidelberg, Germany. The mandible was originally described by O. Schoetensack (1908), who identified it as a new species, *H. heidelbergensis*. The mandible was large in size and combined ancient apomorphies of *H. erectus* and derived characteristics. E. Mayr proposed to classify this individual as late *H. erectus* (1963). F.C. Howell noticed more derived features in this fossil, and attributed it to *H. neanderthalensis* (1960).

The increase in the number of Middle Pleistocene fossils discovered in Africa and Eurasia allowed P.G. Rightmire to attribute a significant part of them to a new species that emerged in Africa ca 900–800 ka BP, and designate the species as *H. heidelbergensis*, after the place of the first find (1988). There has been a long lasting debate about the age of the Mauer mandible. Most researchers have accepted the date proposed by M. Day based on the study of the remains of animals adapted to warm climate—the end of the first interglacial or the onset of the second interglacial (~550–500 ka BP) (Day, 1986). According to the updated data, the age of this fossil is 609 ± 40 ka BP (Wagner et al., 2010).

The *H. heidelbergensis* population migrated to Europe and dispersed over a fairly large area. The northernmost anthropological find comes from the Acheulean site of Boxgrove in England (52°N). This is one of the informative Acheulean sites in Europe, with the largest number of Acheulean handaxes. The site has also revealed a shinbone. C. Stringer and his colleagues carefully studied the fossil and attributed it to the genus *Homo* (Roberts, Stringer, Parfitt, 1994). In some publications, this bone is dated to 524–478 ka BP (Ibid.), in others, 423–362 ka BP (Bowen, Sykes, 1994). It is very likely that in England *H. heidelbergers* encountered late *H. erectus*. At the same latitude, the sites of *H. erectus* with pebble-flake industry, dating back to 800–900 ka BP, have been reported. Another site with the pebble-flake industry was discovered in eastern England in Pakefield (Parfitt et al., 2005). An age estimate of about 700 ka BP was obtained for this locality through several methods. Thus, there is every reason to believe that *H. heidelbergensis* came into contact with late *H. erectus* in England, and the assimilation could have occurred between the newcomers and the indigenous population.

The grotto of Caune de l'Arago, located 30 km from Perpignan, near the small town of Tautavel in the Eastern Pyrenees, is one of the best explored localities. During the excavations (1964–2015), 148 fragments of human remains were found there (Lumley M.-A., 2015). The fossils were deposited in a clear stratigraphic sequence of 15 lithologic units (including the bottom of unit Q, dated to 550 ka BP, and the top of unit C, 400 ka BP) dating back to the period corresponding to MIS 14–11. During this long time, hominins experienced two periods of cold and dry climate, separated by a period of moderately humid climate.

Human remains are represented mainly by cranial fragments. These included the frontal part of Arago 21 skull, which provided the first insight into the physical appearance of the first Europeans. The entire set of finds from Caune de l'Arago—5 mandibles, 123 teeth (isolated or in the alveolar process), several fragments of postcranial skeleton, including 9 fragments of upper and 19 fragments of lower extremities—has been classified and attributed to 30 individuals: 18 adults and 12 children (Ibid.: 303).

This extensive anthropological material is supported by detailed field documentation clearly recording the locations of fossils in the stratigraphic sequence; and has a reliable geochronology. During field work and laboratory research, all finds discovered during excavations were studied by experts of various fields of sciences and humanities, using the most advanced techniques and equipment. The anthropological material was comprehensively studied by one of the most highly qualified physical anthropologists M.-A. de Lumley. She notes that the abundance of bone remains makes it possible to assess the biodiversity and composition of this population (Ibid.: 304).

M.-A. de Lumley draws the attention to the fact that the finds from Caune de l'Arago show certain archaic features not noted in the Mauer mandible. The particular value of these anthropological materials is that they provide the possibility to study the skull and lower limbs of a European Middle Pleistocene hominin simultaneously. Skulls with well-preserved facial parts found in the clear stratigraphic context are extremely rare. The skull of Arago 21, retaining facial bones, is the most complete and best preserved skull from the first half of the Middle Pleistocene in Europe.

The issue of taxonomic identification of the fossils from Caune de l'Arago has caused a lively debate. The first finds from the grotto were designated as pre-Neanderthal (Lumley M.-A., 1970, 1973). The skull of Arago 21 had many features resembling those of the late *H. erectus*. In particular, Arago 21 showed similarities to fossils from Morocco and Algeria. This led to the assumption of a genetic link between European and African hominins of the Middle Pleistocene (Aguirre, Lumley M.-A., 1977). In the course of further comprehensive studies of archaeological and anthropological materials from Caune de l'Arago, the leaders of the work, an outstanding French archaeologist A. de Lumley and his no less famous wife M.-A. de Lumley, came to the conclusion that these fossils should be classified as a separate taxon, *Homo erectus tautavelensis* (Lumley H., Lumley M.-A., 1979). They supported their conclusion with the following evidence: anthropological remains from Caune de l'Arago reveal morphological similarities between each other; the morphology of these hominins shows features characteristic of pre-Neanderthal populations of Europe and distinguishing them from the hominins that settled in Africa and Asia during the same period. These representatives of *H. erectus*, the first inhabitants of Europe, are the ancestors of Neanderthals and modern humans (Ibid.).

M.-A. de Lumley combined various fossils—Arago, Ceprano, Galeria, Swanscombe, Vértesszőlős, Bilzingsleben, Petralona, Biache-Saint-Vaast, and Lazaret—into the subspecies *H. erectus tautavelensis*, which replaced *H. antecessor*. For the developed European *H. erectus*, several stages of evolution can be distinguished, which ended with the emergence of Neanderthals 120 ka BP. M.-A. de Lumley believed that the phenomenon of Neanderthalization would be widely dispersed in Europe starting from 100 ka BP.

The extensive anthropological materials from excavations at Caune de l'Arago have aroused great interest among physical anthropologists. Fossils representing cranial, facial, and postcranial elements have opened up the possibility of comparison with other anthropological finds from Africa and Eurasia.

D. Johanson and E. Blake believe that the Steinheim skull is a reduced copy of Arago 21. They explain the slight difference in size by sexual dimorphism (Johanson, Blake, 1996). J. Schwartz and I. Tattersall argued that the mandibles from Mauer and Arago belong to the same species, despite the differences in the antero-posterior branch and some other details, and pointed out the necessity of comparison of the cranial specimens from Arago, specifically the facial portion of the skull of Arago 21, with other fossil hominin skulls and *H. heidelbergensis*. Given Arago 21 and its fragments as reference models, there are several other relatively well-preserved remains that would be candidates for inclusion in the class of *H. heidelbergensis* (Schwartz, Tattersall, 2005b: 503).

Another fossil dating back to the first half of the Middle Pleistocene was found in France—a mandible from the vertical gallery of La Niche in the Montmaurin Grotto. Excavations in the grotto revealed Mindel faunal remains (~540–470 ka BP) (Lumley M.-A., 2015). M.-A. de Lumley described this mandible as quite different from those of hominins from North Africa and East and Southeast Asia—Atlanthropus, Pithecanthropus, and Sinanthropus. It differs from fossils from East Asia by the curvature of the alveolar arch. European specimens are always characterized by a flattened wall anteriorly at the level of the incisors, while in Pithecanthropus, the front arch of the mandible is of a regular convex shape. In general, the Montmaurin mandible is robust; it retains six molar teeth. The researchers have found isolated teeth and a vertebra.

Based on the thickness of the bones in the symphysis, as well as the shape of the mental region (sharply receding at an angle of 73°), the large width of the ascending ramus, and the low position of the digastric fossa, A.A. Zubov and S.V. Vasiliev classified this mandible as the one close to *H. heidelbergensis*, and based on the size of the teeth, to the Steinheim skull, but more robust than the latter (Zubov, Vasiliev, 2006). Overall, the Montmaurin mandible appears archaic. G. Billy and A. Vallois noted that in some features this mandible was more primitive than those of *H. erectus*, but at the same time it showed a number of derived characteristics; this suggests its classification as “pre-Neanderthal” (Billy, Vallois, 1977).

A Middle Pleistocene hominin skull was first found in 1933 near Steinheim, 30 km north of Stuttgart, Germany. The fossil was discovered by anthropologist F. Berckhemer in the fluvial deposits of a gravel quarry on the banks of the Murr River. It was the skull of a young individual; most of its face, upper molars and premolars were deformed by fossilization. Some scholars attribute these deposits to the Mindel-Riss (Cela-Conde, Ayala, 2007), others estimate their age as ca 475 thousand years (Adam, 1985).

All researchers note a remarkable combination of primitive and advanced features in the Steinheim fossil. The skull demonstrates certain *H. erectus* traits: a small cranial capacity of 1100 cm^3, a low skull cap, a “sloping” forehead, and a robust supraorbital torus. The discoverer and the first researcher F. Berckhemer identified the find as a new species, *Homo steinheimensis* (1936). B. Campbell downgraded the specimen to the subspecies *H. sapiens steinheimensis* (1964). Some anthropologists classified the Steinheim hominin as Neanderthal. The antiquity of the fossil and some morphological features argued against such a taxonomic determination. According to M. Day, the position of the maximum width of the skull, the shape and thickness of its vault bring the Steinheim fossil closer to the Swanscombe find (1986).

The discussion concerning the taxonomic affinity and age of the Ceprano skull is a striking example of the discrepancy between various viewpoints of experts. This fossil was discovered in Central Italy, near the small town of Ceprano, approximately 100 km south of Rome. On March 13, 1994, I. Biddittu, a member of the Italian Institute of Human Paleontology, discovered the first fragment of the skull. In the course of subsequent excavations, researchers found about 50 fragments. The skull was reconstructed over a period of ca 5 years by several researchers (Ascenzi et al., 1996, 2000; Clarke, 2000).

The debate over the place of the Ceprano fossil in the hominin taxonomy stems from the fact that the find was initially dated to ca 0.8–0.9 Ma BP (Ascenzi et al., 1996; Ascenzi, Segre, 1997). The researchers, having studied the Ceprano skull, concluded that the main characteristics of this specimen are comparable with those of Asian *H. erectus*. The cranial vault is low, with a flattened sloping forehead. The supraorbital arches are robust and extremely prominent. They are continuously connected to the glabella, which is equally robust in structure. The bones are thick. Behind the supraorbital torus, there is an extended depression in the form of a groove; the postorbital constriction is pronounced. The inion coincides with opisthocranion; the maximum width is located very low—at the level of the well-developed supramastoid crest. The occipital squama is very large as compared to its width between the asterions. However, the researchers note certain characteristics that distinguish Ceprano skull from *H. erectus*. The capacity of the Ceprano skull is 1185 cm^3, while the largest *H. erectus* skull size rarely exceeds 1000 cm^3. The Ceprano skull does not show a distinct sagittal suture or parasagittal depression in the frontal squama, where, unlike the parietal bones, the vault maintains its continuity. A reduced postorbital narrowing and a relative reduction in the robustness of the vault in relation to the base were noted.

Some scholars proposed to include Ceprano, together with the Atapuerca fossils (TD 6), into the group of the oldest anthropological remains discovered in the Mediterranean region, and to designate these materials as a single species *H. antecessor*; however, they did not exclude the possibility of emergence of two different species in Europe in the late Early Pleistocene (Ascenzi et al., 1996; Clarke, 2000; Bruner, Manzi, 2005).

Finally, in the course of interdisciplinary research, the age of Ceprano skull was established within the range of 430–385 ka BP (Manzi et al., 2010). This result was unexpected for specialists and allowed them to significantly revise the previously stated hypotheses about the place of the Ceprano fossil in the phylogeny of Middle Pleistocene hominins. As it turns out, the Italian fossil dates back to the second half of the Middle Pleistocene rather than to the late Early Pleistocene. At the same time, along with the indisputable morphological features of Neanderthals, scientists noted certain similarities of the Ceprano skull to the Late Pleistocene finds from Western Europe. It has been concluded that the new Ceprano geochronological position indicates the diversity of Middle Pleistocene hominins and a more complex scenario for their evolution than previously thought.

The site of Sima de los Huesos (SH) is one of the most outstanding sites in Europe due to the abundance of hominin finds falling almost within the same time range. It is located in the Atapuerca sector 2 (Cueva Mayor), 500 m from sector 1 (Trinchera del Ferrocaril). Sima de los Huesos, according to one data, revealed about 4000 hominin remains, and according to other data, 3000 and 3600 fragments (Aguirre, 1995; Bermúdez de Castro et al., 1997, 2004; Rodríguez, Carbonell, Ortega, 2001; Falguères et al., 2001).

The SH collection of anthropological fossils is unique in both quantity and morphological diversity. J.M. Bermúdez de Castro and S. Sarmiento (2001) carried out a comparative morphological analysis of human teeth from two Atapuerca localities—Gran Dolina (TD 6) and SH. The SH site yielded 380 teeth, of which 98 were found *in situ*. Most of the teeth (*n*=376) are permanent. The authors of the first publications describing this analysis assumed that the teeth belonged to 32 individuals (Bermúdez de Castro, Nicolás, 1997). The further detailed analysis showed that the SH anthropological remains belonged to 27 individuals.

SH fossils date back to ca 430 ka BP (Arsuaga et al., 2014). The cranial and postcranial morphology of these hominins shares many features with Neanderthals. Therefore, some anthropologists assign SH fossils to this taxon. This hypothesis cannot be considered substantiated, because, according to the results of DNA sequencing, the hominins of the locality in question were in the process of development.

Extraction of an almost complete mtDNA sequence from the femur of a SH individual of such great antiquity should be considered a great achievement of researchers from the Max Planck Institute for Evolutionary Anthropology in Leipzig. The mtDNA sequence of this hominin turned out to be Denisovan rather than Neanderthal, as expected (Meyer et al., 2014). To test this result, the researchers created three phylogenetic trees based on the mtDNA sequences of SH hominin, anatomically modern human, early modern human, Neanderthal, Denisovan, chimpanzee, and bonobo. All three trees demonstrated a topology where mtDNA of the SH individual shared a common ancestor with mtDNA of Denisovan, while mtDNA of the other taxa was out of this process (Ibid.: 404).

Re-sequencing of DNA from two bones of the Sima de los Huesos hominin resulted in extraction of nuclear DNA of Neanderthals rather than Denisovans (Meyer et al., 2016). The nuclear DNA sequence extracted from the AT-5431 femur and an incisor suggests their affinity with the Neanderthal evolutionary lineage. The researchers concluded that the SH hominins were early Neanderthals or a group closely related to the ancestors of Neanderthals after diverging from their common ancestor with the Denisovans (Ibid.: 507).

DNA sequencing of the SH hominins revealed the presence of Denisovan mtDNA in their genome. However, mtDNA can be inherited as a separate unit passed from mother to her offspring; it doesn't fully represent the affinity between individual hominins and the population as a whole. The nuclear genome of SH individuals was sequenced from a femur fragment and an incisor. It was found out that in the genome from the femur, 87 % of the common branch of Neanderthals and Denisovans contains 43 % of the Neanderthal alleles and 9 % of the Denisovan alleles; in 68 % of the incisor, the share of the Neanderthal alleles is 39 % and that of Denisovan is 7 %. The results of genome sequencing are extremely important. These confirm that the SH individuals were not only ancestral to Neanderthals, but in their genome they also retained mtDNA and a small percentage of nuclear DNA of the Denisovans. The initial split of morphological and genetic heredity into two taxonomic lineages (Neanderthals and Denisovans) in *H. heidelbergensis* occurred when a part of their population dispersed to

Europe 700 (600) ka BP. In the course of development of a new Neanderthal taxon on the ancestral basis of *H. heidelbergensis*, the new taxon retained some part of the Denisovan mtDNA for a long time, despite the fact that Denisovans never populated Europe.

The duration of the process of development of the Neanderthal taxon is illustrated by other, younger anthropological fossils found in Europe.

In 1933–1935, excavations of an Acheulean site carried out in England near the small town of Swanscombe, 30 km east of London, in the valley of the Thames River, revealed an occipital bone, as well as left and right parietal bones of one skull. The bones of late Pleistocene animals and Acheulean tools were embedded in a stratum attributed to the second interglacial. First, the stratum was dated to 225 ka BP (Bridgland et al., 1985); later, a date of 423–362 ka BP was derived (Bowen, Sykes, 1994). The skull fragments belonged to a female individual. The cranial capacity is approximately 1325 cm^3. The skull is characterized by thick bones, a low vault, and a rounded occipital region, and combines primitive features and well-expressed features of modern humans. The mosaic combination of traits has sparked discussion about the taxonomic affinity of this fossil. W. Le Gros Clark, who first studied the fossil, and his co-authors designated it as *Homo* cf. *sapiens* (1938).

Later, A. Kennard classified the Swanscombe fossils as a separate species (1942). In many respects, the skull fragments from Swanscombe were similar to the skull from Steinheim (Germany), which showed a mosaic pattern of primitive features and those of modern humans.

F.C. Howell included the fossils from Swanscombe, Steinheim, and Fontéchevade in the group of early Neanderthals, on the basis of their great similarity (1951). M. Wolpoff had a different opinion: he attributed a large group of European Middle Pleistocene fossils from Swanscombe, Vértesszőlős (Hungary), Petralona (Greece), Steinheim, and Bilzingsleben (Germany) to *H. erectus* (1971). The scholar explained the presence of modern human traits in the Swanscombe skull by the fact that it belonged to a female individual, and the morphological differences in the group attributed by him to late *H. erectus* he associated with sexual dimorphism. M. Day, in his study of the Swanscombe fossils, concluded that they belonged to a female individual at the transitional stage between *H. erectus* and *H. sapiens*, which could be regarded as the base of a diverging branch leading to European Neanderthals (1986). There are also other viewpoints on the taxonomic affinity of this fossil. The case of the Swanscombe skull shows how different the conclusions may be, which is explained by the great morphological mosaicity of features in anthropological remains.

The distribution of late hominins bearing evident features of *H. erectus* and *H. sapiens* in Europe is also evidenced by other finds. The site of Vértesszőlős with a pebble-flake industry, located 50 km northeast of Budapest, yielded the teeth of a child in the main culture-bearing layer and the occipital bone from an adult individual in the overlying horizon. Initially, the cranial capacity of the adult individual was estimated as 1400 cm^3; according to the updated information, it is 1325 cm^3. This individual clearly shows some extremely archaic features: very thick bones and a well-protruded occipital torus. Among the deciduous teeth, the lower canine is distinguished by the large size and the absence of a cingulum. The fossils also showed pronounced derived sapient features, which gave reason to attribute these finds to late *H. erectus* and early *H. sapiens*.

In Germany, the Early Paleolithic site of Bilzingsleben revealed bone fragments, which were reconstructed and identified as belonging to two individuals showing significant differences from one another (Schwartz, Tattersall, 2005b). For the cultural layer, the dates of 228 ± 17/12 ka BP (Harmon, Gtazek, Nowak, 1980) and 414 ± 45 ka BP (Schwartz, 1988) were generated. J. Schwartz and I. Tattersall emphasized certain intriguing issues in the morphology of the bone fragments of these individuals.

The fossils were found in a single cultural layer and were initially attributed to a single individual. The head of the field research D. Mania and his co-author, like other specialists, identified this fossil as late *H. erectus* and compared it with Sinanthropus III and with fossil OH 9 from Olduvai, on the basis of the following features: archaic structure of the frontal bones (robust supraorbital torus, sloping forehead), and the abrupt bend of the occipital bones forming a prominent torus (Vlček, Mania, 1977). This site has revealed a rather peculiar lithic industry, consisting mainly of small-sized tools. Consequently, the site with the pebble-flake microindustry was inhabited by a population in which individuals were morphologically different from one another. Special attention should be drawn to this inference, since it is possible that throughout the Middle Pleistocene, two taxa populated Western Europe: late *H. erectus* (*antecessor*?) and *H. heidelbergensis*. Sometimes, they inhabited neighboring or close regions and, in the absence of hostile relations, they could meet, interbreed and produce fertile offspring. This created a highly mosaic pattern in the morphology of hominins in the second half of the Middle Pleistocene. Importantly, the lithic industry of these hominins was different from the Acheulean and Mousterian traditions.

A hominin skull of the final Middle Pleistocene was uncovered in Petralona Cave near Thessaloniki, Greece, in 1939. The skull was hanging from a stalactite, while the rest of the skeleton lay on the ground. Sadly, the skeleton bones were subsequently lost. Near these currently missing bones, a few Middle Paleolithic tools were found (Poulianos, 1971). Dozens of publications discussed the studies of the Petralona fossil. The find is of particular interest to physical anthropologists studying Middle Pleistocene hominins of Eurasia. The Petralona skull (the mandible is missing) is well preserved. Its age is assessed differently. The electron spin resonance method produced a date of more than 700 ka BP (Poulianos, 1978). The most reliable age determination obtained using the ESR method is 250–150 ka BP (Grün, 1996).

The skull from Petralona shows a mosaic combination of very archaic and distinctive *H. sapiens* features: a robust supraorbital torus and thick bones, a significant height of the vault, relatively low orbits, and the incipient canine fossae. A.A. Zubov and S.V. Vasiliev pointed to the "keel-shaped cranium and an abrupt bend of the occiput, with a strongly prominent torus (a feature more typical of *H. erectus*), as well as some Neanderthaloid features (oblique zygomatic region and broad nasal opening). The cranial capacity is 1220 cm^3 (Zubov, Vasiliev, 2006). Because of this combination of archaic and *H. sapiens* features, researchers have differently assessed the taxonomic affinity of this fossil. Anthropologists characterize it as having well-defined features of Neanderthals (Kokkoros, Kanellis, 1960), the earliest representatives of *H. sapiens* (Stringer, Howell, Melentis, 1979), and advanced late *H. erectus* (Hemmer, 1972).

The Petralona fossil is often used in comparative analyses of Middle Pleistocene hominin remains from Africa and Eurasia. I consider it necessary to briefly dwell on the conclusions of J. Schwartz and I. Tattersall based on the results of their comparative analysis of Middle Pleistocene hominins. Considering the affiliation of fossils from Africa and Eurasia to *H. heidelbergensis*, the scholars noted that among other European specimens the first candidate for inclusion in this species is the Petralona skull. Among African fossils, the obvious candidates are the skulls from Bodo, Kabwe, and Saldanha; among the Asian finds, the skulls from Dali and Jinniushan. All of them are comparable in skull size and proportions of facial part relative to the cranium. The Petralona specimen is particularly similar to Arago 21. The same can be said of the finds from Bodo, Kabwe, Saldanha, and Dali. Finds from Jinniushan show less similarity. These are a half of the Narmada skull and part of the Maba skull vault.

J. Schwartz and I. Tattersall thoroughly examined the signs of similarity and difference, and came to the conclusion as to the "fundamental structural similarity among most of them" (2005b). I cite this conclusion in order to emphasize once again that Middle Pleistocene hominins were the descendants of one ancestral species *H. erectus* and retained many common traits evolving along the *H. sapiens* lineage, despite the great divergence and differences in environmental and climatic conditions of their habitats. Middle Pleistocene African-European hominins can be grouped into a single species, *H. heidelbergensis/rhodesiensis*. Asian hominins of this period also evolved into the *H. sapiens* lineage; their morphology shows many derived features similar to those of the *H. heidelbergensis/rhodesiensis* population; there are also differences resulting from divergence.

The possibility of a single evolutionary line of development of hominins in Eurasia toward sapienization was also assumed by other researchers. For example, G. Rightmire noted that "Petralona and Broken Hill crania differ only slightly in orbit size, frontal proportions, and prominence of the torus crossing the occipital bone; in general, they are remarkably alike" (2001: 133). Similarities in the morphology of the late Middle Pleistocene hominins can be traced not only in the African-European anthropological remains, but also in Chinese fossils. Rightmire and some other anthropologists attributed the Dali and Jinniushan fossils from China to *H. heidelbergensis*. The morphological similarity between them is the result of the common pattern of human evolution along the *H. sapiens* lineage, despite divergence, assimilation, and a regional component. It is no coincidence that D. Johanson considered it possible to attribute the Dali skull to *H. sapiens* (Johanson, Blake, 1996). C. Groves argued that the Dali and Jinniushan fossils are similar to specimens of the same age from Africa and Europe rather than to the more ancient hominins from Zhoukoudian and Hexian (Groves, 1994).

Many anthropologists are convinced that the evolution of Neanderthals took place mainly in Western Europe. This is confirmed by anthropological materials from this region, indicating the gradual development of Neanderthaloid features in the morphology of late Middle Pleistocene hominins; furthermore, a Neanderthal nuclear genome was derived from SH hominins. However, there are several hypotheses as to the time when *H. neanderthalensis* began to exist as a separate taxon. Some scholars believe that Neanderthals emerged in Europe as early as the mid-Middle Pleistocene, and F.K. Howell (1960) even considered the Mauer mandible as *H. neanderthalensis*. M.-A. de Lumley attributed the anthropological finds from Lazaret, aged 170–150 thousand years and associated with the handaxe industry, to late *H. erectus* showing features of Neanderthalization, which is designated as pre-Neanderthal (Anténéandertalien). In her opinion, this hominin had cognitive abilities corresponding to conceptual thinking and social organization. He was on the way to a "surge in symbolic thinking" (Lumley M.-A., 2015).

In connection with determining the boundaries of the initial stage of development of the Neanderthal taxon, the discussion of the taxonomic affinity of fossils found in the south of the Peloponnese Peninsula is noteworthy. Two skulls dating to ca 160 ka BP were found in breccia that filled the space between the walls of Apidima A Cave (Pitsios, 1999). M.-A. de Lumley attributes Apidima 1 and Apidima 2 skulls, as well as the human remains from Lazaret, to a population of late European *H. erectus* at the stage of Neanderthalization. In her opinion, they preceded the classic Neanderthals (Lumley M.-A., 2019). She dates classic Neanderthals in Western Europe to 120–37 ka BP. A similar point of view on the taxonomic affinity of anthropological finds from Apidima Cave is shared by G. Bräuer and co-authors: "…from our results it can be concluded that the Apidima crania should be classified as early Neanderthal and taxonomically, as *H. sapiens neanderthalensis* based on a concept of *H. sapiens* s.l." (2020: 1390).

K. Harvati and her co-authors studied virtual reconstructions of both skulls along with the detailed description and the analysis of their morphological features, as well as U-series dating results (2019). The researchers attributed the skull Apidima 2 to the Neanderthal-like type and dated it back to a period prior to 170 ka BP. The skull of Apidima 1, which is over 210 thousand years old, shows a mixture of modern and primitive features. The available data suggest that two groups of hominins inhabited the cave area in the terminal Middle Pleistocene: at first, a population of early *H. sapiens*, and then Neanderthals. The authors of the paper believed that their findings indicated the repeated migrations of anatomically modern humans from Africa to Europe (Ibid.: 500). The conclusions of Harvati and her co-authors as to the taxonomic affinity of Apidima 1 and Apidima 2 are very controversial, since there is no evidence of such early repeated migrations of modern humans from Africa to Europe.

The brief review of various viewpoints on the evolution of Neanderthals in Europe reveals the following attribution of fossils dating to the terminal stage of the Middle Pleistocene: pre-Sapiens, pre-Neanderthals, Anténéandertalien, and late *H. erectus* undergoing the process of Neanderthalization. I am not aware of any anthropological finds older than 200 ka BP attributable to Neanderthals anatomically and genetically. Possibly, the Neanderthal taxon was finally formed by ca 150 ka BP.

Based on the available materials, I propose the following scenario for the development of this taxon. About 700 (600) ka BP, some part of the *H. heidelbergensis* population with the Acheulean industry migrated from the Near East (Levant) to Europe, where they met with *H. antecessor*. The populations of migrants and the indigenous population were small; representatives of these two taxa interbred and produced fertile mixed offspring. Almost all of the so-called species (Mauer, Boxgrove, Arago, Sima de los Huesos, Steinheim, and others) are the result of this assimilation process. Thus, these were not separate species, but subspecies—the result of evolutionary processes associated with the development of a new taxon of *H. neanderthalensis* in Europe. Apparently, in some areas of Europe, there remained small groups with clear erectoid traits (Vértesszőlős, Hungary), which produced a pebble-flake industry.

When considering the hominin industry of the second half of the Middle Pleistocene in Europe, it is important to understand the issue of emergence of the Levallois primary reduction technique. R. Foley and M. Lahr believe that this technology was introduced in Europe owing to the migration to this region of representatives of the hypothetic taxon—*H. helmei* (1997). I am of different opinion: ca 400–350 ka BP, a part of the *H. heidelbergensis* population from the Near East (Levant), which underwent the evolutionary process of division into two lineages—anatomically modern humans and Palestinian Neanderthals—migrated with the Levallois primary reduction technique to Europe. The first migration wave of *H. heidelbergensis* from the Near East (Levant) 700 (600) ka BP brought the Acheulean industry to Europe, and the second wave ca 400–350 ka BP introduced the Levallois primary reduction. Approximately in the same chronological range (400–350 ka BP), another part of the *H. heidelbergensis* population from the Near East (Levant) began to settle over Central Asia. The dispersal of *H. heidelbergensis* into the Near East ca 800 ka BP marked the divergence of modern humans from Neanderthals and Denisovans, which is confirmed by genetic studies (Reich et al., 2010; Meyer et al., 2012), while the migration of one part of *H. heidelbergensis* to Europe, and the other to East Asia, marked the final split of the common ancestral taxon (*H. heidelbergensis*) into two taxa—Neanderthals and Denisovans. Analysis of the sequenced Denisovan genome showed that the split of the population into Denisovans and Neanderthals occurred 430–380 ka BP (Prüfer et al., 2014; Meyer et al., 2014). *H. heidelbergensis* settled in Central Asia and assimilated with late *H. erectus*, which led to the development of the Denisovan taxon (Derevianko, 2022).

The ultimate genetic and anatomical formation of the Neanderthal taxon took place ca 150 ka BP. The oldest Neanderthal mtDNA, which is considered basal for all Neanderthals, was extracted from the remains of the Hohlenstein-Stadel individual, who lived 124 ka BP in the territory of Germany (Posth et al., 2017; Peyrégne et al., 2019). I consider it necessary to emphasize that the process of evolution of the Neanderthal taxon took more than 500 thousand years, and all the identified intermediate forms differed from one another in certain morphological features, but the ultimate anatomical and genetic development of the Neanderthal taxon took place later than 200 ka BP. This process occurred mainly in Western Europe, where most fossils of intermediate forms were discovered. In Eastern Europe and the Caucasus, the earliest age of the Neanderthal remains does not exceed 100–120 thousand years.

A thorough analysis of the origin of the Neanderthal taxon is necessary for consideration of the main issue raised in the present paper—the validity of identifying a special group of Altai Neanderthals among Neanderthals.

Neanderthals of the Altai: Myth or Reality?

In 1984, in the course of field research in the Altai, Okladnikov Cave with Mousterian industry was found (Derevianko, Markin, 1992). The cave revealed anthropological remains, whose sequenced DNA showed that they belonged to Neanderthals (Krause et al., 2007). In 2007, S.V. Markin discovered another, Chagyrskaya Cave, which also yielded Mousterian industry and Neanderthal bone fossils. The migration of classic Neanderthals designated as the Chagyrskaya Neanderthals to the Altai occurred ca 60 ka BP (Derevianko, Markin, Kolobova et al., 2018). In addition to this group of Neanderthals, on the basis of DNA sequencing of anthropological finds and of samples taken from culture-bearing deposits, another Neanderthal group was identified in Denisova Cave—the Altai Neanderthals.

The complete genome sequence of the Altai Neanderthal was derived from the fossil Denisova 5 (proximal phalanx of the toe) (Prüfer et al., 2014) found in the East Chamber of the cave, in the bottom of cultural layer 11.4 dating to 123 ± 7 ka BP (Jacobs et al., 2019: 594, fig. 3).

M.B. Mednikova, who studied the find, came to the conclusion that this toe phalanx is more developed in width than in height (2011a). This feature distinguishes the hominin from Denisova Cave from most modern humans and brings it closer to Pleistocene *Homo* of various taxonomic affinities. The bone is more robust and wide than those of Neanderthals and anatomically modern humans. The Altai Neanderthals show indications of hypertrophy in plantar ligaments and muscles. The metatarsal facet is canted dorso-proximally rather than proximally as in most modern humans, which may be explained by the habit of a kind of "athletic" or "marathon" (heel off) running (Ibid.: 138). So far, according to Mednikova, this phalanx finds the "closest" morphological parallels in the structure of the corresponding skeleton elements of West Asian Neanderthals from Shanidar Cave and early modern humans from Tianyuan Cave, China (Ibid.: 134).

DNA sequencing from Denisova 5 showed the Neanderthal affinity. This find provided the grounds for identification of a special group of the Altai Neanderthals (Prüfer et al., 2014). It was established that the evolutionary lineage of Neanderthals was ca 20 % shorter than that of Denisovans. This made it possible to assume that the toe phalanx of the Neanderthal (Denisova 5) is older than the phalanx of the little finger of the Denisovan hand (Denisova 3) from layer 11.2 of the East Chamber of Denisova Cave. The comparative analysis of the mtDNA of Denisova 5 and that of other Neanderthals has shown that Denisova 5 is most closely related to the mtDNA of child 1 ca 60–70 thousand years old from Mezmaiskaya Cave in the Caucasus (Ibid.).

The Altai Neanderthal genome contains several long runs of homozygosity indicating that the parents of this individual were close relatives. Since the individual found in the Altai was a woman and her X chromosome had a long run of homozygosity, it can be assumed that both X chromosomes were inherited from close common ancestors—two consecutive males in the pedigree (father and grandfather). The parents of the individual under study were either half-siblings with a common mother, or double first cousins, or uncle and niece, or aunt and nephew, or grandfather and granddaughter, or grandmother and grandson. The experts believe that such marriage relationships were common among Neanderthals (Ibid.: 45).

DNA sequencing has shown that heterozygosity in Denisovans is increased in those regions of the genome where there is one allele from a Neanderthal and one from a Denisovan. This indicates the gene flow from Neanderthals into the Denisovan population, and that at least 0.5 % of the Denisovan genome is the Neanderthal contribution. The Denisovan genome shares more alleles with those of the Altai Neanderthal than with the Vindija Neanderthal (33.19) from Croatia, or with the Neanderthal genomes of the Caucasus; this suggests a gene flow from the Altai Neanderthal population into the Denisovan population (Ibid.: 46–47). In this regard, I consider it necessary to note that this finding may indicate not the flow of genes from Neanderthals to Denisovans (this is quite possible, since both had the open genetic systems), but the residual ancestral heritage of Denisovans from *H. heidelbergensis*, which was common to both Denisovans and Neanderthals.

When studying more than 2 thousand bone fragments from Denisova Cave layer 12 through the technique of peptide mapping for protein identification using mass spectrometry, a small fragment of a hominin bone (24.7 mm long and 8.39 mm wide) designated as Denisova 11 was identified (Brown et al., 2016). During the preliminary genetic analysis of Denisova 11 and comparison with the available complete Neanderthal mtDNA, it was established that the sample from Denisova Cave has five differences from the Neanderthal Okladnikova 2, 12–17 differences from the Neanderthals of Western and Southern Europe, and 31 difference from Mezmaiskaya 1 in the Caucasus and from the Neanderthal Denisova 5 from layer 11.4 of Denisova Cave (Brown et al., 2016: 4).

The mtDNA sequencing from Denisova 11 showed that it was a female (first generation) hybrid, whose father was a Denisovan and mother was a Neanderthal (Slon et al., 2018). The direct radiocarbon analysis produced the date of more than 49.9 ka BP (OxA-33241) for the fossil, while the bone was recovered from layer 12.3 accumulated in the chronological range of ca 140–135 ka BP. The thickness of compact tissue showed that Denisova 11 individual was at least 13 years old at the time of death (Ibid.).

To identify the group of hominins from which Denisova 11 originated, the researchers used the DNA fragments derived from the analysis of bone materials from Denisova Cave, as well as the genomes of modern Africans, and studied the ratio of proportions of alleles in the genome of the Altai Neanderthal (Denisova 5) and the Denisovan (Denisova 3). For Denisova 11, phylogenetic information sites show 38.6 and 42.3 % of alleles from the genome of Neanderthals and Denisovans, respectively, which suggests approximately the same contribution of the two populations to the genetic material of this individual (Ibid.: 113).

According to the researchers, it is unlikely that the genomes of the Altai Neanderthal (Denisova 5) and the Denisovan (Denisova 3) were identical to those of the individuals who contributed to the genetic material of Denisova 11. Therefore, several experiments were carried out; the derived data indicated that the father of Denisova 11 had some Neanderthal ancestral genetic material. Most likely, there was more than one Neanderthal ancestor in his genealogy. Notably, heterozygosity in the runs of Neanderthal origin in Denisova 11 is higher than in the same runs in Vindija 33.19 or in the Altai Neanderthal (Denisova 5); this suggests that the Neanderthal ancestors of Denisova 11's father and mother belonged to different populations.

In connection with the latest inferences, I propose another solution to this issue. As noted, the Neanderthal genomic heritage in Denisova 11's father was the result not of direct interbreeding with Neanderthals, but of preservation of ancestral residual DNA. The Neanderthal mother of Denisova 11 originated not from the Altai Neanderthals, but from the later classic European Neanderthals—Chagyrskaya.

In order to clarify how the Denisova 11's mother is related to the two Neanderthals (Denisova 5 and Vindija 33.19), whose high coverage genomes are now available, the portions of the Denisova 11 genome fragments that matched the derived alleles from either of the two Neanderthal genomes were examined. In the genome of Denisova 11, the proportion of the derived alleles common with the genome of the Altai Neanderthal (Denisova 5) is 12.4 %, while in the genome of Vindija 33.19 this figure reaches 19.6 %, indicating that the mother of Denisova 11 comes from a population that is closer to Vindija 33.19 than to the Altai Neanderthals. The results of sequencing of mtDNA from the specimen of Chagyrskaya 8 support the fact that the mother of Denisova 11 belonged to the late classic Neanderthals, in particular, to the Chagyrskaya Neanderthals in the Altai. It was found that the genome of Chagyrskaya 8 has more derived alleles with the genome of the Denisova 11's mother than that of Vindija 33.19. Moreover, among the currently known Neanderthals, Chagyrskaya 8 is genetically most closely related to the mother of Denisova 11 (Mafessoni et al., 2020: 15133).

The proposed brief review of the genetic and morphological features of the Altai Neanderthals shows the insufficiency of data for a full characterization of this taxon. First of all, the question arises of when and where the so-called Altai Neanderthals migrated from, who are genetically different from Chagyrskaya Neanderthals, although show some common features with them.

A great achievement of paleogeneticists from the Max Planck Institute for Evolutionary Anthropology in Leipzig is the technique developed under the leadership of Svante Pääbo for the extraction of mtDNA directly from culture-bearing layers (Slon et al., 2017).

I am forced to note that our colleagues-geneticists, with whom we have been collaborating for many years, are not familiar with the results of archaeological research, and when discussing joint publications it is almost impossible to convince them of the fairness and validity of our viewpoint if it does not correspond to the sequencing results. Disagreements arise due to a lack of hard evidence in favor of one opinion or another, and more often due to the belief of researchers, representing different scientific disciplines, in the greater significance of their finds.

Paleogenetics is of great importance in the studies of evolution of the genus *Homo* and the origin of modern humans. But this branch of molecular biology is still very young. Its study methods are constantly being improved, new instrumentation is emerging, making it possible to extract the maximum amount of information about DNA from a fossil under study and, more recently, about DNA obtained directly from the lithological layer.

In Denisova Cave, Neanderthal DNA was extracted from cultural deposits in the Main Chamber, accumulated 168–86 ka BP (layers 19, 17, and 14); East Chamber, 205–172 ka BP (layer 14); and from the fossils found in the East Chamber (Denisova 9 – 118–150 ka BP, and Denisova 5 – 93–132 ka BP) (Jacobs et al., 2019: 596).

Establishing the time of the earliest habitation of Denisova Cave is extremely important for solving the issue of existence of the Altai Neanderthals. Z. Jacobs and her co-authors provide information about the extraction of Neanderthal mtDNA from layer 14 of the East Chamber, dated to the range from 193 ± 12 to 187 ± 14 ka BP (2019: 596, fig. 3). E. Zavala and co-authors attribute the sample from layer 14 to layer 11.4 (2021); but the reasons for this remain unclear. They make a reference to Appendix 1 to their publication, which should contain a corresponding explanation, but it also does not provide arguments justifying such a change. Moreover, another paper addressing the issues of collection of samples from the stratigraphic sequence for endogenous analysis and presenting the results of this analysis reports the extraction of Neanderthal mtDNA from layer 14 (Slon et al., 2017).

Jacobs argued that the cave was inhabited by Denisovans between 287 ± 4 (or at least 203 ± 14) and 55 ± 6 ka BP and later, while Neanderthals settled there in the range from 193 ± 12 to 97 ± 11 ka BP (Jacobs et al., 2019: 597). K. Douka and co-authors also came to the conclusion that Neanderthals settled in Siberia at the end of the warm stage of MIS 7 (about 190 ka BP) (2019: 644).

Researchers draw attention to "the presence of Neanderthal mtDNA before 175 ka" (Zavala et al., 2021: 403). Thus, Neanderthals started to inhabit the cave with Denisovans prior to 175 ka BP. I consider it necessary to cite another conclusion of the researchers: sediments of Denisova Cave, belonging to the chronological range of 130–100 ka BP (and maybe even a longer period, taking into account the hiatus in sedimentation recorded in the interval 97–80 ka BP), contain mtDNA and fossil evidence only of Neanderthals (Ibid.: 401).

The genetic age of the most complete mtDNA sequence of a Neanderthal from the Main Chamber (M65) is 140 thousand years (Ibid.: 401). The mother of Denisova 11 came from a population that was closely related to Neanderthals living in Europe (Vindija 33.19), rather than to the earlier Neanderthals from Denisova Cave. This points to the migrations of Neanderthals from the eastern and western parts of Eurasia about 120 ka BP (Slon et al., 2018: 113).

There are also other arguments of geneticists that confirm the Altai Neanderthal occupation of Denisova Cave in the late Middle Pleistocene. Ultimately, on the basis of genetic research, experts are convinced of the following: 1) Neanderthals began living in the cave prior to 175 ka BP; 2) Neanderthals and Denisovans inhabited the cave in succession, replacing each other; 3) there were long periods when the cave was inhabited exclusively by Altai Neanderthals; 4) the Middle Paleolithic industry of Denisova Cave could have been produced by Denisovans and Neanderthals.

All the four conclusions contradict the data derived during excavations in Denisova Cave and other Paleolithic sites in the Altai, as well as the available information about the origin of the Neanderthals, their material culture, and their dispersal in Eurasia in general. Let's consider some of the inferences.

Neanderthals gained their anatomical and genetic features in Western Europe no earlier than 200–150 ka BP. They produced the Mousterian industry, which is characterized (despite the great variability) by special techniques of primary reduction, particular types of tools, and methods of their manufacture. The dispersal of representatives of the Neanderthal taxon from Western Europe to the east of Eurasia proceeded slowly because of their small number. It took a long time to cover the huge distance of several thousand kilometers to the Altai. No remains of Neanderthals older than 100–120 thousand years have been discovered anywhere in Eastern Europe and West Asia so far. Perhaps the earliest Neanderthal fossil is a tooth from occupation layer 5c of Matuzka Cave in the Caucasus, but the geochronology of these deposits remains controversial. This particular layer has not been dated, but the age of the overlying layer 4d was determined to be 191 ± 29 thousand years (LU); the underlying layer 7 produced the IR-OSL date of 80.1 ± 8.3 ka BP (RLQG-2497-048); and layer 6, the date of 77.5 ± 6.1 ka BP (RLQG-2498-048) (Golovanova et al., 2022: 174). Consequently, the age of this fossil is not older than 100 thousand years.

Currently, no sites with the Mousterian industry or, even more so, Neanderthal anthropological remains older than 100 thousand years have been found either in Central Asia or the Urals, i.e., along the possible transit route of Neanderthal dispersal. The only find is the bone remains of a Neanderthal child from Teshik-Tash in Uzbekistan; these are younger than 70 thousand years old. Thus, the available archaeological data indicate that the assumption as to the settlement of Altai Neanderthals in Denisova Cave 175–150 ka BP is not supported by any evidence.

Archaeological materials convincingly prove that the early Middle Paleolithic industry discovered in the lowest archaeological layer 22 was produced by Denisovans. In the course of forty years of excavations at Denisova Cave, a huge amount of materials has been accumulated (Derevianko, Shunkov, Agadjanian et al., 2003; Derevianko, 2022; and others). The uniqueness of Denisova Cave lies in the fact that it contains 14 cultural layers in three "rooms": Main Chamber, East Chamber, and South Chamber. Culture-bearing layers yield different amounts of stone tools and bones of wild animals. The Upper Paleolithic layers also contain bone items and various kinds of personal ornaments made of stone, bone, and shells. Based on finds from culture-bearing layers, five stages of development of the lithic industry have been identified: early, middle, and late Middle Paleolithic, transitional Middle to Upper Paleolithic, and initial Upper Paleolithic. Most importantly, the entire set of evidence discovered in Denisova Cave is a homogeneous complex clearly demonstrating the development continuity of the industry at all the stages of the Middle Paleolithic, the Middle to the Upper Paleolithic, and the initial Upper Paleolithic. This well-developed industry was produced by the Denisovans. This population took part in the evolution of modern humans, and thus should be designated as *H.s. altaiensis* (Derevianko, 2012, 2019, etc.).

The continuity of the Denisova Cave lithic industry is evidenced by its homogeneity. There is no reason to assume that any representatives of another taxon (Altai Neanderthals) with a different industry lived in the cave. In the Middle Paleolithic, Denisovans and Neanderthals produced completely different lithic industries; hence, occupation of Denisova Cave by Neanderthals with a different industry would immediately lead to a change in the technical and typological complex of lithics. Therefore, the assumption as to the long-term residence of Neanderthals in the cave, and especially the identification of certain periods when only Neanderthals inhabited the cave, contradicts the archaeological evidence. Based on the results of DNA sequencing, the researchers conclude that in the chronological range of 130–100 ka BP Denisova

Cave was populated only by Neanderthals (Jacobs et al., 2019; Zavala et al., 2021). In the East Chamber of Denisova Cave, this interval is represented by cultural layers 12.3, 12.2, 12.1, and 11.4, which yielded the fossils of a Denisovan (Denisova 8), Altai Neanderthals (Denisova 9, Denisova 5) and a hybrid (Denisova 11); in the Main Chamber, by layers 17, 14.3, 14.2, and 14.1, which produced the mtDNA of Altai Neanderthals. Researchers of Denisova Cave have no doubt that the lithic industry of all the listed cultural layers is homogeneous, corresponds to the Denisova Middle Paleolithic culture, and is completely different from the Mousterian. All the archaeological materials indicate habitation of Denisova Cave exclusively by Denisovans with their Middle Paleolithic industry during that period.

Due to the fact that the results of genetic and archaeological studies reveal significant contradictions, I have proposed the following hypothesis (Derevianko, 2019, 2022). Denisovans and Neanderthals evolved on a single ancestral basis—*H. heidelbergensis*; representatives of this taxon with the Acheulean industry migrated from Africa to Eurasia ca 800 ka BP. The process of morphological and genetic development of Denisovans and Neanderthals took more than 500 thousand years. Moreover, in the course of dispersal in Eurasia, they interbred with late *H. erectus*. During the evolution of the genetic sequence, Denisovans and Neanderthals retained parts of their ancestral heritage for a long time. This is evidenced by the results of DNA sequencing of hominins from Sima de los Huesos in Spain, dating back to more than 400 ka BP: their mtDNA turned out to be close to Denisovan, and nuclear DNA to Neanderthal (Meyer et al., 2014, 2016). In the course of development of the genetic sequence, Denisovans could also retain part of their ancestral heritage for a long time.

Two finds are important evidence that forms the basis for the assumption of Neanderthal habitation in the cave: the phalanx of a toe (Denisova 5) from layer 11.4, and a small bone of a hybrid (Denisova 11) born from a Denisovan father by a Neanderthal mother, from layer 12.3. The occurrence of these fossils in culture-bearing layers 12.3 and 11.4 can be explained only by post-depositional disturbances of the stratigraphic sequence: these materials were shifted from the upper sediments to the underlying layers. This version is supported by the results of DNA sequencing of Denisova 11; according to them, the mother of this individual came from a population that was closer to Vindija 33.19 than to the Altai Neanderthals (Slon et al., 2018: 115). This suggests the possible interbreeding between a Denisovan father and a mother descended from the Chagyrskaya Neanderthal population, which migrated to Altai from Europe ca 60 ka BP (Derevianko, Markin, Kolobova et al., 2018). Furthermore, individual Chagyrskaya 8 is genetically most closely related to the mother of Denisova 11 (Mafessoni et al., 2020: 15133), which suggests its origin from the Chagyrskaya Neanderthals. According to geneticists, the split between the population to which the mother of Denisova 11 belonged and the population of Denisova 3 took place approximately 7 thousand years before the birth of the latter, i.e. ca 60–55 ka BP (Jacobs et al., 2019).

Individual Denisova 11 was a female, same as Denisova 5. It is very likely that the inhabitants of Denisova Cave accepted only women from the Chagyrskaya group of Neanderthals. The absence of the Mousterian industry in the cave in the period of 60–40 ka BP is a reasonable ground for this assumption. Small fossil fragments might have shifted from overlying layers into the underlying sediments, which is indicated by depositional stratigraphic changes. For example, researchers note that the Denisova 11 sample is very small in size and could have moved down from the overlying layer (Zavala et al., 2021).

Thus, all the above arguments allow us to draw the following conclusion: the identification of Altai Neanderthals in Denisova Cave on the basis of genetic studies is not supported by archaeological materials from Denisova Cave and other Middle Paleolithic sites of the Altai, as well as by the data of analyses of anatomy and genome of the Neanderthal taxon in Western Europe and the time of dispersal of Neanderthals in Eurasia.

Conclusions

The creative team of experts in four scientific disciplines—archaeologists, physical anthropologists, paleogeneticists, and geochronologists—is of utmost importance for solution of many issues of the evolution of the genus *Homo*, development of new taxa, dispersal of new human populations over Europe, and relationships between the indigenous population and the migrants. Interdisciplinary research requires that the involved scholars show respect for the findings of their colleagues, especially in discussion of controversial issues.

I have always acknowledged that many significant discoveries have been made owing to the creative collaboration between Svante Pääbo and his team and the Institute of Archaeology and Ethnography SB RAS. The most important breakthrough is the identification of a new taxon—Denisovans. Creative collaboration between scientists is important and effective; it can be even more fruitful if the data of archaeological research are fully taken into account in the discussion of final conclusions.

This article is based on the assumption that hominins were an open genetic system and were able to interbreed and give birth to fertile offspring throughout the almost three-million-year evolution of genus *Homo*. This idea is based on the existence of three hominin taxa at the final stage of the phylogenetic history of the genus *Homo*, 200–100 ka BP: early modern humans in Africa, *H. sapiens neanderthalensis* in Europe; *H. sapiens denisovan* in Central and Northern Asia. Representatives of these taxa interbred, and the hybrids were fertile. And this was not interspecific, but intraspecific assimilation. Consequently, throughout the entire evolutionary process from *H. erectus* to *H. sapiens sapiens*, hominins retained an open genetic system and ability to assimilate, and were able to produce fertile offspring.

From my point of view, the most debatable issues are the identification, on the basis of genetic studies, of the Altai Neanderthals, who migrated to Southern Siberia from Europe prior to 175 ka BP; and the possibility of alternate occupation of Denisova Cave by the Altai Neanderthals and the Denisovans. I have made my conclusions on the basis of archaeological realities, and I hope that future research will clear up these issues.

Neanderthals and Denisovans had a common ancestor—*H. heidelbergensis*, who was formed in Africa ca 900 (800) ka BP on the ancestral basis of late *H. erectus*. During the same period, *H. heidelbergensis* with the Acheulean industry migrated to the Near East in Eurasia. About 700 (600) ka BP, part of them, with the Acheulean industry, started settling in Europe; as a result of assimilation with the indigenous population (*H. antecessor*), natural selection, and regional specificity of hominins, 200–150 ka BP, a new taxon was developed—*H.s. neanderthalensis*.

1. At such an early time, Neanderthals could not have expanded so far east up to the Altai from the center of their origin in Western Europe, because morphological and genetic evolution of this taxon was finished no earlier than 200–150 ka BP. Moreover, no anthropological remains of Neanderthals nor archaeological sites with the Mousterian industry older than 100–120 thousand years have been discovered in Eastern Europe; and in the transit region of Central Asia, only the anthropological remains of a child from Teshik-Tash Cave younger than 70 thousand years have been found. The dispersal of Neanderthals over the Altai prior to 100 ka BP was possible only through charter flights connecting Western Europe with Denisova Cave.

2. Occupation of Denisova Cave simultaneously or alternately by Denisovans and Altai Neanderthals, moreover, habitation of the cave exclusively by Neanderthals ca 130–100 ka BP should have been supported by the occurrences in the cave of two lithic industries—the Denisovan Middle Paleolithic and the Neanderthal Mousterian, with different technical and typological characteristics. The stratigraphic sequence of Denisova Cave (layers 22–11) clearly shows the continuity in the development of the Middle Paleolithic industry from the early stage (300 ka BP) to the initial Upper Paleolithic of 55 (50)–45 ka BP. And there is absolutely no basis for the assertion as to the presence of the Mousterian industry in the stratigraphic sequence of the cave; hence, the possibility of habitation of the cave by representatives of any taxon other than Denisovans is excluded. Only with the emergence of Chagyrskaya Neanderthals in the Altai ca 60 ka BP, their assimilation with the indigenous population, the Denisovans, became possible.

3. The only possible explanation of the presence of Neanderthal mtDNA in the culture-bearing layers of Denisova Cave is the specific anatomical and genetic evolutionary development of the Neanderthal and Denisovan taxa. Both of them originated from a single ancestral basis—*H. rhodesiensis/heidelbergensis*. It was developed in Africa ca 900 (800) ka BP; then, ca 800 ka BP, part of this population (*H. heidelbergensis*), with the Acheulean industry, moved to the Near East (Gesher Benot Ya'aqov). After 700 (600) ka BP, a part of the *H. heidelbergensis* population, with the Acheulean industry, migrated to Europe and mixed with the indigenous *H. antecessor* population. In the process of assimilation of these two taxa, natural selection, adaptation to changing environmental and climatic conditions in Europe, new taxon *H.s. neanderthalensis* evolved over 500 thousand years, by 200–150 ka BP. The Neanderthal taxon gradually formed the increasing amount of derived Neanderthaloid morphological features and the Neanderthal genetic sequence. However, Neanderthals also retained some ancestral genetic heritage for a long time. This is confirmed by the results of mtDNA sequencing of hominin remains from Sima de los Huesos (Spain), dating back to

more than 400 ka BP. These hominins had Denisovan mtDNA (although Denisovans never settled in Europe) and Neanderthal nuclear DNA.

H. heidelbergensis from the Near East began to migrate to East Asia ca 400–350 ka BP. In Central Asia, they met the indigenous population—late *H. erectus*; a as a result of the assimilation of two taxa, natural selection, adaptation to changing environmental conditions, over the course of 300–200 thousand years, a new taxon emerged—*H.s. denisovan*. We don't know its morphology yet. However, it is known that part of the ancestral heritage was preserved in the emerging genetic sequence of the new taxon. This is precisely what was reflected in the Neanderthal mtDNA extracted from the cultural layers of the cave. In the sample from layer 15 of the East Chamber, in the Denisovan genomic sequence, 5 % of the Neanderthal genetic heritage was recorded (Slon et al., 2017: 3), which indicates that not only mtDNA, but also nuclear DNA of Neanderthals was preserved in genome of the emerging Denisovan taxon.

The proposed scenario for the genesis of the Denisovan taxon and the explanation of identification of the Neanderthal mtDNA in the deposits of Denisova Cave contradict the findings of genetic studies. But the available archaeological materials exclude the identification of any group of the Altai Neanderthals in the Altai apart from the Chagyrskaya Neanderthals.

The miniature bone, discovered in layer 12.3, of individual Denisova 11, whose father was a Denisovan and whose mother was a Neanderthal, is considered a confirmation of the assumption that Denisova Cave was inhabited by the Altai Neanderthals. The occurrence of this sample in layer 12.3 is explained by depositional stratigraphic disturbances. The age of the find is 50–60 thousand years. This age estimation confirms the assumption that the mother of the Denisova 11 hybrid was genetically close to Chagyrskaya Neanderthals, rather than to the Altai Neanderthals. Among the currently known Neanderthals, individual Chagyrskaya 8 is most closely related to the mother of Denisova 11 (Mafessoni et al., 2020: 15133). Neanderthals who migrated from Europe ca 60 ka BP interbred with Denisovans, and produced fertile offspring. The mtDNA sequenced from the female phalanx of the fourth or fifth toe (Denisova 5) from layer 11.4 of the East Chamber of Denisova Cave and compared with the mtDNA of other Neanderthals has shown the closest relationship with the mtDNA of a child from Mezmaiskaya-1 Cave (Caucasus) aged ca 60 thousand years. This individual possibly belonged to the late classic European Neanderthals, too. The fossil comes from the overlying layer, same as Denisova 11 does. On the basis of archaeological findings, we can conclude: the Altai Neanderthals identified by genetic studies are a myth, not a reality.

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