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The Origin of *H. s. denisovan* and Their Dispersal Across Iran

*Before the early 2000s, anthropologists spoke of two taxa existing in the Late Middle and Early Upper Pleistocene: anatomically modern humans in Africa and Neanderthals associated with the Mousterian industry in Eurasia. Therefore, all Eurasian Paleolithic sites dating to that period were believed to be Mousterian and were associated with Neanderthals. In 2010, owing to the sequencing of mtDNA from a fragment of the distal phalanx of the hand found in Denisova Cave, a third species was introduced, genetically different from both anatomically modern humans and Neanderthals. This new taxon was termed *H. s. denisovan*—or simply Denisovan. Further studies showed that this population dispersed in the Late Middle and Early Upper Pleistocene across vast territories of Central and Southeast Asia. A question arose as to where Denisovans had originated and which routes they had taken to get to the Altai. A series of articles forthcoming in this journal will address these questions. The first of them focuses on the origin of Denisovans on the basis of *H. heidelbergensis* and on their migration via Iran to Central Asia.*

Keywords: *H. heidelbergensis, H. s. neanderthalensis, H. s. denisovan, Early and Middle Paleolithic industries.*

Introduction

Since 1983, archaeological studies of nine cave and eleven open-air sites with long historical and cultural stratigraphic sequences have been carried out by researchers from the Institute of Archaeology and Ethnography of the Siberian Branch of the Russian Academy of Sciences, with the involvement of scientists from various other disciplines. These long-lasting and large-scale annual works resulted in accumulation of extensive material on the archaeology, geology, chronostratigraphy, paleontology, and paleogeography of the Altai. The most significant diagnostic material was collected during excavations in Denisova Cave; in its lowermost cultural layer 22.2, dated to the range of 282–256 ka BP (RTL-548), a biface reminiscent of the Acheulean handaxe was discovered. In 2001, in the course

of analyzing the collected material, I came to a number of ideas that were subsequently reviewed, some of them got additional confirmation and served as a basis for further inferences (Derevianko, 2001).

1. Since the lowermost cultural layer yielded bifacially worked artifacts, the lithic industry of Denisova Cave was attributed to the Acheulean, Middle Paleolithic.

2. The closest parallels not only to the Middle, but also to the Upper Paleolithic industry of the Altai Mountains can be traced in the Levant. A striking similarity in the evolution of the industries can be explained only by a common more ancient basis. The absence of indigenous population in the Altai Mountains during the migration of hominins from the Levant to the region allowed them to preserve more primary features in the industry than in the transit territories of the Central Asian-Kazakhstan region inhabited at that time by man.

3. This industry provides the sufficient grounds to trace its development from the early to the terminal stage and the transition from the Middle to the Early Upper Paleolithic. In the initial Upper Paleolithic, two development trends have been distinguished—the Ust-Karakol and Kara-Bom, which were formed on the basis of terminal Middle Paleolithic industries.

4. The Altai lithic industry developed on the basis of the Acheulo-Yabrudian complex of the Levant. The migration route of hominins from the Levant to the Altai passed through Central Asia; this is supported by Mongolian lithic industries sharing many features with the Denisova industry. In Uzbekistan, westwards from the Altai, the Obi-Rakhmat culture was identified at the Obi-Rakhmat site; its industry, same as the Denisova, showed the parallel flaking strategy dominating in core utilization, with elongated blade blanks and microblades being the target products.

5. Judging by the sparse anthropological finds in the late 1990s, it was concluded that the second wave of hominin migration from the Near East was conducted by the early humans, archaic *H. sapiens*, or the evolutionary lineage that gave rise to the anatomically modern human (Ibid.: 97).

In 2010, the sequencing of mitochondrial and nuclear DNA from Denisova 3 has revealed that a tiny nail-bone fragment belonged to a new taxon that was genetically distinct from both modern humans and Neanderthals (Krause et al., 2010; Reich et al., 2010). Thanks to the genetic studies, it has been established that the Denisova industry belonged to a newly identified taxon named Denisovan, after the place of its discovery.

The question of the origin of the Denisovans has arisen. I am sure that this population with the Acheulo-Yabrudian industry migrated from the Levant through the Iranian Plateau and Central Asia to the Altai, therefore, the homeland of this taxon must be sought in the Near East.

Origin of *H. s. denisovan*

I have addressed the issues of the origin of *H. s. denisovan* in various publications (Derevianko, 2019, 2020, 2022; Derevianko, Shunkov, Kozlikin, 2020; and others); therefore, I will briefly dwell on it. J. Rightmire put forward a hypothesis as to the process of speciation of a new taxon *H. heidelbergensis*, which took place in Africa ca 800 ka BP or somewhat earlier (1996, 1998b). Many experts in physical anthropology supported his hypothesis, but designated the new taxon differently: *H. heidelbergensis*, *H. rhodesiensis*, *H. sapiens* (Rightmire, 1996, 1998a, b; 2008, 2009a, b; 2013; Tattersall, Schwarz, 2000; Bräuer, 2001a, b; Hublin, 2001; Stringer, 2002; Foley, Lahr, 2003; and others). Discussions about the role and place of this

taxon in the evolution of the genus *Homo* continue to this day (Athreya, Hopkins, 2021; Roksandic et al., 2022).

H. rhodesiensis and *H. heidelbergensis* belonged to the same biological species evolved from the ancestral base of *H. erectus*, but they had different phylogenetic histories: *H. rhodesiensis* settled in Africa, and 200–150 ka BP provided the ancestral base for the formation of early modern humans; *H. heidelbergensis*, with the Acheulean industry, migrated to Eurasia ca 800 ka BP, and became ancestral for *H. s. denisovan* and *H. s. neanderthalensis*. Moreover, the available DNA sequences showed that these three taxa retained an open genetic system—they were able to interbreed and produce fertile offspring (Derevianko, 2019).

The split of *H. erectus* into two lineages (*H. rhodesiensis/heidelbergensis*) was the most important event in the evolution of the genus *Homo*; it marked the beginning of the formation of modern humans in Africa, and Neanderthals and Denisovans in Eurasia. Genetic studies show that this split occurred in the range of 812–793 ka BP (Reich et al., 2010; Meyer et al., 2012)*. The migration of *H. heidelbergensis* with the Acheulean industry to Eurasia is confirmed by the lithic industry from the site of Gesher Benot Ya'aqov, which has been studied for many years in Israel (Goren-Inbar et al., 2018).

The genetic and morphological evolution of modern humans in Africa took a long period of time, about 600 thousand years. For Neanderthals and Denisovans, in Eurasia this was long, too. Moreover, both branches continued to retain some features of their common ancestral genetic heritage (Derevianko, 2024).

Around 700 ka BP, tribes of *H. heidelbergensis* with the Acheulean industry from the Near East (Levant) started their dispersal across Europe and South Asia. In Europe, as a result of assimilation with late *H. erectus* (*H. antecessor*), the process of evolution of the Neanderthal taxon began, since representatives of these taxa belonged to an open genetic system (Derevianko, 2019, 2022), as well as owing to natural selection and adaptation to changing environmental conditions. The second split of the late *H. heidelbergensis* lineage occurred around 400 ka BP. At that time, part of *H. heidelbergensis* practicing the Levallois primary reduction technique settled in Europe, where they underwent further evolution to the Neanderthal taxon with the Mousterian industry, which genetically and morphologically evolved ca 200–150 ka BP (Derevianko, 2024). The other part of *H. heidelbergensis* dispersed in the east of Asia 400–

*There is no general consensus on the time of divergence of modern humans from Neanderthals and Denisovans, as well on the divergence between Neanderthals and Denisovans. This is explained by differences in the determination of the time of split of great apes and Australopithecus, and in the assessment of frequency of mutations per year, and other reasons.

350 ka BP; they met the indigenous population—late forms of *H. erectus* with a pebble-flake industry. Both taxa belonged to a genetically open system and could interbreed; hence, fertile offspring were born, and a diffusion of lithic industries occurred. The occupation of the vast territory of eastern Iran and Central Asia continued over 100–150 thousand years. In the course of dispersal, several crucial processes took place: assimilation between the migrants and the indigenous population, natural selection, adaptation to changing environmental settings, and genetic and morphological evolution of a new taxon—Denisovans and their lithic industry. About 300 ka BP, this evolving taxon began to settle in the Altai. In the lowermost culture-bearing layer 22.2 at Denisova Cave, along with the Early Middle Paleolithic industry, a deciduous molar tooth was found. The DNA sequencing of the molar showed that it belonged to a Denisovan child. This find indicates that Denisovans were the first settlers in the cave.

Thus, three stages can be distinguished in the process of evolution of Denisovans. The first stage was the migration of *H. heidelbergensis* from Africa to Eurasia ca 800 ka BP. This marked the genetic split of a single ancestral taxon *H. erectus* into modern humans evolving in Africa, and Neanderthals and Denisovans who evolved in Eurasia. The second stage was the dispersal of one part of late *H. heidelbergensis* from the Near East (Levant) ca 400 ka BP to Europe, and of the other to Asia, which led to the genetic separation between Neanderthals and Denisovans. The third stage was the genetic and morphological formation of the Denisovan taxon in the process of migration of late *H. heidelbergensis* from the Near East (Levant) to Central Asia in the period of 400–350 ka BP and their assimilation with the indigenous population (Derevianko, 2019, 2022).

Dispersal of late *H. heidelbergensis* across Iran and the initial stage of development of Denisovans

Dispersal of hominins across Iran during the Pleistocene depended largely on environmental changes. Iran is a mountainous country located mainly in the subtropical zone, between 25 and 40° N. The West Asian highlands demonstrate a great diversity of landscapes. Their main feature is the combination of high mountain ranges alternating with valleys where the arid climate prevails, with an excess of evaporation over influx of moisture. Mountain ranges with individual peaks reaching a height of 4–5 thousand meters form two huge arcs that stretch across the entire territory of Iran: the northern range runs from the Iran-Turkey border to the east along the Caspian coast; the southern range stretches from western and eastern Azerbaijan to Pakistan in the southeast. The

vast deserts of Dasht-e Kavir, Dasht-e Lut, and others are located between these orographic systems.

In the Pleistocene, hominins could have migrated to South, East, and Southeast Asia from Africa only through the Iranian Plateau. During the cool periods, the climate was arid here, and the drylands of the Iranian Plateau became unsuitable for habitation and hardly passable for hominins heading to the east of the Asian continent. At that period, the most beneficial west to east routes for hominins were those along the border of the Kavir Desert, passing through the northern foothills of the Alborz Mountains and the plains of the Caspian Lowland; the southern route passed along the coast of the Persian Gulf. There are about 60 deserts of varying sizes in Iran. The availability of lithic resources and permanent water sources was of great importance for the dispersal of hominins (Shoaei et al., 2023).

During almost 70 years of studying the Iranian Paleolithic, only 13 Early Paleolithic, 30 Middle and 39 Upper Paleolithic sites have been discovered in the area of transit for the hominins exiting Africa and moving to South, Central, and East Asia (Ibid.; Shoaei, Nasab, Petraglia, 2021). During the same time, in India, several hundred Early and Middle Paleolithic sites have been discovered; and in Mongolia, the Joint Soviet-Mongolian and Russian-Mongolian expeditions have found about one thousand Stone Age sites in the recent 40 years alone.

Acheulean sites in Iran

The majority of the Acheulean sites in the region have been identified as short-term camps with a disturbed surface cultural layer, containing small amounts of finds. The sites were discovered mainly in the western part of the country.

In northwestern Iran, in the Sahand Range (Central Iranian Range), on river terraces at an altitude of 1400–1800 m, seven open-air localities and three cave sites were examined, yielding a small number of Lower Paleolithic artifacts. On the terraces, cultural remains were redeposited; and near the caves, artifacts lay on the surface. The assemblages of lithic artifacts include choppers, pebble cores, retouched flakes, polyhedrons (Fig. 1, 4), spheroids, and a pick-type tool (Fig. 1, 7).

Several Paleolithic sites were established along the Mahabad River, to the south of Lake Urmia, southwards of the Sahand Range. Among these, the Shiwatoo site presents the greatest interest (Jaubert et al., 2006). It is located on the left bank of the Mahabad River, at an altitude of 1380 m asl. Lithic artifacts (ca 100 spec.) were scattered over an area of approximately 1 hectare. Most of the artifacts were made of andesite, quartz, and basalt boulders. The finds include single- and multiplatform

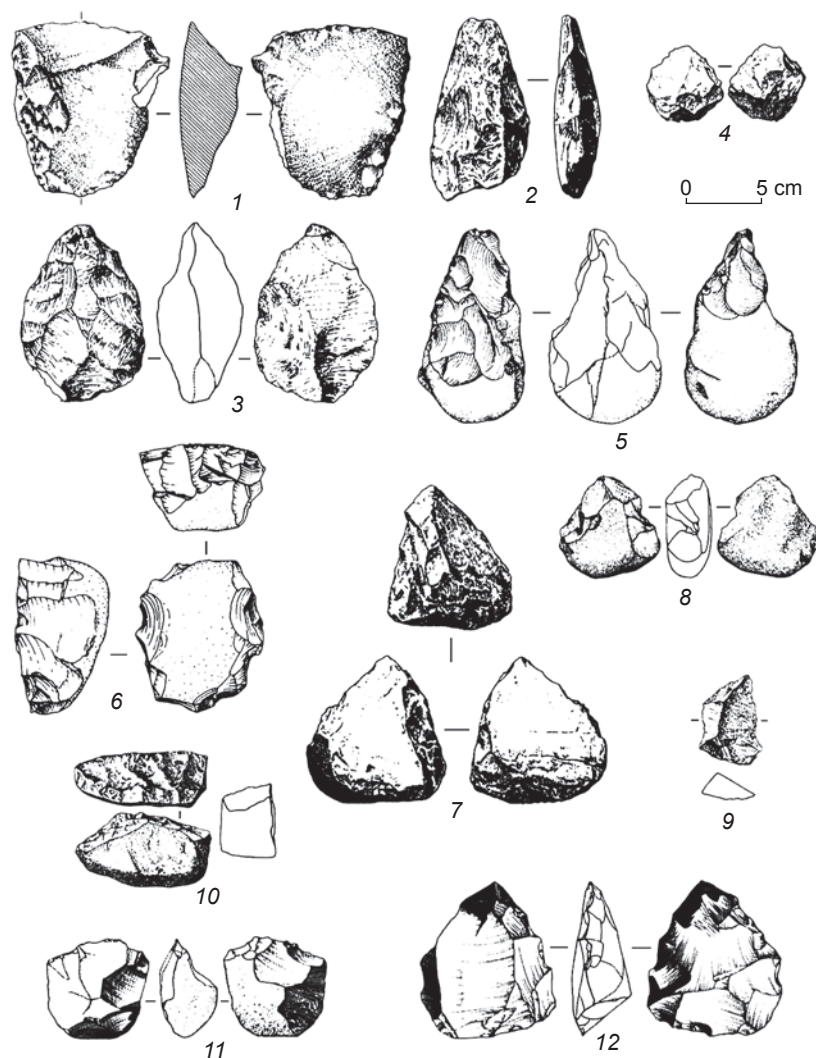


Fig. 1. Lithic tools from the sites with the Acheulean industry (after (Biglari, Jahani, 2011)).

1 – Shiwato; 2 – Quri Gol; 3, 6 – Ganj Par; 4, 7 – Sahand; 5, 8 – Amar Merdeg; 9, 10 – Kashafrud; 11, 12 – Pal Barik.

1 – cleaver; 2, 3, 5, 12 – bifaces; 4 – polyhedron; 6 – end-scraper on core; 7 – trihedron (pick); 8 – pointed chopper (partial biface); 9 – flake; 10 – single-platform core; 11 – chopping tool on core.

cores, discoidal cores bearing negative scars of radial flaking, and pebble cores. A cleaver-like tool made on a cortical flake was identified (Fig. 1, 1). One of its edges bears the continuous negatives of small flake removals and retouch; the opposite edge bears discontinuous traces of flaking.

In the southwest of Iran, in the hilly Zagros region, approximately 10 km southwest of the Kermanshah Valley, on one of the terraces of the Qarasu River at an altitude of 1260 m asl, the expedition headed by R.J. Braidwood (1960) found a biface and a large number of flakes and cores. These lithic artifacts clearly belonged to various chronological periods; most of them referred to the Late Stone Age. The biface, probably Acheulean, is 16.5 cm long, almond-shaped. In 2006, two bifaces,

Levallois cores, and debitage were found 25 km from the village of Gakia, near Harsin.

Some 150 km southeast of the village of Gakia, at the foots of the southwestern slopes of Zagros, in the Amar Merdeg area, small amounts of stone tools were found among pebbles on tops of hills at an altitude of 200–300 m. Chopping-like cores prepared on rounded pebbles are noteworthy. Some of them, after being used as cores, could have served as heavy-duty chopping tools. There are pebbles with traces of unifacial treatment, which the researchers called “pointed choppers” (partial bifaces?) (Fig. 1, 8). The site also yielded prepared cores of various types, including Levallois, and four bifaces. One triangular biface bears various-sized signs of careful continuous trimming over one face, except for the proximal end retaining pebble crust (Fig. 1, 5). The opposite end is worked by small flake removals and retouch. All lithic artifacts are made from local raw materials—chert, sandstone, and quartzite pebbles.

The Acheulean site of Pal Barik is located 65 km from the Kermanshah Valley, in western Iran. It sits on a flat hilltop, at an altitude of 975 m asl. An area measuring 50 × 80 m yielded heavily patinated lithic artifacts (89 spec.). The cores included single- and double-platform, discoidal, and orthogonal varieties. Side- and end-scrapers, denticulate-notched tools, chopping tools (Fig. 1, 11), and other implements were fashioned on flakes.

There was also a small biface (Fig. 1, 12) showing traces of large and small flake removals all over the surface; its distal end was especially well treated by small flake removals and retouch.

In northern Iran, 1 km southeast of Lake Quri Gol, a sub-triangular biface with a truncated top made of quartzite sandstone was found (Fig. 1, 2). Its surface showed flaking scars of various sizes, was covered with a deep patina, and smoothed.

Typologically, the lithic assemblages from the three Acheulean sites in central part of western Iran have much in common. The main difference is that at Gakia and Amar Merdeg, Levallois cores were often used for primary reduction, while at Pal Barik only one small core of this type was found.

An Acheulean site was discovered in the western skirt of the Desert of Dasht-e Kavir, in central Iran. The site of Geleh is located at an altitude of 1100 m asl, on the eastern slopes of the Karkas Mountains. Two shallow riverbeds run to the east and west from Geleh. A total of about 30 lithic artifacts were collected here (Biglari, Shidrang, 2006). The assemblage includes large flakes and pebble cores up to 27 cm long. Primary flakes are large in number. Some flakes demonstrate signs of discontinuous retouch. The category of large prepared flakes includes cleaver-shaped artifacts made on primary flakes, and a large broken biface, with its faces worked by flaking and the lateral edges by retouch.

The earliest Acheulean site, Ganj Par, is located in the western part of the Alborz Range, in northern Iran (Biglari, Heydari, Shidrang, 2004; Biglari, Shidrang, 2006; Biglari, Jahani, 2011). It is situated on the terrace of the Sefid-rud River on the Rostamabad Plain. The terrace rises 230 m asl and 90–100 m above the valley floor. The site is located above terrace IV; researchers do not exclude that the archaeological materials were previously deposited in more ancient terraces (Biglari, Jahani, 2011).

During three visits of archaeologists, about 140 lithic artifacts were discovered at this site, with an area of ca 0.5 hectare, judging by the distribution of finds. The artifacts were made of red sandstone, quartzite, andesite, basalt, and tuff. The well-rounded pebbles and boulders lying on the surface and in the river alluvium served as blanks. The share of small flakes is minor among the finds, which suggests that most of these were transported by water currents from their original location to another place.

The assemblage contains single- and multiplatform, discoidal, amorphous, and bipolar cores. These were made mostly from silicified limestone. The tool kit includes choppers fashioned on cores, side-scrapers, hammerstones, bifaces (Fig. 2, 1), cleavers (Fig. 2, 2), and a trihedron. The sub-triangular and oval shaped bifaces were prepared on large flakes and pebbles. Their both faces show negative scars of large and medium-sized flake removals, the edges were additionally prepared with retouch. The cleavers were made on flakes (Fig. 2, 2). Carinated side-scrapers are typical of the Early Paleolithic sites in the Caucasus (see Fig. 1, 6). Researchers point to certain common features of the Ganj Par lithic industry with those of the Caucasian Acheulean (Biglari, Shidrang, 2006: 166).

Darband cave site was discovered 16 km east-southeast of Ganj Par. This is a single-chamber cave 21 m long, with the entrance zone 7 m wide (Ibid.). The lithic collection includes side-scrapers on flakes, core-like and end-scrapers, notched tools, borers, a chopper on core, and retouched flakes. Most of the stone products are heavily patinated. The presence of a flake that could have been removed from a biface suggests that the biface

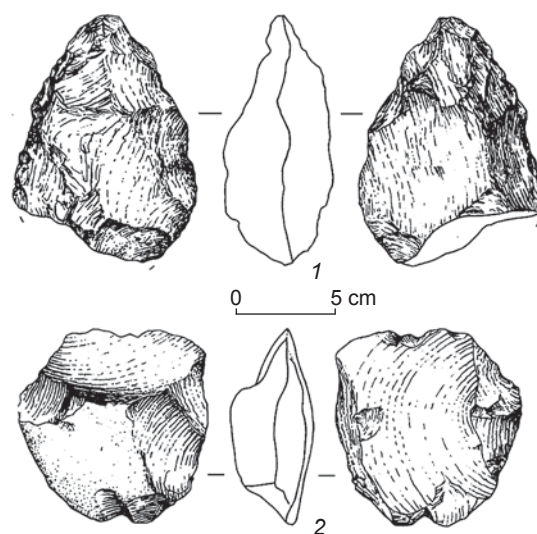


Fig. 2. Biface (1) and cleaver (2) from the site of Ganj Par (after (Biglari, Jahani, 2011)).

was used as a core; hence, the Acheulean technique was practiced at the site (Ibid.). Notably, the faunal remains in the cave were dominated by bones of the cave bear of the Caucasian population.

At most Acheulean sites where culture-bearing layers were either destroyed or scattered on the surface, only a few dozens of artifacts were discovered: cores, flakes, choppers, side-scrapers, as well as solitary bifaces and cleavers. Thus, all these sites are non-stratified and are characterized by a small number of stone tools.

Two types of Acheulean sites have been established in Iran: the first with large cores from which large flakes were removed and used as blanks for tool manufacturing, including flakes with traces of bifacial working, resembling cleavers and bifaces; the second with cores and blanks typical of the Levallois strategy of primary reduction. These archaeological materials apparently evidence two migration flows of hominins from the Near East to Iran. The first migration wave was associated with the dispersal of *H. heidelbergensis* with the Acheulean industry, moving from the Levant to Iran and South Asia around 700 (600) ka BP. The technical and typological characteristics of the Acheulean industry was similar to the industry of Gesher Benot Ya'aqov, which was based on removing large flakes from large cores and on manufacturing bifacially prepared tools—bifaces, cleavers, and pick-type tools (picks, hoes). The second wave was associated with the dispersal of late *H. heidelbergensis* (in the course of morphological and genetic evolution towards Denisovans), moving from the Levant to Iran and South Asia around 400–350 ka BP; this explains the appearance of Acheulean sites with the Levallois technique of primary reduction in these territories.

Summarizing the data of the review of the Early Paleolithic of Iran, and the Acheulean industry in particular, we should emphasize the paucity of Acheulean sites so far discovered in this region. There are two main reasons for this. One of them is the insufficient amount of knowledge on the regional archaeology. The other reason is rather harsh living conditions, especially during cold periods, when the arid climate became even more arid, hominins could not survive at such places for a long time and migrated to more favorable areas. The small number of stratified complexes is a problem that requires further study, because Iran during the Pleistocene could have been the only transit territory for the migration of hominins from Africa and the Near East and their dispersal over the eastern regions of the Asian continent.

Middle Paleolithic sites in the territory of Iran

In the area under consideration, 30 Middle Paleolithic sites have been identified (Shoae et al., 2021). Despite the hypothesis that in the second half of the Middle Pleistocene small hominin populations could have settled in this region even in the most extreme environmental conditions, it is hardly possible to trace the continuity between the Early and Middle Paleolithic industries because of the small number of Acheulean sites.

The lithic industry attributable to the terminal stage of the Middle and first half of the Upper Pleistocene in Iran is often correlated with the Zagros Mousterian, although it differs significantly from the European Mousterian in many technical and typological features. Taking this into account, I believe it is correct to attribute this industrial complex to the Zagros Middle Paleolithic. The industrial complexes from the mentioned sites show the greatest similarity with those of the Levantine Middle Paleolithic. Nevertheless, owing to the small number of anthropological finds, I do not rule out that both Denisovans and Neanderthals could have settled in Iran in the Late Middle to the first half of the Upper Pleistocene. It is quite understandable that all researchers associate the Zagros Mousterian only with Neanderthals: before the discovery of the Denisovan taxon, the Middle Paleolithic of Eurasia was associated mainly with the Mousterian industry and Neanderthals. The study of the Denisovan taxon is just beginning, and I am sure that in the future many generally accepted points of view on the Middle Paleolithic of Eurasia will be revised, because the Denisovans dispersed over a vast territory of the Asian continent.

The largest number of Late Pleistocene sites have been discovered in the western and northwestern parts of Iran, especially in the Zagros Range: the ecological conditions in the intermountain depressions were

quite beneficial for human habitation. The areas of the Kermanshah and Khorramabad valleys and others in the western Central Zagros were a kind of refuge for hominins. Mountain ranges prevented penetration of cold air masses to the valleys. Archaeological studies have shown the availability of permanent sources of fresh water and sources of high-quality raw materials for the manufacture of lithic tools in the valleys. During the Late Pleistocene, a relatively dry and cool climate prevailed in the valleys (Van Zeist, Bottema, 1977; Kehl, 2009). The environmental conditions in Iran were especially beneficial for hominin habitation during the period corresponding to MIS 5 (Shoae et al., 2023).

The sites in the caves and rock shelters of Kunji, Warwasi, Bisitun, Yafteh, Ghamari, Arjeneh, Mar-Aftab, Mar-Dodard, Buf, Qaleh-Bozi, and others provided the greatest amount of information. One of the key Middle Paleolithic sites is Bisitun Cave; it was excavated by C.S. Coon in 1949 (Coon, 1951). Archaeological materials from this rockshelter were also studied by J. Skinner (1965) and H. Dibble (1984).

Dibble provided the most profound and comprehensive analysis of the Bisitun lithic industry; he drew attention to the drawbacks made by Skinner when studying the excavation materials. Dibble noted that many cultural remains were discovered by researchers in the 1930s and 1940s, when excavation methods were far from being perfect and stratigraphy issues remained unresolved; consequently, there was a problem of identifying the exact position of artifacts in lithological layers relative to each other (Ibid.: 24). These problems evidently existed during the excavations carried out by Coon. He reported that in two weeks, 39 m³ of cave deposits were removed in Bisitun Cave, while in Denisova Cave, for example, it takes three months to excavate no more than 3 m³. Removal of Denisova deposits is carried out in strict accordance with stratigraphy, interlayers 3–5 cm thick are removed in order to accurately record the position of each find in the sequence. After the removal of cultural layers, all loose sediments are washed and sieved in order to collect the smallest archaeological finds.

Dibble conducted a thorough analysis of the Bisitun lithic industry. The vast majority of artifacts in the collection were side-scrapers of various shapes (Fig. 3, 1–3, 5, 8). Most of these were made on flakes, mainly Levallois flakes, and showed traces of careful retouching. Dibble identified three types/classes of side-scrapers: longitudinal, double, and convergent.

A small number of other tools were also found in Bisitun Cave. All the burins, except one, were made on fragments of retouched items (Fig. 3, 4, 6, 7). These tools can be classified as combination tools. Dibble identified more than ten typical borers in the tool kit, seven of which were made on flakes. Among the small number of typical and atypical backed knives, the scholar distinguished a

Fig. 3. Lithic tools from Bisitun Cave (after Dibble, 1984)).

1–3 – convergent side-scrapers; 4, 6, 7 – burins; 5 – tool with the retouched distal end and the pointed tip prepared by multifaceted retouch on the ventral face (Kostenki-type knife); 8 – convergent side-scraper; 9 – small Levallois flake with the truncated proximal end; 10–15 – Levallois blades.

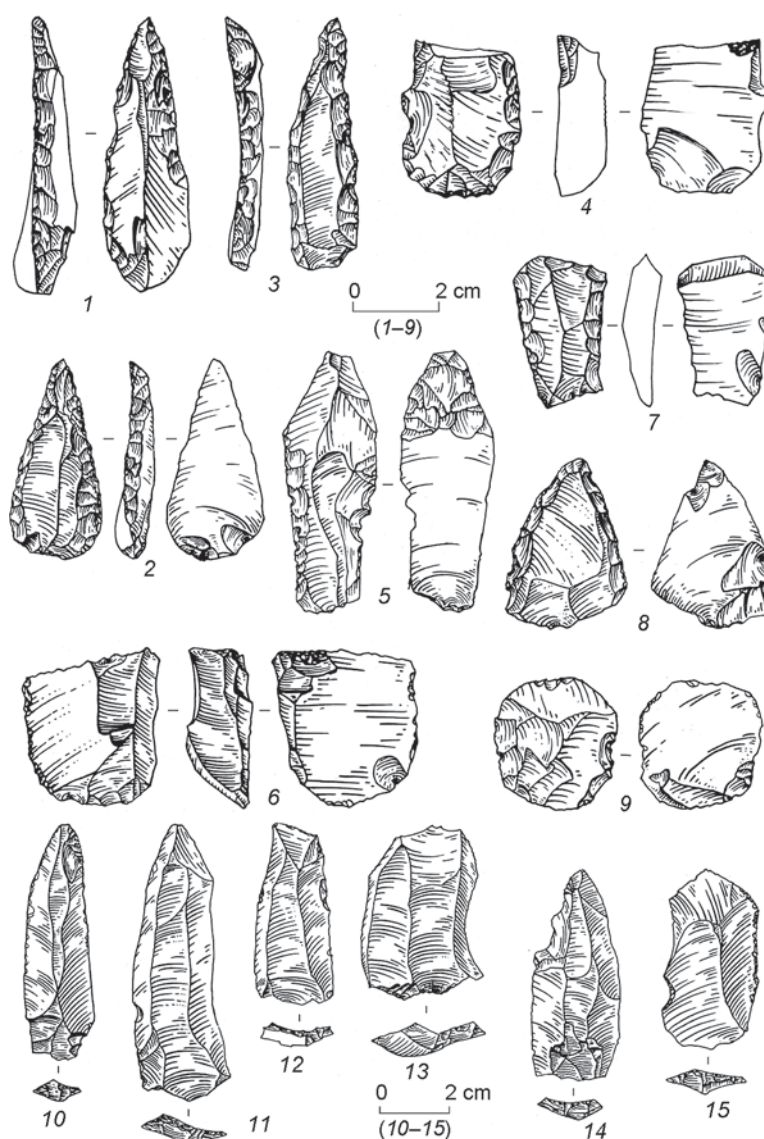
special Kostenki type (Fig. 3, 5). Based on the retouch over ventral surface of the distal ends of these items, Coon classified the artifacts as points that were attached to shafts.

According to Dibble, the Bisitun reduction technique is characterized mainly by unidirectional and bidirectional knapping. The share of blades (Fig. 3, 10–15) is small, while that of laminar flakes is large.

The role of Levallois reduction in producing blanks is important for understanding the character of the Bisitun industry. Skinner recorded only 15 atypical Levallois flakes in the collection, with an IL_{ty} index of 2.4. Dibble identified more than 100 typical and atypical Levallois flakes, which, in his opinion, corresponds to IL_{ty} of 10.6, and the Levallois index value including the share of the retouched Levallois flakes is 55.8 for the entire collection. Dibble concluded that the finds from Bisitun Cave are almost indistinguishable from the products from Jerf Ajla and Nahr Ibrahim. However, there exists another assessment of the Bisitun Cave industry (Baumler, Speth, 1993).

Dibble's conclusion is partially acceptable, because numerous parallels to the Bisitun stone products have been recorded in the archaeological materials from the Middle Paleolithic sites of the Near and Middle East, as well as Central Asia (Obi-Rakhmat Cave site in Uzbekistan). Similarities in technical and typological features over a vast territory can be attributed to the dispersal of Denisovans and Palestinian Neanderthals, because their lithic industry was developed largely on the basis of the Acheulo-Yabrudian and Amudian traditions of the Levantine Paleolithic.

The lack of the Early Paleolithic sites with reliable geochronological data in Iran does not make it possible to determine the time of occupation of this territory by either the first wave of *H. heidelbergensis* migrants with the Acheulean industry (it can be dated to ca 700 (600) ka BP), or the second wave, Denisovans (400–350 ka BP). The earliest date established by a bone fragment from the



Khumian site in Iran is 148 ± 35 ka BP. However, the date raises doubts because of the controversial assessments of the stratigraphic position of the bone (Shoae, Nasab, Petraglia, 2021: 19).

Since only one taxon, *H. s. neanderthalensis*, inhabiting Eurasia in the Late Middle to Early Upper Pleistocene, has been known until recently, a small number of anthropological fossils dating from the first half of the Upper Pleistocene found in Iran were also attributed to Neanderthals.

The earliest archaeological find, a hominin tooth, originates from Qaleh Kurd, dated to 150 ka BP. Fossils from Bisitun Cave also refer to early periods. According to Coon, a tooth and a fragment of radius were found in the Middle Paleolithic layer. These materials were later examined by E. Trinkaus; he identified the tooth as the left 12th or 13th lower incisor, possibly of a bull (Trinkaus, Biglari, 2006). The other fossil turned out to

be the proximal half of the diaphysis of a human radius. Its both ends were broken off obliquely. The comparative analysis of the remains of Neanderthals and early modern humans showed that the morphology of the Bisitun fossil shared many features with the fragments of Neanderthal bones from Shanidar Cave and other sites in the western part of Eurasia.

Notably, the Denisovan dental system with many archaic features could have developed in the course of Denisovan dispersal across Central Asia, as a result of assimilation with the indigenous population. Interbreeding was possible because these taxa had an open genetic system. It cannot be ruled out that the physical abilities allowing Denisovans to master the highlands were gradually evolved in the course of their adaptation to local conditions during the occupation of the Tien Shan and Pamir regions.

The two taxa—Neanderthals and Denisovans—having evolved 400–350 ka BP on the ancestral base of *H. heidelbergensis* had common morphological features. However, in the process of dispersal across the territory of Iran and Central Asia, assimilation into the indigenous population, and adaptation to new environmental conditions, Denisovans acquired certain new morphological and genetic characteristics that distinguished them from the Neanderthals. Apparently, at the initial stage of settling in Iran, the Denisovans' morphology differed insignificantly from that of the indigenous population.

Some experts do not exclude the possibility of existence of two different groups of hominins with slightly different industries in the region under consideration during the period corresponding to MIS 3. One group, with the Mousterian industry, settled in Zagros (Shoae et al., 2023). These hominins rarely used the Levallois knapping strategy. Their sites yielded numerous well-retouched side-scrapers; the tool kit included denticulate-notched items and quite few bifacially processed tools such as handaxes. Researchers attribute this industry to Neanderthals and date it to the period of 70–42 ka BP. The Middle Paleolithic sites located in the northern regions of Iran contained a lithic industry close to the Levantine Middle Paleolithic.

Possible migration routes of the emerging Denisovan taxon from Iran to Central Asia

In the eastern part of Iran, as compared to the western, quite few Paleolithic sites from the Pleistocene period have been found that could evidence the dispersal of Denisovans to East Asia. Apparently, this disproportion should be associated with the harsh environmental conditions for human habitation during that period,

as well as with the insufficient field investigations in this territory.

The sites of Kashafud and Darungok seem to have produced the earliest Paleolithic finds in the eastern Iranian Plateau, but owing to their small number and the lack of diagnostic stone implements (despite their evident Early Paleolithic morphology) it is hardly possible to attribute these sites with surface occurrence of cultural remains either to the pre-Acheulean or Acheulean period.

Over the recent 20 years, in the eastern Iranian Plateau, scholars discovered several Paleolithic sites with surface occurrence of artifacts, mainly attributable to the Middle Pleistocene (Barfi, Soroush, 2014; Nikzad, Sedighian, Ghasemi, 2015; Nasab, Hashemi, 2016, 2018; Sadraei et al., 2017, 2018, 2019; Sadraei, Anani, 2018; Sadraei, Garazhian, Sabori, 2021; and others).

Reconstruction of possible migration routes of hominins in the Middle Pleistocene should be based on field materials from the Nishapur intermountain valley in northeastern Iran (Sadraei, Garazhian, Sabori, 2021). The valley is bounded by the Binalud range in the north, the Neyzehband, Siah Kooh, and Namak mountains in the south, the Milajough and Yalpalang heights in the east, and the Sabzevar valley in the west. A total of 37 archaeological sites with various concentrations of lithics were discovered in the Nishapur plain. Four sites were identified in the southern part of the Binalud foothills, at an altitude over 1400 m asl. One of them was attributed to the Early Paleolithic, the other three to the Middle Paleolithic. The hominins inhabiting these sites used mainly flint rocks; chert, quartz, and jasper were less common (Ibid.: 5).

The above-mentioned sites yielded small numbers of artifacts. From the site of Mushan Tappeh, attributed to the Early Paleolithic, 13 items were reported: cores (4 spec.), tools (retouched, 4 spec.), and fragments (5 spec.). The category of tools contained three side-scrapers (including a bifacial one) and a core-chopper.

The small lithic assemblages from the Middle Paleolithic sites of Ali Abad, Qezel Tappeh, and Dar Behesht comprise 9, 13, and 14 items, respectively. The Dar Behesht site yielded cores and core-like items (3 spec.), flakes (4 spec.), formal tools (5 spec.) including a déjeté-type scraper, and fragments (2 spec.). The Ali Abad site also produced formal tools (5 spec.) and retouched items (2 spec.). The Qezel Tappeh collection was dominated by flakes, and included two cores (Ibid.: 8).

The sites of Kaftar Kouh, with products of Levallois reduction (flakes and blades) (Sadraei et al., 2017), and Kalat-e-Shour (Sadraei, Anani, 2018) have been attributed to the Middle Paleolithic.

The industry of the sites under consideration presents four main flaking strategies: unidirectional, typical of unifacial cores and core-choppers; bipolar; parallel

flaking, recorded on at least two cores; and centripetal, recorded on three cores. Researchers did not identify the Levallois reduction technique; however, in the lithic assemblages, they recorded Levallois flakes, a bifacial scraper made on a Levallois blade, and a fragment of a Levallois point with irregular retouch. A series of Middle Paleolithic sites was found in South Khorasan (Barfi, Soroush, 2014).

In general, in the eastern Iranian Plateau, a considerably small number of Middle Paleolithic sites have been found. According to A. Sadraei and his co-authors, between the Kashaf Rud site in the Mashhad Plain and Kiarām Cave in the Gorgan Plain, in a 500 km long area, no important sites with Middle Paleolithic industry have been established (Sadraei et al., 2017). In case this conclusion is based on the results of a thorough survey of this area, it means that some regions of Iran were very sparsely populated by hominins. It should also be noted that almost all the local Middle Paleolithic sites are characterized by surface occurrence of cultural remains and the small number of finds.

The Sorheh complex, located in the southern slopes of the Alborz Mountains, 80 km northwest of Tehran, is of great interest (Hariryan et al., 2021). It includes six caves and rock shelters. In one of these karst cavities, the stratigraphic sequence was severely disturbed by amateur excavations. Five other rock shelters, located 20–70 m from each other, yielded only thin loose deposits. The Sorheh collection contains 118 lithic artifacts, including 12 tools. The industry is clearly blade-based. Blanks are dominated by blades, Levallois blades, and points.

Another locality, Mirak, is an open-air site in the northern part of the Central Iranian Range. Seven hills from of 4 to 11 m high were discovered in the area of 2.5 km on the southern slopes of the Alborz mountain system, 5 km south from the modern city of Semnan. This hills are surrounded by several seasonal and permanent water sources, including the permanent watercourse of the Geyno River, which were very important for the hominin dispersal in this extremely dry region. At Mirak, researchers identified two relatively large sites with a lot of artifacts assembled from the surface (Nasab, Clark, Turkamandi, 2013; Nasab et al., 2019; Rezvani, Nasab, 2010).

Taking into account the significant area of lithic artifact dispersion (1.6 km²) and the large number of surface collected items, the researchers divided the site into eight sections. The sections for artifact collection, measuring 4 × 10 m each, were established arbitrary. All lithic material was collected at each section. A total of 7744 artifacts were collected, including 6222 blanks subdivided into flakes (5504 spec.), blades (304 spec.), and small bladelets (414 spec.). The radial flaking predominated in primary reduction at the site; the Levallois index was

high, IL = 46.0. According to the Levallois index, the Mirak collection was second only to the Bisitun site (IL = 55.8) and surpassed the Kunji (IL = 10.1) and Warwasi sites (on average, IL = 10). Other features of the Mirak industry included the predominance of tools on flakes; the predominance of faceted and dihedral striking platforms; a high proportion of flakes without pebble crust (89 %), which suggests that the primary reduction most probably took place beyond the site; a high share of complete blanks (more than 50 %) with traces of use, edge wear, and damage, indicating their use without retouching the working blade; the most frequent use of such raw materials as flint and chalcedony; partial retouching—hominins did not aim at changing the shape of blanks or standardizing tools; low intensity of retouch in general, although 3816 artifacts showed varying degrees of edge retouching.

The collection of tools is dominated by side-scrapers with longitudinal or transverse working edges (36 %), as well as uni- and bifacial convergent forms. A small number of pointed tools, denticulate-notched tools, and Upper Paleolithic type tools were found. There are no geochronological data for the Mirak locality; however, on the basis of technical and typological features, it was dated to the Late Middle Paleolithic.

I have presented the data on a small number of finds from the Middle Paleolithic sites in Iran. However, in recent years, the amount of available information has significantly increased. In 2015–2016, the team of the Iranian-French expedition carried out excavations at Mirak 8, where the greatest number of surface artifacts were recorded (Nasab et al., 2019). During the works, they exposed deposits at an area of 36 m², subdivided into three sections (19, 12, and 5 m²) on the northern, eastern, and southern slopes of the mountains. The excavations revealed 6266 artifacts, including 2709 recovered from stratigraphic context at a depth of 4–7 m. Along with stone tools, heavily modified bones and teeth of large animals, including teeth belonging to equine species, were found.

In the stratigraphic sequence (9 m), two units were identified. The lower unit was an alluvial horizon, while the upper one consisted of wind-blown sediments. Each unit was subdivided into separate smaller strata. The OSL-dating of the lower strata, containing three main culture-bearing layers, produced the following dates: layer 1 – 28 ± 2 ka BP; layer 2 – 28 ± 2 to 38 ± 2 ka BP; layer 3 – 47 ± 2 to 47 ± 4 ka BP (Ibid.).

The artifact collection from upper layer 1 was dominated by blades and bladelets, but there were neither Arjeneh points, nor Dufour blades typical of the Baradostian or Zagros Aurignacian. Only ten tools were identified, most of which were burins. Cultural layer 2 contained the mixed Upper Paleolithic industry: blades and bladelets occurred along with Levallois flakes with

typical *chapeau de gendarme* platforms. The observed combination provided the grounds to characterize layer 2 as a mix of the Upper and Middle Paleolithic industries.

The materials recovered from layer 3 demonstrated that primary flaking was carried out mostly by Levallois technique; blades and small bladelets accounted for about 5 % of the debitage. The tool kit included numerous Middle Paleolithic implements; dominated by side-scrapers and points with faceted striking platforms. In general, the industry of layer 3 showed distinct Middle Paleolithic features. The Mirak lithic industry, collected both from the surface and from the stratified context, was attributed to the terminal Middle and Early Upper Paleolithic. It showed similarities with the Zagros Middle Paleolithic complexes.

The lack of sites with long stratigraphic sequences and chronological determinations in the territory of Iran, as well as the small number of anthropological finds, do not provide reasonable grounds for establishing the taxa that could have inhabited this region in the late Middle to the first half of the Upper Pleistocene. It cannot be ruled out that both Denisovans and Palestinian Neanderthals occupied the region at that time, since both taxa had an open genetic system; they could interbreed and produce fertile offspring. As a result of acculturation, very diverse lithic industries were developed; such variability is observed at sites of both the Middle and Upper Paleolithic.

The eastern part of the Iranian Plateau is the only possible area through which Denisovans could have migrated to Central Asia and Southern Siberia. H.V. Nasab with co-authors (Nasab, Clark, Turkamandi, 2013), on the basis of the Paleolithic sites found in this area, proposed three possible migration routes passing through intermountain depressions.

Route A (Southern) consists of two parts: through the Strait of Hormuz (from Balochistan to Makran); from the strait along the northern shore of the Persian Gulf. Route B (Northern) runs along the southern coast of the Caspian Sea and the northern foothills of Alborz. This route provided the way for hominins to go east—towards Turkmenistan and Afghanistan, and west—reaching the territory of Ukraine. Route C is an internal corridor between the southern foothills of Alborz and the northern part of the Iranian Central Desert.

With the discovery of new Paleolithic sites, Sadraei and co-authors proposed two possible routes through the northeastern part of the Iranian Plateau (Sadraei, Garazhian, Sabori, 2021: 10). The first corridor, designated Hezar Masjed – Binalud, may have passed through the mountain plains where the large cities of Ashkhaneh, Bojnord, Quchan, and Mashhad are currently located (Fig. 4, *a*). The second corridor can be subdivided into two parts covering the southern portion of the Binalud and Jaghatai Mountains. This corridor borders the Jajarm and Esfaryen plains in the north, and Sabzevar and Nishapur plains in the south (Fig. 4, *b*). The researchers noted that the reconstruction of the two routes was carried out taking into account the ecological potential of the region and the small amount of available data (Ibid.).

Although all Paleolithic sites in the area are localities with surface occurrence of artifacts, scholars believe in the great archaeological potential of these two corridors, which hominins could have used to move from the Iranian Plateau to Central Asia.

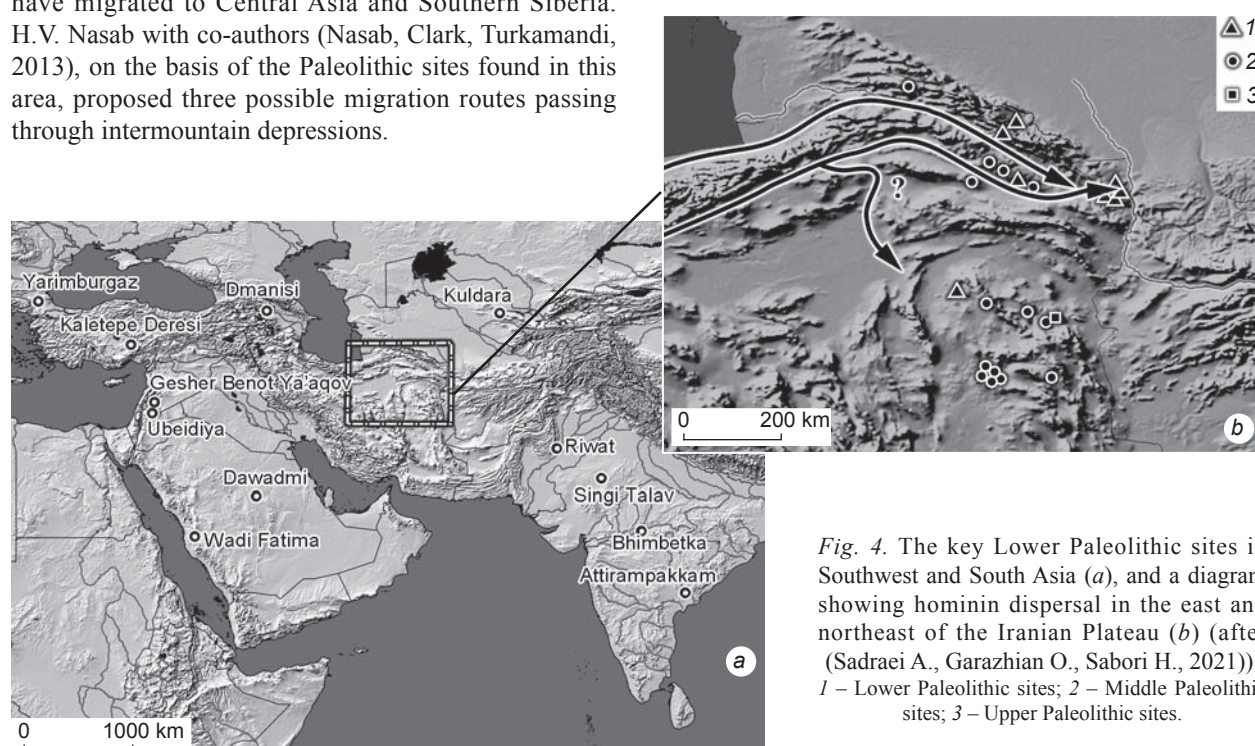


Fig. 4. The key Lower Paleolithic sites in Southwest and South Asia (*a*), and a diagram showing hominin dispersal in the east and northeast of the Iranian Plateau (*b*) (after (Sadraei A., Garazhian O., Sabori H., 2021)). 1 – Lower Paleolithic sites; 2 – Middle Paleolithic sites; 3 – Upper Paleolithic sites.

Conclusions

Owing to the lack of well-stratified sites of the Early and Middle Paleolithic, with reliable geochronological determinations and representative anthropological evidence, it is hardly possible to convincingly prove that the territory of Iran was a transit area for the hominins inhabiting South and Central Asia. Nevertheless, certain irrefutable facts allow us to accept this assumption as the main hypothesis. There were several migration flows.

1. The early migration flows led to the dispersal of *Homo erectus* populations. In Georgia and Dagestan, *H. erectus* sites with pebble-flake industry dating back 1.75–1.6 Ma BP have been found (Gabunia et al., 2002; Messenger et al., 2010; Amirkhanov, Trubikhin, Chepalyga, 2009; Derevianko, 2015; and others). The Pabbi Hills and Riwat sites in South Asia are dated by researchers to the Late Pliocene to the initial Early Pleistocene (Hurcombe, Dennell, 1993; Dennell, 2004a, b). In Tajikistan, the Kuldara site with microlithoid industry dating back 800–900 ka BP has been discovered (Ranov, 1988; Ranov et al., 1987), in the Altai the Karama site with pebble-flake industry dating back to about 800 ka BP (Derevianko, Shunkov, 2005; Derevianko et al., 2005). Thus, the dispersal of *H. erectus* populations from Africa across Central and South Asia could have occurred only through the Iranian Plateau.

2. Emergence of the Acheulean industry in South Asia ca 700 (600) ka BP could have also been the result of the migration of the first wave of *H. heidelbergensis* from the Levant to the territories of Pakistan and India (Derevianko, 2018: 132, 181). Hundreds of Acheulean sites have been discovered in India.

3. In the Indian Acheulean, the early and the late stages have been identified (Shipton, Petraglia, Paddayya, 2009). The Late Acheulean, in contrast to the early one, is characterized by small, thinner, and shorter bifaces, bearing a large number of flake negative scars, indicating thorough treatment. But most importantly, the primary reduction strategy shows traces of the Levallois technique. The Levallois method of primary reduction is particularly evident in the assemblages from the sites in western Pakistan. The emergence of the Levallois reduction in western regions of South Asia can be associated exclusively with the second migration flow of late *H. heidelbergensis* (evolving Denisovans) from the Levant. Notably, the Denisovan genetic heritage can be traced in some populations of South Asia (Bergström et al., 2021; Skoglund, Jakobsson, 2011). Around 400–350 ka BP, a small group of Denisovans from the Levant could have migrated through the Iranian Plateau to the western regions of South Asia and assimilated into the indigenous population.

4. The initial stage of the Denisovan dispersal over Central Asia is represented by bifacially prepared tools

of the handaxe type reported from the western regions of Turkmenistan (Okladnikov, 1953; Vishnyatsky, 1996). The Denisovans migrated from Iran to the territory of Turkmenistan along the most ecologically beneficial corridor between the Caspian Sea and the northern foothills of the Alborz mountain system. The Karakum Desert in southern Turkmenistan was not beneficial for early human habitation; no Acheulean-type sites indicating the presence of Denisovans have yet been discovered in the region.

The hypothesis that Iran was the only transit area for hominins migrating from Africa and the Near East (Levant) to South and Central Asia is currently insufficiently evidenced. Nevertheless, the emergence of a new Denisovan taxon can be described as follows: Denisovans' homeland was the Levant; their dispersal to the Altai could have occurred only through Iran and Central Asia. The aim for future studies is the search for new archaeological sites that could support the idea on the existence of this migration route.

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