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The Earliest Paleolithic Assemblages from Denisova Cave in the Altai

The article presents the results of multidisciplinary studies of the Early Middle Paleolithic assemblages from the lower part of the Denisova Cave Pleistocene sequence in the East Chamber and the Main Chamber of the cave. Data on geochronology, small and large vertebrate fauna, palynology, stratigraphy and micromorphology of sediments containing the earliest archaeological finds at the site, as well as on petrography, traceology and archaeozoology are presented. We describe human fossils and aDNA studies based on them. These materials demonstrate that the first inhabitants of the cave and those associated with the Early Middle Paleolithic traditions were Denisovans. On the basis of the collection, which includes over 35,000 artifacts, the technology and typology of the Denisova industry are reconstructed. We focus on the comparison of the Denisova Early Middle Paleolithic with chronologically closest industries of North and Central Asia. The most similar industry is the Acheulo-Yabrudian of the Near East. Parallels concern primary reduction techniques and tool types. A hypothesis explaining the appearance of Middle Paleolithic traditions in Southern Siberia is proposed. We demonstrate continuity in the evolution of the lithic industries of Denisova up to the autochthonous emergence of the Upper Paleolithic ca 50,000 years ago.

Keywords: *Altai, Denisova Cave, Pleistocene, Early Middle Paleolithic, lithic industry, Denisovans.*

Introduction

Archaic pebble tools from the deposits of the first half of the Middle Pleistocene, which were discovered at the Early Paleolithic stratified Karama site in the valley of the upper Anuy River, testify to the first appearance of prehistoric humans in the Altai and the entirety of North Asia (Derevianko, Shunkov, 2005; Bolikhovskaya, Derevyanko, Shunkov, 2006). The Karama lithic assemblage includes side-scrapers, choppers, tools with spike-like protrusions, and carinated core-shaped end-scrapers made from pebbles of spherulite effusives, as well as denticulate, notched, and beak-shaped tools made from massive pebble fragments. Ulalinka, located in the basin of the lower Katun River, is another Early Paleolithic site of the Middle Pleistocene in the Altai (Okladnikov, 1972; Pospelova, Gnibidenko, Okladnikov, 1980). The quartzite lithic items found at the site included core-shaped pieces with prepared striking platforms and negative scars of subparallel removals, scraper-like tools on flattened pebbles, choppers, chopping tools, and tools with distinctive spike-like protrusions on massive pebbles.

The next stage in the peopling of Southern Siberia began after a long break, probably caused by general deterioration of the natural environment at the end of the first half of the Middle Pleistocene. The stage was associated with the carriers of the Middle Paleolithic, who appeared in the Altai ca 300 ka BP and left traces of their presence in the lower cultural layers of Denisova Cave, located 15 km from the Karama site upstream the Anui River (Fig. 1). For a long time, first habitation stages by prehistoric humans in the cave were known only from sparse archaeological finds of the Early Middle Paleolithic discovered in basal deposits in the Main Chamber of the cave (Prirodnaya sreda…, 2003: 114–118). Comprehensive studies in the last decade have significantly expanded the number of sources from the lower part of cave deposits. Over 35,000 lithic items were found during the excavations of lithological layers 15 and 14 in the East Chamber of the cave. These finds have made it possible to reevaluate the technical and typological traditions of the Altai population in the Early Middle Paleolithic. Judging by the anthropology and paleogenetics data, these humans were the Denisovans.

Archaeological, zooarchaeological, and microstratigraphic studies have revealed that the lower layer of sediments in the Main and East chambers emerged in a time of the most active human habitation in the cave. The Denisovans who left the earliest artifacts in the cave knew the physical properties of stone pebbles from the nearby Anui channel. To produce tools, they selected the pieces that were homogeneous in their key characteristics, had a hardness of 5–6.5 on the Mohs scale, and were mainly sedimentary rocks, such as siltstones and sandstones (70 %), less often volcanic aphyric or porphyritic effusive rocks (Kulik, Shunkov, Kozlikin, 2014).

Two species of horse *Equus ovodovi/ferus*, red deer *Cervus elaphus*, roe deer *Capreolus pygargus*, bison *Bison priscus*, gazelle *Gazella gutturosa*, and Siberian ibex *Capra sibirica* were the main prey for the first inhabitants of the cave (Vasiliev, Shunkov, Kozlikin, 2017). The main part of the taphocenosis in layers 15 and 14 of the East Chamber resulted from human hunting activities. Most of the bones were crushed; cuts commonly appeared on bone fragments. As compared to other layers, these deposits contained the largest amount of bone remains with thermal impact traces, as well as numerous charcoal microparticles (Morley et al., 2019). The edges of lithic tools from layer 15 had microremains of animal fat, and traces of cutting and scraping (Bordes et al., 2018).

This article discusses the lithic processing technologies and typology of implements among the inhabitants of Denisova Cave in the Early Middle Paleolithic, as well as the emergence of the Middle Paleolithic traditions in North Asia.

Fig. 1. Location of Denisova Cave.

Geochronology of Pleistocene deposits and paleogeographic stages of their formation

The periods when the lower unit of Pleistocene deposits was accumulated in the Main and East chambers of Denisova Cave were identified using the results of biostratigraphy and OSL-dating (Jacobs et al., 2019). The earliest Paleolithic evidence was found in the upper part of layer 22 in the Main Chamber, with its roof's OSL-age being 287 ± 41 ka BP (Fig. 2). The formation of this part of the section coincided with wide distribution of forests around the cave, in a stable natural environment, with small fluctuations in temperature and humidity within the interglacial climate. The lithological and stratigraphic equivalents of these deposits in the East Chamber were those of layer 17.1, dated from 305 ± 37 to 284 ± 32 ka BP. Spore and pollen spectra from the lower part of layer 17.1 indicate a warm climate, with the widest possible development of forest biotopes, which gave way to relative cooling during the accumulation of its roof (Bolikhovskaya et al., 2017). Dust-like coating of carbonates on the bones, the presence of lemmings among small mammals, and a complete absence of frogs suggest a short-term cooling in this part of the section (Agadjanian, Shunkov, Kozlikin, 2021). The deposits of layer 17.1 contain numerous primary teeth of bears and the highest content of their DNA (Brown et al., 2021), which suggests the active use of the East Chamber by carnivores in this period, while the more spacious and better-illuminated Main Chamber of the cave was already visited by hominins on a periodic basis.

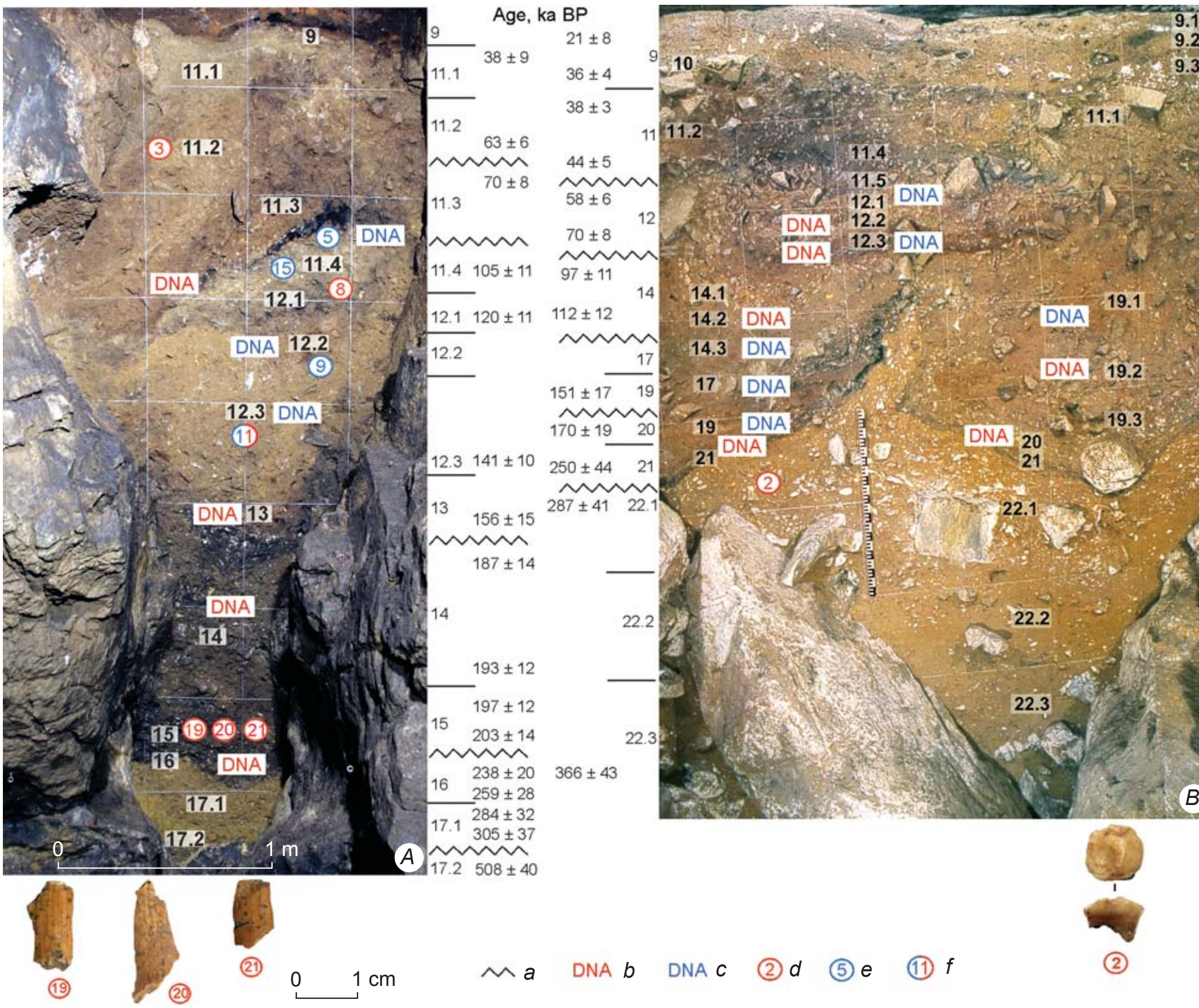

Fig. 2. Pleistocene deposits in the East Chamber (*A*) and Main Chamber (*B*) of Denisova Cave, with an indication of geochronological and paleogenetic evidence, and places of anthropological finds.
a – break in sedimentation; *b* – DNA of the Denisovans from the deposits; *c* – DNA of the Neanderthals from the deposits; *d* – bone remains of the Denisovans; *e* – bone remains of the Neanderthals; *f* – bone remains of a hybrid individual.

The overlying deposits in the Main and East chambers emerged after a long break in the sedimentation process. The sequence of layers 21 and 20 in the Main Chamber was formed in the period of 250 ± 44 to 170 ± 19 ka BP. Relatively cold and moderately humid climate was reconstructed for the accumulation time of layer 21. Deposits of layer 20 correspond to a warm and dry climate showing extensive growth of pine and birch forests, with the presence of broad-leaved species (Prirodnaya sreda …, 2003: 109).

The equivalent of the archaeologically sterile black sooty noncarbonate loams at the base of layer 21 were the deposits of layer 16 in the East Chamber, which showed an age of 259 ± 28 to 238 ± 20 ka BP. Pollen evidence from layer 16 included sporadic pollen grains of dwarf birch, which reflects cold climate. The deposits of the middle and upper parts of layer 21 in the Main Chamber correspond to layer 15 sediments in the East Chamber, dated to 203 ± 14 to 197 ± 12 ka BP. The composition of microtheriofauna from layer 15 suggests a relatively cold natural environment in the beginning of its accumulation. The middle and upper parts of that layer were formed under a more favorable climate, which contributed to expansion of the area of forest vegetation. Molars of water vole *Arvicola* were found in these deposits, with the morphological features that were intermediate between the Middle Pleistocene *A. mosbachensis* and the Late Pleistocene *A. cf. Sapidus*. The formation of layer 20 in the Main Chamber corresponds to the period of sedimentation for layer 14 in the East Chamber, which was 193 ± 12 to 187 ± 14 ka BP. According to biostratigraphy, the deposits of layer 14 emerged in a climate warmer than today's. Mixed forests with broad-leaved species, including hornbeam associations with addition of oak and linden, dominated around the cave at that time.

Lithological and stratigraphic columns of the lower part of the Pleistocene deposits in the Main and East chambers generally complement each other, and reflect the development of a natural environment during two warm and relatively cold climatic periods in the second half of the Middle Pleistocene, corresponding to oxygen isotope stages 9–7.

Anthropological and paleogenetic evidence

Human bone remains from the lower part of Pleistocene deposits in the Main Chamber of the cave include a left lower deciduous second molar (dm_2) found in layer 22.1. This tooth, which was designated as *Denisova 2*, belonged to a child ca 7–8 (Shpakova, Derevianko, 2000) or 10–12 years of age (Slon, Viola, Renaud et al., 2017) according to current standards. The paleogenetic analysis has revealed that the tooth belonged to a Denisovan (Ibid.). The probable age of *Denisova 2*, modeled by the Bayesian method using chronometric (OSL-dating), stratigraphic, and genetic data, is 194,400–122,700 BP (Douka et al., 2019), while the OSL-age of the upper part of the deposits in layer 22 is 287 ± 41 ka BP (Jacobs et al., 2019).

Three fragments of *Homo* representatives (*Denisova 19*, *20*, and *21*) were identified using collagen fingerprinting among the morphologically unidentifiable bone remains from layer 15 in the East Chamber. From these samples, the Denisovan mtDNA was sequenced (Brown et al., 2022). The identity of the mitochondrial sequences of *Denisova 19* and *21* suggests that they belonged to the same person or to maternal relatives. *Denisova 20* sample differed from them by four mtDNA substitutions. The phylogenetic analysis has shown that *Denisova 19*, *20*, and *21* were approximately of the same age or slightly older than *Denisova 2*.

The fragments of the Denisovan mtDNA were discovered in fifty samples of sediments from layers 21 and 20 in the Main Chamber, and layers 15 and 14 in the East Chamber of the cave (Zavala et al., 2021) (Fig. 2). Two samples from the roof of layer 20 in the Main Chamber contained nucleotide sequences of the mtDNA of the Neanderthals, which can be associated with the base of overlying deposits. Initially, the sample containing Neanderthal mtDNA from the East Chamber was erroneously assigned to layer 14 (Slon, Hopfe, Weiß et al., 2017), although in fact it was taken from layer 11.4 (Zavala et al., 2021). Thus, currently available anthropological and paleogenetic evidence from the lower part of the cave's deposits indicates that the Denisovans were the first inhabitants of the cave, and carriers of the Early Middle Paleolithic.

Archaeological evidence

The earliest lithic artifacts in the cave were discovered in the upper part of layer 22 of the Main Chamber. This small collection includes seven items from stratigraphic unit 22.2 and 312 artifacts from deposits of layer 22.1 (Prirodnaya sreda…, 2003: 114–118). Rare core-like items and flakes testify to parallel, radial, and irregular reduction methods. Artifacts made using Levallois technique have also been found. The most distinctive series of side-scrapers in the toolkit includes backed varieties and tools with stepped retouch of the Quina type. Production waste prevails among the finds from layers 21 (293 spec.) and 20 (908 spec.). Several cores belong to parallel single-platform and radial varieties. Shortened flakes with smooth or irregular dorsal scar pattern and smooth or natural striking platforms dominate among the spalls. Pieces with traces of secondary treatment include side-scrapers, as well as denticulate, notched, and spur-like artifacts.

The highest density of Paleolithic artifacts was observed in layers 14 (26,996 spec.) and 15 (9411 spec.) in the East Chamber. Despite significant differences in quantitative indicators, lithics from these layers were identical in their technical and typological features, and can be identified as a single complex.

Within the industry, tools for stone-knapping include hammerstones (13 spec.) and retouchers (7 spec.). Hammerstones are large, rounded, subrectangular, and angular pebbles ranging from 82 × 53 × 50 to 148 × × 74 × 50 mm in size, with intense microflaking on the protruding ribs and ends. Retouchers of 71 × 55 × 38 to 75 × 67 × 30 mm show traces of slight microflaking on faces or ends.

Core-shaped pieces (0.8 %) include typologically identifiable cores (105 spec.) and core-shaped debris (168 spec.). The most diverse are radial bifacial cores (56 spec.) of rounded, more rarely subrectangular or angular, shapes, corresponding to various stages of reduction: from pebble blanks, with traces of initial trimming, to severely exhausted residual pieces. Core sizes range from 46 × 37 × 27 to 137 × 130 × 56 mm, with 60–100 mm on average. Most of the cores were made on large pebbles (Fig. 3, *13*); some of them were made of large massive flakes (Fig. 3, *9*). Several cores

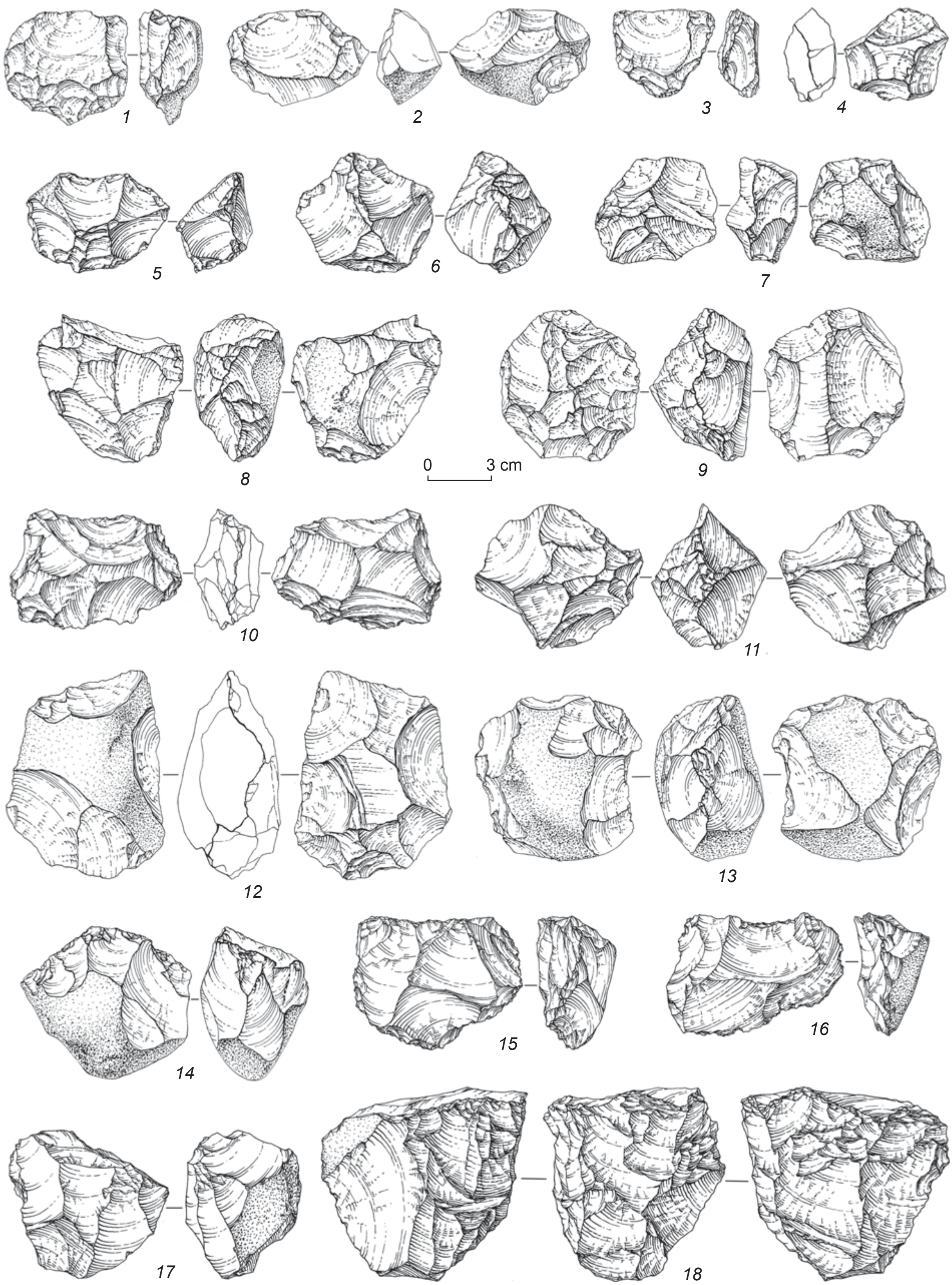

Fig. 3. Cores of the Early Middle Paleolithic from layers 15 and 14 in the East Chamber of Denisova Cave.

do not allow us to establish the type of their blanks, owing to their heavy exhaustion (Fig. 3, *6*, *10*, *11*). Most artifacts show that removals were taken along the entire perimeter of the flaking surface, without preliminary preparation of the edge (Fig. 3, *7*). Radial unifacial cores (28 spec.) are rounded items ranging from 51 × 44 × 24 to 108 × 52 × 25 mm in size, made on large massive flakes or on large pebbles (Fig. 3, *5*, *8*). The flaking surface was most commonly located on the ventral side (Fig. 3, *4*, *12*), and less often on the dorsal side of the blank. Flaking was carried out both from the unprepared edge and from the striking platform fashioned along the perimeter of the core.

Parallel technology is represented mainly by single-platform unifacial cores (15 spec.) of subrectangular shape, made of pebbles (Fig. 3, *14*) or large flakes (Fig. 3, *16*). These items vary in size from 43 × 27 × 19 to 77 × 74 × 66 mm. In most cases, the striking platform was prepared by one large removal, less often by several removals; it could also retain the pebble's surface. In one core, the flaking-arc occupies almost the entire circle of the striking platform (Fig. 3, *18*); in the rest of the cores, flaking-surface is confined to a single face. Double-platform unifacial cores (Fig. 3, *15*, *17*) show negative scars of bidirectional reduction from striking platforms prepared by one or several large removals (3 spec.). They are subrectangular, range in size from 64 × 67 × × 50 to 123 × 73 × 64 mm, and are made of large pebbles.

The utilization of the Levallois reduction method is confirmed by three cores: two were made of flakes, and one was made of pebble (Fig. 3, *1*). These items are processed almost along the entire perimeter of the frontal surface, and show one negative scar of a large removal (Fig. 3, *2*, *3*).

Core-shaped debris (168 spec.) are typically angular stone jointings with single removals or traces of several irregular removals, as well as severely exhausted, typologically unidentifiable cores. Their sizes vary from 37 × 35 × 19 to 132 × 79 × 42 mm.

The spalls (44.4 %) are dominated by flakes (16,850 spec.), including a series of radial core *débordantes* (165 spec.) (Fig. 4, *2*) and Kombewa flakes (179 spec.), both classic forms (Fig. 4, *1*) and lateral removals (Fig. 4, *4*). Complete flakes are medium (1424 spec.) and large (1957 spec.), shortened and short (88 %), or elongated (12 %), with smooth (64.2 %), natural (23.6 %), or unidentifiable (7.5 %) residual striking platform without any traces of overhang reduction. Dorsal scar pattern is mostly longitudinal unidirectional (36.4 %), orthogonal (18.0 %), smooth (13.2 %), or unidentifiable (26.4 %). About a half of the flakes completely (13 %) or partially (35 %) retain pebble surface on their dorsal face. A few blades (81 spec.) show smooth or natural platforms, longitudinal or orthogonal (Fig. 4, *3*) scar pattern; half of them retain a partial or complete pebble-surface. Production waste (52.7 %) includes split pebbles (143 spec.), debris (16,465 spec.), and chips (2575 spec.).

Tools (774 spec., 2.1 %) were mostly made of large short or shortened flakes and fragmented spalls. Most of them were shaped by dorsal marginal or invasive steep subparallel strongly modifying retouch, including stepped Quina-type retouch. Items with thinning are common.

Artifacts subjected to secondary treatment are dominated by large ventral thinned flakes (214 spec.): longitudinal single (70 spec.) and double (61 spec.) (Fig. 4, *7–10*, *12–14*), transverse single (43 spec.) (Fig. 4, *6*) and double (17 spec.) (Fig. 4, *5*, *11*), longitudinal-transverse (15 spec.), and semi-circular (8 spec.). Complete items are mostly short (80 spec.) or shortened (55 spec.), less often elongated (22 spec.), treated with direct ventral percussion by large removals 10 to 60 mm wide.

The second most important group consists of proximally truncated spalls (110 spec.). These are large short or shortened flakes, with their striking platforms removed by a series (64 spec.) (Fig. 4, *15–17*) or a single (46 spec.) large ventral removal. The negative scar width of truncation spalls varies from 5 to 40 mm; in several items, the proximal edge was removed by a large (40–50 mm wide) detachment.

Side-scrapers (73 spec.) show the greatest typological diversity. They include longitudinal items with straight (12 spec.) or convex (18 spec.) (Fig. 5, *7*, *11*) retouched edges, including implements formed on ventrally thinned (Fig. 5, *5*) and proximally truncated blanks, as well as backed items (13 spec.); diagonal side-scrapers with straight (12 spec.) or convex (4 spec.) (Fig. 5, *10*) retouched edges, transverse side-scrapers with convex (14 spec.) (Fig. 5, *3*, *4*) or straight (2 spec.) retouched edges; double (3 spec.) and convergent (7 spec.) (Fig. 5, *1*, *2*, *6*, *8*, *9*) varieties, as well as a semi-circular side-scraper.

The group of denticulate, notched and spur-like tools comprises mainly the items with denticulate longitudinal edges (45 spec.), including backed varieties—with natural back (11 spec.) (Fig. 5, *17*), back-facet (4 spec.), and broken off back (3 spec.), with diagonal (9 spec.) (Fig. 5, *16*), transverse (22 spec.) (Fig. 5, *14*), or longitudinal-transverse (4 spec.) retouched edge, with two working edges (3 spec.) (Fig. 5, *18*), convergent (3 spec.) items, and semi-circular implements (8 spec.). Notched tools (33 spec.) are represented by retouched notches formed on longitudinal (22 spec.) (Fig. 5, *15*) or transverse (11 spec.) edge of the blank, including

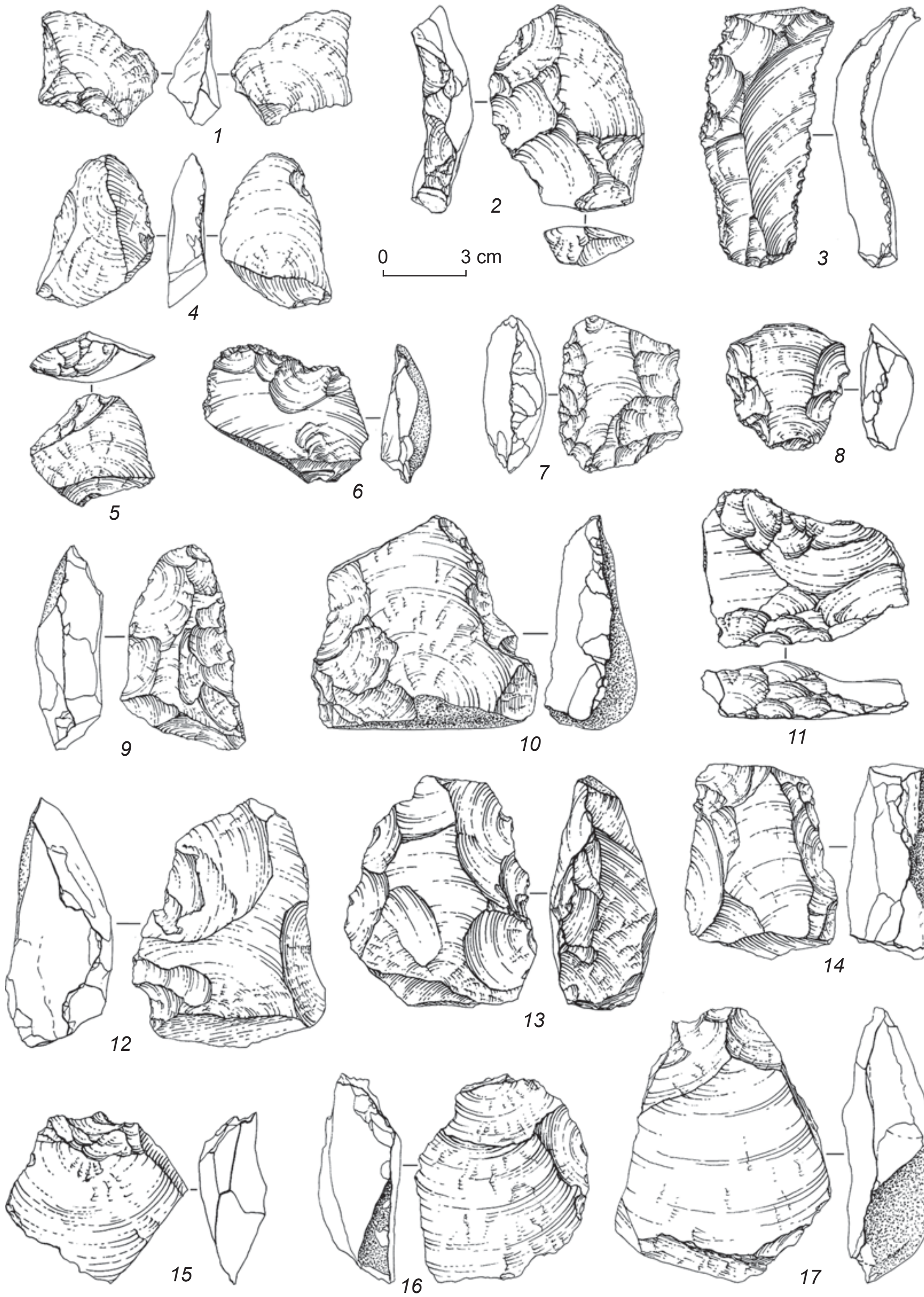

Fig. 4. Lithic artifacts of the Early Middle Paleolithic from layers 15 and 14 in the East Chamber of Denisova Cave.
1, *4* – Kombewa flakes; *2* – radial core *débordantes*; *3* – blade; *5–14* – ventrally thinned flakes; *15–17* – proximally truncated flakes.

backed varieties on marginal and fragmented spalls. The working element in spur-like tools (31 spec.) is located in the middle part of the distal (16 spec.) (Fig. 5, *12*, *13*) or longitudinal (8 spec.) edge, as well as at the corner of the transverse and longitudinal edges (7 spec.).

The collection also comprises 171 flakes and a blade with local retouch, as well as 50 unidentifiable tool fragments.

Generally, the Early Middle Paleolithic industries in Denisova Cave are illustrated by radial and parallel

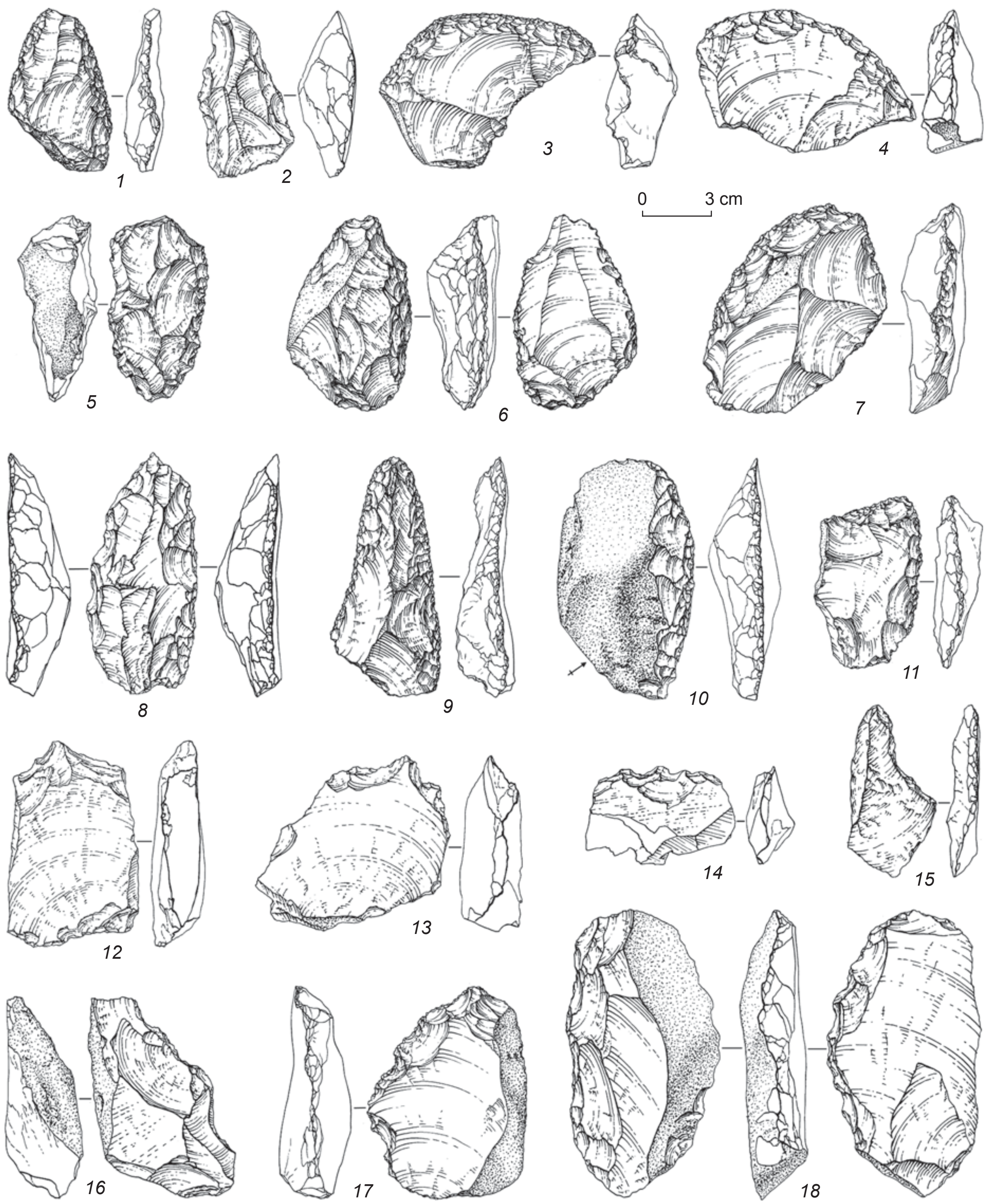

Fig. 5. Lithic artifacts of the Early Middle Paleolithic from layers 15 and 14 in the East Chamber of Denisova Cave. *1–11* – side-scrapers; *12*, *13* – spur-like tools; *14*, *16–18* – denticulate tools; *15* – notched tool.

unifacial single-platform cores made of massive flakes or small boulders. There is some evidence of the use of Levallois technique. Large massive flakes with ventral thinning resulting from wide removals from the distal or one or two longitudinal edges dominate among the artifacts subjected to secondary treatment. Another typical variety of artifact includes basally truncated flakes, with proximal edge truncated by ventral detachments. Side-scrapers with longitudinal, diagonal, transverse, convergent, and angular retouched edges, including those similar in morphology to Quina-type items, as well as spur-like, denticulate, and notched pieces, appear in large numbers.

Discussion

Among the Altai Middle Paleolithic complexes, the chronologically closest evidence to the earliest industries from Denisova Cave was obtained from alluvial layer 19 of the stratified Ust-Karakol site, and was dated by the RTL-method to 133 ± 33 ka BP (RTL-661) (Derevianko, Shunkov, 2002). These deposits contain sparse corroded lithic artifacts with well-distinguished traces of parallel technology, identified as longitudinal and convergent side-scrapers, an end-scraper, spur-like items, denticulate and notched tools with Clactonian and retouched notches, spalls with traces of secondary treatment, and a truncated spall.

Supposedly, the age of layer 19 at the site corresponds to the lower strata of layers 10 and 9 in Ust-Kan Cave. By several teeth of gray voles of the *Allophaiomys* genus, these deposits were dated to the Late Middle Pleistocene (Agadjanian, Serdyuk, Postnov, 2002), and artifacts found therein were attributed to the Early Middle Paleolithic (Derevianko et al., 2001). However, this was clearly insufficient to confirm the Middle Pleistocene age of the deposits. Numerous remains of the Upper Pleistocene microtheriofauna were found in these layers, together with the *Allophaiomys* teeth. In paleontology and taphonomy, deposits are dated according to the latest components of taphocenosis. In addition, publications provide only a general description of the industrial complex of this stratified site, and the technical and typological appearance of the finds from the lower stratigraphic levels of the cave was unclear. Generally, the Levallois technique was typical of the Middle Paleolithic industry of the cave. The toolkit mainly consists of Levallois spalls, such as flakes, blades, and points, mostly medium-sized and short. Longitudinal and convergent side-scrapers (including those made on large Levallois blades) and Mousterian points dominate among the retouched items. Denticulate and notched tools are scarce, although quite diverse.

In the second half of the Middle Pleistocene, the Middle Paleolithic traditions began to emerge in the Altai, while in other areas of Southern Siberia that period was most likely dominated by pebble industries of Early Paleolithic appearance. Such a distribution of cultural manifestations may reflect specific regional developments in the Early Paleolithic ecumene in the eastern part of Eurasia (Derevianko, 2017: 89–128).

In southern Tuva, the second half of the Middle Pleistocene may be represented by surface finds from the Torgalyk localities, whose most probable age corresponds to the end of oxygen isotope stage 8 (Astakhov, 2008: 29–37). Primary technology in these industries includes flat parallel and radial cores, as well as artifacts with the Levallois reduction elements. The toolkit contains side-scrapers, spur-like points, denticulate, notched, and beak-shaped forms, bifacially treated pebble artifacts, and, according to the published evidence, ventrally thinned and proximally truncated flakes.

In the north of the Minusinsk Basin, corroded pebble artifacts have been found at Razlog II, Razliv, Kamenny Log, and Berezhekovo, in the zone of erosion of Pleistocene deposits by the waters of the Krasnoyarsk Reservoir (Drozdov et al., 2000). Some items may belong to the Middle Pleistocene; this is indirectly indicated by the remains of fossil fauna of the early mammoth complex, such as *Mammuthus chosaricus* and *Equus caballus chosaricus*, found together with pebble artifacts. Core-shaped items in these industries include radial and orthogonal cores, and artifacts in the form of chopping tools with the traces of convergent flaking. Scraper-like tools with backs on “citron” spalls and retouched flakes have also been discovered.

These collections are similar in appearance to surface finds from high terraces in the upper Angara River at the Igetei, Tarakhai, Olonskaya, and other sites (Medvedev, 1975). These industries are based on reduction of radial cores, with some elements of Levallois technique, and of single and double-platform parallel cores. There are also side-scrapers of longitudinal, transverse, and combination variants shaped by steep stepped retouching, and bifacially treatment items.

The small number and apparently uneven age of archaic pebble industries in Tuva and Eastern Siberia make it difficult to assess the level of cultural interaction or possible continuity between them. However, we should note the developed industry of the Torgalyk site, which includes elongated spalls removed from flattened cores and the simplest forms of bifacial pebble tools. The Angara and (to some extent) Yenisey industries show the greatest technical and typological diversity, well-developed methods of bifacial-radial, convergent, and parallel techniques, use of blanks of a deliberate shape, and production of various side-scrapers and other specialized tools.

Some similarities between the Altai industries of the second half of the Middle Pleistocene and the corroded Angara-Yenisey materials are manifested in the wide use of radial reduction along with parallel and Levallois techniques. The predominant tools are side-scrapers of various types, including the items shaped by stepped retouch, as well as denticulate and notched items, and spalls with ventral thinning and proximal truncation. Given the ambiguity of the chronological context and lack of anthropological evidence at the Angara-Yenisey sites, the question concerning the carriers of these archaic pebble traditions remains open.

Anthropological finds from Baishiya Cave in the northeast of the Tibetan Plateau testify to the wide spread of the Denisovans to the east of Asia. A hominin dated to ca 160 ka BP, a fragment of whose mandible was found in the cave, was identified (on the basis of a paleoproteomic analysis) as a Denisovan (Chen et al., 2019). During further studies of the cave deposits accumulated during 100–60 ka BP, mtDNA fragments of the Denisovans that formed a clade with *Denisova 3* and *4* samples were sequenced (Zhang et al., 2020). According to preliminary data, the lithic industry of Baishiya was dominated by simple methods of knapping pebble raw materials aimed at obtaining flakes (the illustrations show the use of the radial method); typologically expressed tools were rare, and flakes with use-wear traces were predominant.

In the western part of Central Asia, the Early Middle Paleolithic is probably represented by the finds from Selungur Cave in the Fergana Valley, in the western Tian Shan. Although, initially, the cultural and chronological attribution of the site was associated with the Early Paleolithic (Islamov, Krakhmal, 1995), the evidence from the cave is presently considered a new industrial variant of the Middle Paleolithic of Central Asia (Krivoshapkin et al., 2016). The upper complex of the cave was preliminarily dated by the thorium-uranium method to 126 ± 5 ka BP (Krivoshapkin et al., 2017). According to its technical and typological features, the complex is similar to the industries from the lower cultural layers of Denisova Cave. Primary technology in the Selungur industry was aimed at producing shortened massive flakes with large smooth striking platforms, without overhang reduction in a system of radial, orthogonal, or parallel techniques. The toolkit was dominated by various kinds of longitudinal and transverse side-scrapers, including carinated varieties and items with the edge in the proximal part of the blank; ventrally thinned and proximally truncated flakes were common. Specific forms of tools were flat-convex bifacially treated points and side-scrapers, Tayacian points, and Mousterian chisels.

The Early Middle Paleolithic industries of the Altai show the closest similarity with the Acheulo-Yabrudian Cultural Complex (AYCC) in the Middle East (Derevianko, 2018: 112, 264; Derevianko, Shunkov, 2002). This complex was identified by A. Rust, who used the evidence from the Yabrud I rock shelter in Syria (1950). It includes three main industries: Acheulo-Yabrudian, Yabrudian, and Amudian, dating back to 420–200 ka BP (Barkai, Gopher, 2013; Zaidner, Weinstein-Evron, 2016). In the Acheulo-Yabrudian industry, primary reduction was aimed at producing flakes; handaxes and side-scrapers were predominant among the tools. The Yabrudian industry was also mostly flake-dominated, with small number of blades and various side-scrapers of the Quina and semi-Quina type. The Amudian industry had a distinctive laminar appearance.

The evidence from the stratified Misliya and Qesem caves in Israel, which was substantiated by reliable geochronological and paleogeographic research, is a notable part of AYCC (Barkai, Gopher, 2013; Zaidner, Weinstein-Evron, 2016). The Acheulo-Yabrudian industry from Misliya Cave shows three lithic reduction technologies: bifacial; removal of thin flakes from prepared cores, including some elements of the Levallois technique; and detachment of large massive flakes from unprepared cores, which served as blanks for handaxes and scrapers of the Quina and semi-Quina type. All main components of AYCC appeared in different proportions in the stratigraphic sequence of Qesem Cave. The Amudian tradition was dominated by distinctive laminar technologies. The Yabrudian industry of the cave included Quina scrapers and a relatively small share of blades. Rare handaxes appeared in both industries. Such variability was caused by changes in the economic structure and adaptation strategies of cave inhabitants rather than by the change in the carriers of cultural traditions. Geochronological data suggest the coexistence of the Amudian and Yabrudian industries (Barkai, Gopher, 2013).

The earliest assemblage from Denisova Cave and the Middle Eastern evidence were compared to reveal the presence of numerous so-called cores-on-flakes in both industries. For example, materials from Tabun Cave include several hundreds of such items appearing in different variants: with prepared striking platform and without traces of special preparation, with a negative scar of one flake or a series of removals from the ventral or dorsal sides (Shimelmitz, 2015). The use of parallel reduction technique aimed at producing elongated flakes was another important indicator of similarity. The role of blades in the earliest Denisovan industry was insignificant, but individual expressive specimens and carefully prepared cores testify to the developed methods of blade production. Judging by a few items, the Levallois reduction was uncommon; it became widely used in the next stage of the Middle Paleolithic.

A key technical and typological feature of the Denisovan industry denoting possible genetic links with the AYCC cultural traditions are representative series of ventrally thinned flakes and proximally truncated artifacts. The *Nahr Ibrahim* technique in Levantine industries was based on removal of small flakes from large spalls, both from the prepared limited area of the striking platform and from unprepared edge of the blank (Solecki R.L., Solecki R.S., 1970). Older flakes with patinated or rounded surfaces also often served as blanks in the Levant and Denisova Cave industries (Barkai, Gopher, 2013; Shimelmitz, 2015). This technique might have been used to obtain smaller blanks, or to adapt the implement to its fastening in a haft (Prévost, Zaidner, 2016). In Denisova Cave, the evidence of possible use of basal thinning for accommodation has been observed in a series of side-scrapers, and denticulate and spur-like tools.

The Early Middle Paleolithic industry of Denisova Cave and the Levantine complexes demonstrate the typologically expressive series of side-scrapers shaped by the Quina retouch. Their blanks were mainly large, shortened massive flakes (including radial core *débordantes*) and primary flakes. Cores for removing large tool blanks have not been discovered either in Denisova Cave or in Misliya Cave.

The share of bifacially shaped tools in the Altai Early Middle Paleolithic assemblages and at other Siberian sites, supposedly associated with the second half of the Middle Pleistocene, was insignificant, while in the AYCC industries bifacial techniques were important. In this regard, an interesting model was proposed by R. Barkai and A. Gopher. They suggested that the dietary stress caused by the disappearance of elephants from the Middle East led to the replacement of *Homo erectus* by hominins of a new lineage, who were better adapted to hunting smaller and faster animals (Barkai, Gopher, 2013). Biological replacement occurred along with significant cultural changes, resulting in the emergence of AYCC and development of laminar techniques on its basis. Increased mobility contributed to the spread of early populations beyond the Middle East, in particular, deep into Asia, which was accompanied by changes in the appearance of lithic industries affected by new landscapes and climate.

Methods of ventral thinning of massive flakes, widely used by the inhabitants of Denisova Cave, might have been a "residual" manifestation of bifacial technique. The question of whether such flakes, like numerous proximally truncated ones, were tool-like or core-like pieces, still remains open. In the earliest industry of Denisova Cave, flakes less than 5 cm were not subjected to secondary treatment. The use of small (1–3 cm) flakes, detached from the ventral surfaces of larger flakes, without any additional trimming, has been observed in the materials from Qesem Cave (Barkai, Lemorini, Gopher, 2010). Experiments have revealed the high efficiency of such flakes, lenticular in cross-section, with thin sharp edge and back, as knives, especially while cutting carcasses of small and medium-sized animals. In the Early Middle Paleolithic industries of Denisova Cave, the share of thinning flakes, as well as other types of small flake, is rather high, but the purpose of these artifacts is still unclear.

Conclusions

The arrival of carriers of the Middle Paleolithic traditions in Southern Siberia ca 300 ka BP is most likely associated with the eastward migration of the *Homo heidelbergensis* population from the Levant ca 450–350 ka BP (Derevianko, 2019). According to paleogenetic studies, at that time, late *Homo heidelbergensis* separated and populations of the Denisovans and Neanderthals emerged on the ancestral basis (Prüfer et al., 2014; Meyer et al., 2014). While settling in Western, Southern, and Central Asia, late populations of *Homo heidelbergensis* adapted to local environments and came into contact with the descendants of the Asian *Homo erectus*, which resulted in the emergence of a new taxon, i.e. the Denisovans, who inherited a small share of archaic genes through adaptive introgression (Prüfer et al., 2014).

Members of this wave of migration, first identified in Denisova Cave, brought to the Altai the methods of stone tool manufacture on flakes of deliberately prepared shape, removed from well-prepared cores: in particular, strategies of parallel and Levallois techniques. The origins of the technical and typological traditions of the early Denisovans can be observed in the Acheulo-Yabrudian industries of the Levant (Derevianko, 2018; Derevianko, Shunkov, Kozlikin, 2020).

The industry of the Early Middle Paleolithic in the Altai in the second half of the Middle Pleistocene is in good agreement with the evidence from traditional regions of research into the Eurasian Paleolithic. Pre-Mousterian and Early Mousterian industries without Acheulean bifaces, but with stable tool forms on flakes, evolved in Western and Central Europe within the period corresponding to the beginning of oxygen isotope stage 8, along with typical Acheulean complexes (Kuhn, 2013; Kozłowski, 2016). For some Early Mousterian industries, the most typical tools on flakes were still side-scrapers, as well as notched and denticulate items. According to the data on the geochronology of the Paleolithic complexes of Tabun and Misliya caves, the appearance of the Middle Paleolithic industries in the Near East corresponded to ca 250 ka BP (Zaidner, Weinstein-Evron, 2012).

The lithic industry from the lower cultural layers of Denisova Cave testifies to well-developed lithic technologies and successful adaptation by its dwellers to the natural environment and climate of the Altai Mountains in the second half of the Middle Pleistocene. According to the data of fossil DNA sequencing from anthropological remains and cave deposits of the Middle Pleistocene sediments, the Denisovans were the carriers of the Early Middle Paleolithic traditions (Slon, Viola, Renaud et al., 2017; Slon, Hopfe, Weiß et al., 2017; Zavala et al., 2021; Brown et al., 2022).

Further development of Middle Paleolithic traditions in Denisova Cave is reflected in the evidence from deposits that emerged at a time corresponding to oxygen isotopic stages 6–4. They include industries with different variants of parallel, Levallois, and radial techniques. The toolkit is based on side-scrapers and notched and denticulate tools; Levallois artifacts and Upper Paleolithic varieties occur widely. The typological diversity of cores expands and the number of blades among the spalls increases up the section. The share of tools of the Upper Paleolithic group gradually increases in the toolkit, with a simultaneous decrease of Levallois and denticulate-notched components. Approximately 50 ka BP, an Upper Paleolithic culture with a distinctive set of stone and bone tools, personal ornaments, and items of symbolic activity began to emerge among the inhabitants of the cave on a local Middle Paleolithic basis.

The presence of Denisovans in the cave during the Upper Pleistocene is indicated by anthropological finds and sequenced DNA from the deposits of layers 14 and 12 in the Main Chamber, at the boundary of layers 12.1/11.4 and in layer 11.2 in the East Chamber, and in the lower part of layer 11 in the South Chamber (Krause et al., 2010; Reich et al., 2010; Meyer et al., 2012; Sawyer et al., 2015; Slon, Hopfe, Weiß et al., 2017; Zavala et al., 2021; Brown et al., 2022). Anthropological and paleogenetic evidence of the prolonged stay of the Denisovans in the cave is consistent with the cultural continuity in the development of lithic industries. This suggests that the Denisovans were an autochthonous population, which was associated with the development of the Middle Paleolithic and the emergence of the Early Upper Paleolithic (Derevianko, Shunkov, Kozlikin, 2020). In the Middle Paleolithic layers of Denisova Cave, remains of the Neanderthals have also been found, their DNA has been sequenced from these sediments (Mednikova, 2011a, 2013; Prüfer et al., 2014; Slon, Hopfe, Weiß et al., 2017; Zavala et al., 2021; Brown et al., 2022); a bone has been discovered from a girl whose father was a Denisovan and whose mother was a Neanderthal (Slon et al., 2018). Archaeological evidence from the stratified column of cave deposits indicates the absence of drastic changes in the composition of the technocomplexes, and suggests joint habitation of the Denisovans and the Neanderthals in the cave. The role of Neanderthals in the development of the Middle Paleolithic culture of the Altai has yet to be established. Notably, Okladnikova and Chagyrskaya caves, located 100 km from Denisova Cave and inhabited by the late Neanderthals (Krause et al., 2007; Mednikova, 2011b; Buzhilova, 2013; Mafessoni et al., 2020), yielded lithic industries of the Micoquian appearance, based mainly on radial technique. These industries include predominantly convergent side-scrapers and bifacial tools (Mezhdistsiplinarniye issledovaniya…, 2018: 153–230; Kolobova et al., 2020).

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