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Denisovans, Neanderthals, and Early Modern Humans: A Review of the Pleistocene Hominin Fossils from the Altai Mountains (Southern Siberia)

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Abstract

This paper reviews significant issues related to the fossil hominins from the Altai Mountains of Siberia (Russia), namely Denisovans, Neanderthals, and early modern humans. Uncritical acceptance of the recovered information by some authors has resulted in unreliable chronologies of the Middle and Upper Paleolithic artifact assemblages and the animal and hominin fossils. We examine the chronostratigraphic contexts and archaeological associations of hominin and animal fossils and the lithics discovered at the Denisova, Okladnikov, Strashnaya, and Chagyrskaya cave sites. Taphonomic, site formation, and geomorphological studies show evidence of disturbance and redeposition caused by carnivore activity and sediment subsidence at these sites, which complicates the dating of the human remains. Our analysis indicates that the Middle Paleolithic is dated to ca. 50,000–130,000 years ago, and the Upper Paleolithic to ca. 12,000–48,000 years ago. The best age estimate for Denisovans is ca. 73,000–130,000 years ago. The ages of Neanderthals can be determined as more than 50,000–59,000 years ago, and of modern humans at roughly 12,000–48,000 years ago. Denisovan and Neanderthal fossils are associated with Middle Paleolithic complexes only.

Keywords Hominin fossils · Stratigraphy · Chronology · Artifacts · Paleolithic · Altai Mountains · Siberia

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Introduction

Investigations of cave sites in the Altai Mountains of Siberia, Russia, have discovered lithic artifact assemblages and animal and archaic hominin fossils (Neanderthals) since the 1980s to late 2000s. Application of ancient DNA (aDNA) analysis since 2010 has identified a previously unknown Pleistocene hominin group called Denisovans (e.g., Reich et al. 2010). These results generated wide scientific interest (e.g., Dennell 2019; Gibbons 2019). The recent discovery in Tibet of a mandible interpreted as Denisovan (Chen et al. 2019) increases the importance of the Altai fossils. Using the data provided by aDNA for the Denisovans, an attempt was recently made to reconstruct the anatomical profile of these hominins (Gokhman et al. 2019). Therefore, reliable information about the age and environmental conditions of Denisovans is crucial for understanding their place in human evolution.

Since the discovery of Denisovans at Denisova Cave (e.g., Reich et al. 2010), issues related to the chronology and archaeological association of the Altai paleoanthropological finds became important, not only for Siberia but also for the entire region of Eurasia and even for the whole world. This includes the relationship between Denisovans and Neanderthals and between Neanderthals and ancient modern humans (e.g., Nielsen et al. 2017; Yang and Fu 2018). Without more secure information of the chronology of two Late Pleistocene hominin species—Neanderthals and modern humans—and of Denisovans, our understanding of the interaction between these hominins is limited (e.g., Nielsen et al. 2017; Skoglund and Mathieson 2018). For the history of Paleolithic modern humans in Eurasia, the Siberian materials are extremely important (see reviews: Skoglund and Mathieson 2018; Yang and Fu 2018).

Another issue, still enigmatic, is why in several Paleolithic DNA samples from early modern humans in Asia (see Devièse et al. 2019; Fu et al. 2014; Raghavan et al. 2014; Sikora et al. 2019; Yang et al. 2017), there is no trace of admixture with Denisovans, while it is detected in a few early modern humans from East Asia (Massilani et al. 2020) and in extant populations of Asia and Melanesia (e.g., Browning et al. 2018; Sankararaman et al. 2016; Vernot et al. 2016). In other words, where and when did the interbreeding between Denisovans and early modern humans occur? Without knowing the age of the Denisovans in the Altai, it is impossible to shed light on this problem.

With respect to the taxonomic status of Denisovans, Reich et al. (2010) reason that more Denisovan genetic information and fossils are needed for a more complete diagnosis of this hominin group. This should hopefully allow us to determine if Denisovans are a separate species or a subspecies. So far, researchers have not referred to a holotype. The study of the history of Neanderthals also requires a solid chronological basis (e.g., Kuhlwilm et al. 2016; Meyer et al. 2012; Prüfer et al. 2014; Villanea and Schraiber 2019), and data from the Altai caves are crucial for this research. An overall understanding of human evolution in the Middle–Late Pleistocene would be incomplete without data on the Altai hominins (e.g., Galway-Witham et al. 2019).

We here review the geoarchaeological aspects of four cave sites in the Altai: Denisova Cave, Okladnikov Cave, Strashnaya Cave, and Chagyrskaya Cave (Fig. 1). Our focus is on the stratigraphic, taphonomic, and chronological contexts of the archaeological and anthropological materials; the regional Middle and Upper Paleolithic artifact assemblages associated with the Pleistocene hominin fossils are also

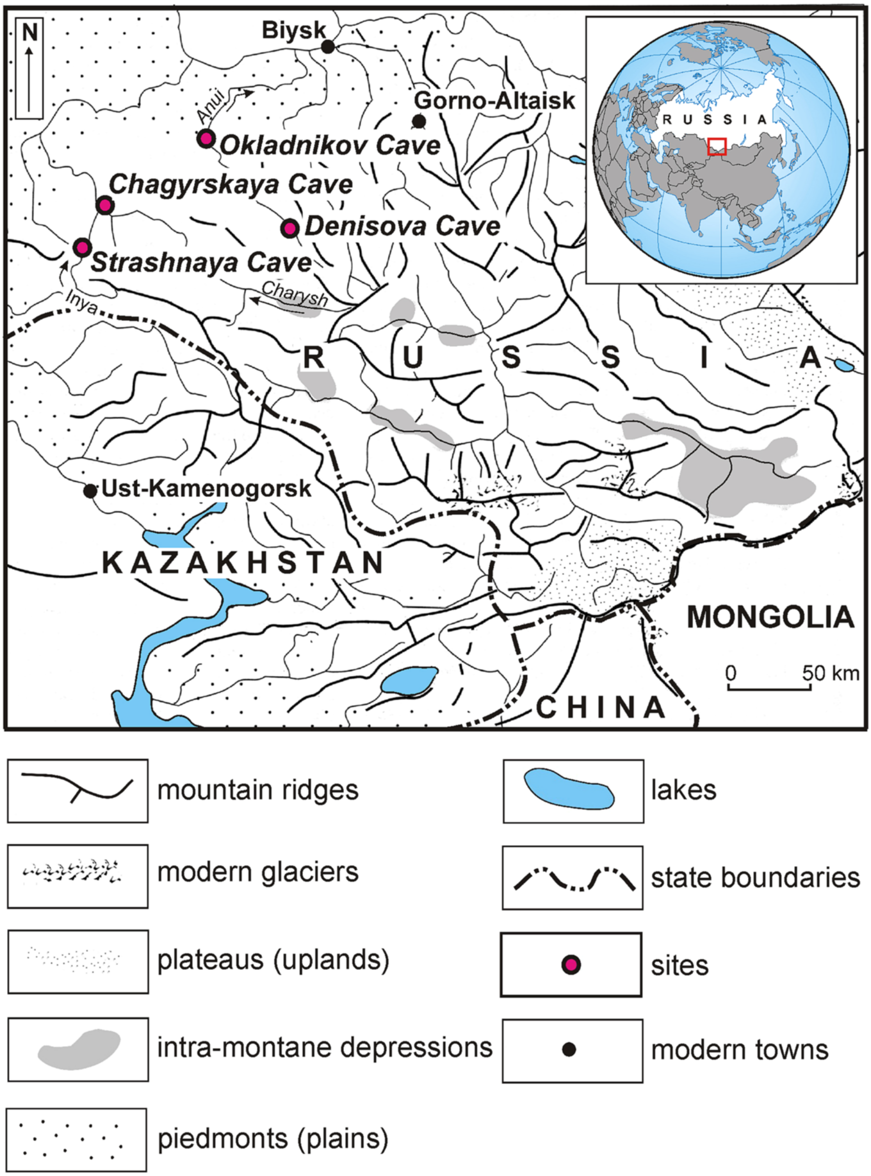


Fig. 1 The Altai Mountains and main geomorphological features (after Shahgedanova et al. 2002, p. 318; modified by Y. V. Kuzmin)

considered. Of especial importance is the evaluation of the dating methods used in the studies of these sites and their results and interpretations. We also review and evaluate issues related to the correspondence between hominin species and lithic assemblages in the Altai. Based on these, we put forward a hypothesis that links the Denisovans with the Middle Paleolithic, which existed in the first half of the Upper Pleistocene, with a simple parallel and radial knapping technique and the use of scrapers and denticulate-notched tools.

This is the first attempt of critical analysis of the geoarchaeology of Pleistocene hominin fossils and cultural complexes from the Altai, especially relevant in the light of recent progress made in Pleistocene hominin aDNA studies in Eurasia (see, e.g., Nielsen et al. 2017; Yang and Fu 2018) and in Siberia (e.g., Fu et al. 2014; Sikora et al. 2019). A well-founded chronostratigraphic framework is essential for understanding the patterns of the macroevolution of hominins and genetic distance between fossils.

Material and Methods

Our analysis of the hominin fossil record and its context in the Altai is to a large extent with reference to earlier publications on the archaeology and anthropology (Derevianko 2001; Derevianko and Markin 1992; Derevianko et al. 2003a, 2013a, b, 2014, 2018; Douka et al. 2019; Jacobs et al. 2019; Kolobova et al. 2020; Krivoshapkin et al. 2018; Otte 2019), geomorphological and sedimentological analyses (Baryshnikov and Maloletko 1998; Derevianko et al. 2003a, pp. 47–65; Morley et al. 2019), taphonomic and zooarchaeological studies (Derevianko et al. 2003a, pp. 178–196, 2018; Ovodov and Martynovich 2004; Rudaya et al. 2017; Turner et al. 2013; Vasiliev 2013; Vasiliev and Zenin 2009, 2010), and chronological information (Douka et al. 2019; Jacobs et al. 2019).

In their research of Pleistocene sites in Siberia, Turner et al. (2013) defined perimortem taphonomic variables and applied them to the paleontological and archaeological assemblages allowing both quantitative and qualitative examinations of bone damage. These taphonomic studies conducted at the Altai cave sites are of especial interest. They provide solid evidence of natural and biogenic disturbance and redeposition of the cultural layers, especially at the Denisova, Strashnaya, and Okladnikov sites (e.g., Turner et al. 2013). These processes have implications for interpretations of the fossils and artifacts; here, we reevaluate how they impact on our understanding of the chronological framework.

The chronology of the Altai cave sites has been examined based on different methods: radiocarbon (^{14}C), Uranium-series (U-series), and three luminescent techniques—radiothermoluminescence (RTL) (Vlasov and Kulikov 1989), optically stimulated luminescence (OSL), and post-infrared stimulated luminescence (post-IRSL) (Jacobs et al. 2019). Uncalibrated ^{14}C dates are given as "BP"; calendar dates obtained upon calibration of original ^{14}C dates are given as "cal BP" (Tables 2, 3, 4, 5, 6, 7) and "years ago" (in the main text). The U-series and luminescence chronologies are expressed in "years ago".

Several morphological investigations of Pleistocene hominin fossils have been conducted (Bennett et al. 2019; Buzhilova 2013; Derevianko et al. 2018; Mednikova 2011; Shpakova 2001; Turner 1990; Zubova et al. 2017a, b). Turner applied the Arizona State University Dental Anthropology System (ASU-DAS; see Scott and Turner 1997; Turner et al. 1991) to the Altai finds, while Shpakova (2001) used the Russian dental classification (see discussion in Turner et al. 2013, pp. 383–384). Zubova et al. (2017a, b) combine these two systems in their study. Ancient DNA studies of hominin fossils and Pleistocene sediments were conducted by Douka et al. (2019), Krause et al. (2007, 2010), Prüfer et al. (2014), Reich et al. (2010), Sawyer et al. (2015), Slon et al. (2017a, b, 2018), Mafessoni et al. (2020), and Petr et al. (2020).

One of the coauthors of this overview, Tsybankov, excavated the Denisova Cave in 2006–2011 under the leadership of Prof. Shunkov. Some of the factual data used in this review were gathered and observations of the Altai Paleolithic sites (including Denisova Cave) were undertaken by the present authors, including visits and examination of artifacts and fossils in 1998 and 2002–2003, and a brief visit to Denisova Cave in 2017. The idea to investigate the DNA of animals and hominins from caves in the Altai Mountains and apply direct ^{14}C dating to the fossils was conceived by Keates in 2002. Keates and Prof. Agadjanian at Denisova Cave began work in 2002 after a consensus reached with Profs. Derevianko and Pääbo.

The main object of this review, Denisova Cave, has been known since the late 19th century. Ovodov conducted the first scientific exploration in 1977 and discovered artifacts and animal fossils (see Okladnikov and Ovodov 1978). Excavations have been ongoing since 1982. Denisova Cave is situated in the Anui River valley (coordinates 51°24′ N, 84°40′ E), in the northern part of the Altai Mountains (Fig.1), at a height of ca. 25–30 m above the Anui River and an elevation of ca. 690 m above sea level (a.s.l.) (Fig. S1). It consists of the Main Chamber, East Gallery, South Gallery and the Entrance; the most intensively excavated parts are the Main Chamber, the East Gallery, and the entrance to the South Gallery (Figs. S2–S3).

The Okladnikov Cave was discovered in 1984 and excavated in 1984–1987. The site is located in the piedmont zone of the Altai Mountains (coordinates 51°44′ N, 84°02′ E) (Fig. 1), on the steep left bank of the small Sibiryachikha River, a tributary of the Anui River, at a height of 14 m above the floodplain (ca. 320 m a.s.l.) (Figs. S4–S5). The main parts of the cave are the Entrance (also called "Shelter" and "Terrace zone under the roof"), Grotto, and five galleries (e.g., Krause et al. 2007) (Fig. S6). Most of the archaeological and osteological materials were recovered from the Entrance area (Ovodov and Martynovich 2004). The hominin fossils are associated with Mousterian lithic technology (Derevianko et al. 2013a).

The Strashnaya Cave was discovered in 1966, and Okladnikov and Ovodov initiated excavations in 1969. Investigations continued from 1989–1994, later from 2006–2009, and since 2013. The cave is situated in the western part of the Russian Altai (coordinates 51°10′ N, 83°02′ E), near the middle stream of the Inya River, a tributary of the Charysh River (Fig. 1). The height of the cave above the river level is ca. 45 m (ca. 520 m a.s.l.) (Fig. S7). The cave shape is a horizontal tunnel, ca. 20 m long, with a relatively flat floor that inclines gently towards the entrance. The width of the entrance is ca. 2 m; height and width increase toward the interior of the cave (Zenin and Kandyba 2006).

The Chagyrskaya Cave is located in the western part of the Russian Altai (coordinates 51°27′ N, 83°09′ E), on the steep bank of the Charysh River, which drains the Tigirek Ridge (Fig. 1), about 25 m above the water level (ca. 360 m a.s.l.) (Fig. S8). It was discovered in 2008, and excavations are ongoing. The cave has two chambers (ca. 130 m^2 large) and three galleries.

All lines of evidence—geomorphological, stratigraphic, taphonomic, zooarchaeological, chronological, archaeological, and anthropological—were taken into account in this review. This kind of evaluation of the Altai fossil hominins has not been done before, and the results obtained by the excavators are usually accepted at face value (e.g., Galway-Witham et al. 2019; Kaifu 2017). The issues related to the correspondence between hominin species and archaeological assemblages, as well as the evolutionary model of the development of Paleolithic complexes in the Altai Mountains, are also discussed in the contexts of chronology, archaeology, and hominin taxonomy.

Pleistocene Hominin Remains from the Altai Sites

In Denisova Cave, there are now a total of 12 hominin fossils. These derive from the Main Chamber (layers 9.1 and 22.1), the East Gallery (layers 9.3, 11.2–11.4, and 12.3), and the South Gallery (layers 11.1 and 22[?]) comprising four Neanderthals, four Denisovans, one Neanderthal/Denisovan offspring, and three Hominin indeterminate; the majority of fossils are fragmentary (Tables 1, S1). The first fossil found (Denisova 3) was divided and sent to two aDNA labs; while the smaller part was delivered to the Max Planck Institute for Evolutionary Anthropology in Leipzig (Germany) (e.g., Reich et al. 2010), the larger part of the bone seemed to have been lost (Pääbo 2014, pp. 233–234). Only later was it traced and studied (Bennett et al. 2019).

Analysis of the mitochondrial DNA (mtDNA) of a phalanx fragment (Denisova 3) and nuclear DNA of Denisova 3 and 4 identified a previously unknown archaic hominin, named Denisovans. The mtDNA of a phalanx (Denisova 5) from layer 11.4 in the East Gallery is from a Neanderthal individual. Ancient DNA analyses identified a nuclear genome sequence of the Denisova 8 molar as Denisovan. Sediment samples yielded Neanderthal mtDNA in the East Gallery (layers 11.4 and 14) and the Main Chamber (layers 14.3, 17, and 19.1), and Denisovan mtDNA in the East Gallery (layer 15) (Douka et al. 2019).

Okladnikov Cave was first excavated in 1984 by Petrin, after which around 20 large plastic bags (ca. 25 kg each) with sieved and cleaned fossils were brought to the Institute of Archaeology and Ethnography in Novosibirsk. Five hominin teeth and some cranial and postcranial bones were discovered in the spring of 1985 by Ovodov by pure chance when he was able to look through the contents of one of the bags left at the institute (Ovodov and Martynovich 2004; see also Turner et al. 2013, pp. 200–201). The location of the rest of the bags remains unknown; they seem to

Table 1 Pleistocene hominin fossils from the Altai Mountains (early 2021)[a]

Cave	Location, layer	Fossils	Claimed cultural association	Species[b]
Denisova	Main Chamber, layer 9.1	Bone	Upper Paleolithic	Hominin indet.
	Main Chamber, layer 22.1	Tooth	Middle Paleolithic	D[c]
	East Gallery, layer 9.3	Bone	Upper Paleolithic	Hominin indet.
	East Gallery, layer 11.2	Bone	Initial Upper Paleolithic	D
	East Gallery, layer 11.4	Bone	Middle Paleolithic	N
	East Gallery, layer 11.4	Bone	Middle Paleolithic	N
	East Gallery, layer 11.4	Teeth	Middle Paleolithic	D, Hominin indet.
	East Gallery, layer 12	Bone	Middle Paleolithic	N/D
	East Gallery, layer 12.3	Bone	Middle Paleolithic	N
	South Gallery, layer 11.1	Tooth	Initial Upper Paleolithic	D
	South Gallery, layer 22(?)	Bone	Middle Paleolithic	D
Okladnikov	Entrance, layer 1	Bones	Middle Paleolithic	N
	Entrance, layer 2	Bone and tooth	Middle Paleolithic	N, Hominin indet. (AMH?)
	Entrance, layer 3	Bones and teeth	Middle Paleolithic	N
	Gallery 1, layer 7	Tooth	Middle Paleolithic	N
Strashnaya	Layer 3_1a, horizon 2	Bones and teeth	Upper Paleolithic	AMH
	Layer 3_1b	Tooth	Upper Paleolithic	?
	Layer 3.3	Bone	Upper Paleolithic	?
	Not identified	Bones	Not identified	?
Chagyrskaya	Layer 5	Bone	Middle Paleolithic	N
	Layer 6a	Bones and teeth	Middle Paleolithic	N
	Layer 6b	Bones and teeth	Middle Paleolithic	N
	Layer 6c/1	Bones and teeth	Middle Paleolithic	N
	Layer 6c/2	Bones and teeth	Middle Paleolithic	N
	Layer 6d	Bone	Middle Paleolithic	N

[a]List of references in Table S1

[b]D = Denisovan; N = Neanderthal; N/D = Neanderthal–Denisovan offspring; AMH = anatomically modern human

[c]Shpakova and Derevianko (2000) determined it as AMH; Turner (1990) assigned it to Neanderthal

have been lost, and it is clear that the curation of these hominin fossils was below the usually accepted requirements (e.g., Turner et al. 2013, pp. 201–202).

Twelve hominin postcranial bones and five teeth have been recorded for Okladnikov Cave by Buzhilova (2013; see also Mednikova 2011) of which eight fossils are listed by Krause et al. (2007) (Table S1). Initial study of the teeth was conducted by Turner (1990), who identified four adult molars from layers 2–3 in the Entrance and a deciduous tooth from layer 7 in Gallery 1. He considered the molars to be premodern and most like Neanderthal teeth, especially one of the layer 3 specimens (Turner 1990). In a subsequent study by Shpakova and Derevianko (2000, p. 137), the teeth were classified as modern human; they also identified some “eastern features.” According to Mednikova (2011), the postcranial bones can be compared to Neanderthal morphology.

A few other cranial and postcranial fragments from Okladnikov Cave total ten specimens (which Ovodov listed in a catalog compiled after 1987), for some of which the location is currently unknown (Ovodov and Martynovich 2004; Turner et al. 2013, p. 211): a humerus fragment from layer 1 of the Entrance; two skull cap fragments and a metapodial fragment from layer 1 of the Grotto; a humerus fragment, a calcaneus, and two patellae from layer 2 of the Entrance; a femur fragment from layer 3 of the Entrance; and a tooth root from layer 7 of Gallery 1. Only the two humeri are mentioned by Mednikova (2011) and Buzhilova (2013).

MtDNA studies using Neanderthal specific primers demonstrated the presence of Neanderthal DNA in samples of the two subadult femora (OK1 and OK2), while the adult humerus contained no Neanderthal DNA and also cannot be classified as modern human (Krause et al. 2007, p. 902, supplemental table 3). One possible explanation is that the DNA from the humerus has a mutation in the primer sequences and, thus, failed to react.

Teeth and bones of Neanderthal-like hominins were discovered in Strashnaya Cave in 1989 and 2009, the latter fossils deriving from layers 3_1a, 3_1b, and 3.3 (Vasiliev and Zenin 2010, p. 19; Zenin et al. 2006, p. 144; Tables 1, S1). Identification as Neanderthal was preliminary and was subsequently not confirmed by physical anthropologists, who state that the modern human fossils—eight teeth and a humerus—were discovered in 1989 in layer 3_1a (Zubova et al. 2017b) (Tables 1, S1). Krivoshapkin et al. (2018) mention that eight teeth, classified as modern human, were found in their 2013–2017 investigations in layer 3_1a, but the teeth illustrated are the same as those found in 1989 (cf. Krivoshapkin et al. 2018, fig. 5; Zubova et al. 2017b, fig. 2).

For Chagyrskaya Cave, 74 hominin fossils were recorded (Kolobova et al. 2020, supplementary information, pp. 15–18; see also Buzhilova 2013; Derevianko et al. 2018, pp. 244–271), mainly in layers 6b and 6c (Tables 1, S1). Different parts of the skeleton were found (often fragmentary). Analysis of the lower premolars shows that the remains belong to a minimum of four or five adult individuals (Derevianko et al. 2018, p. 274). According to Buzhilova (2013) and Derevianko et al. (2018), these fossils are the Altai group of Neanderthals, morphologically between Eurasian Neanderthals (Europe and Levant) and anatomically modern humans. Neanderthal mtDNA was identified from sediment samples (Slon et al. 2017b). The nuclear DNA of Chagyrskaya 8 (a manual phalanx, layer 6b) identifies it as Neanderthal (Mafessoni et al. 2020; see also Kolobova et al. 2020).

Main Archaeological Assemblages Associated with Hominin Remains from the Altai Sites

Here, we present the main features of the lithic assemblages of the four Altai caves with Pleistocene hominin fossils; more detailed information is available in Slavinsky and Tsybankov (2020). The major focus is on Denisova Cave as the most investigated and prolific Paleolithic site in the Altai.

Denisova Cave

Lithic artifacts from Denisova Cave belong to two main assemblages (see Derevianko et al. 2003a, p. 364; Jacobs et al. 2019): Middle Paleolithic in layers 12–21 of the Main Chamber and in layers 11.3–15 of the East Gallery (Fig. 2); and Upper Paleolithic in layers 9–11 of the Main Chamber, layers 9–11.2 of the East Gallery, and layers 9–11 of the South Gallery (Figs. S9–S11).

Krause et al. (2010) and Reich et al. (2010) describe layer 11 based on the lithic industry with both Upper Paleolithic and Middle Paleolithic elements. The collection is represented by a rich inventory of stone tools and a variety of bone tools and adornments (Shunkov et al. 2020a). The joint presence of Upper Paleolithic elements with leaf-shaped bifaces, scrapers, and grooved tools with Mousterian artifacts (as well as Levallois points) is difficult to explain. One possible interpretation is post-depositional mixture, but Upper and Middle Paleolithic elements found at other sites in the Altai Mountains (Derevianko 2001) indicate that this combination is a characteristic feature of the Early Upper Paleolithic in this region. For example, Middle Paleolithic elements were also found in the Initial Upper Paleolithic horizons 5 and 6 at the Kara-Bom site, and refitting studies by Zwyns (2012) indicate the absence of vertical movement between these horizons and the underlying Middle Paleolithic level MP1 (Krause et al. 2010). Bifaces and Levallois elements also occur in the Early Upper Paleolithic of Ust-Karakol 1 site.

Thus, the researchers of Denisova Cave, based on the results of technotypological analysis, determined that the archaeological collection of layer 11 (present in the Main Chamber, the East Gallery, and the South Gallery) belongs to the Upper Paleolithic (Derevianko et al. 2009, 2010, 2011). Later, however, the layer 11 lithic industry was reassessed, and the materials of layers 11.3–11.4 are now associated with the Middle Paleolithic (Derevianko et al. 2017; Shunkov and Kozlikin 2016). In our opinion, such a change in interpretation of archaeological collections due to the new dating is stipulated by the mixed character of the industry of layer 11 in the East Gallery. We, therefore, suggest that the archaeological materials of layers 11.3 and 11.4 and the top of layer 12 in the East Gallery are mixed.

As for the presence of bone points in the East Gallery directly ^{14}C-dated to ca. 41,200–42,900 BP (Douka et al. 2019, extended data, fig. 2), caution should be taken in determining these specimens as human-modified bones or the result of hyena gnawing (see Kuzmin and Keates 2020). In several cases, chewing and gnawing by animals with powerful jaws can result in the creation of pseudo-artifacts (e.g., Villa and d'Errico 2001). Because no use-wear study was done on these specimens

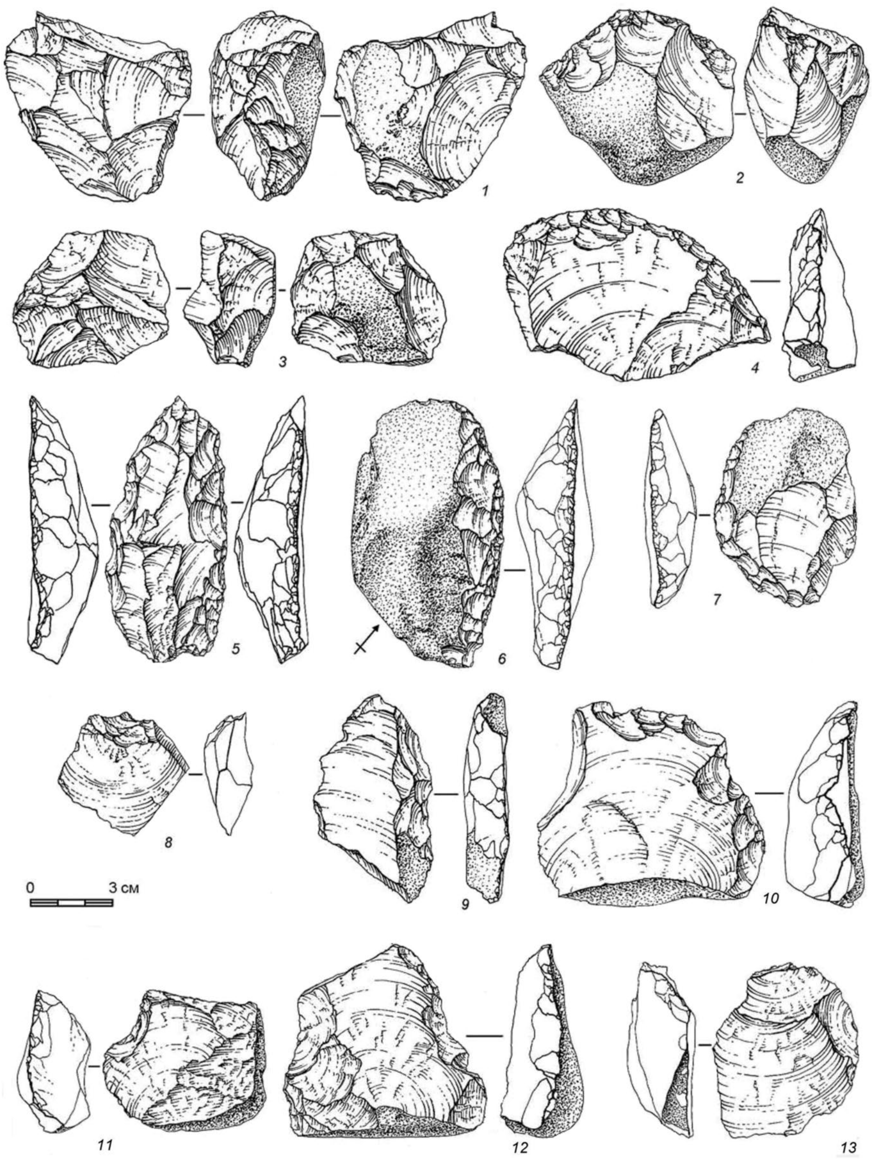


Fig. 2 Lithic artifacts of the early stage of the Middle Paleolithic from Denisova Cave (after Kozlikin 2016; modified by Y. V. Kuzmin): 1–3—cores; 4–7—side-scrapers; 8, 13—proximally truncated-faceted flakes; 9–10—denticulate tools; 11—notched tool; 12—flake with ventral trimming of longitudinal edges

(e.g., Shunkov et al. 2020a), one should be careful when such an early appearance of bone points in the Upper Paleolithic of Siberia is declared.

The collection of stone artifacts from layers 14–15 of the East Gallery has more than 15,000 items. Primary knapping is radial, aimed to obtain short blanks. The basic tool set consists of denticulate, notched, and spur-like tools, and scrapers. Levallois cores and points, typical for the overlying layers, are completely missing, as are stone artifacts of Upper Paleolithic appearance such as end and prismatic cores, scrapers, burins, and borers. According to Kozlikin (2016), based on a set of lithological and biostratigraphical data and preliminary results of luminescence dating (OSL and post-IRSL), the deposits of layers 14–15 were accumulated in the favorable climatic conditions of the Shirta interglacial of Siberia (corresponding to Marine Isotope Stage [MIS] 7). The age assessment and the technological and typological appearance of the industry indicate that layers 14–15 of the East Gallery can be correlated with the materials of the early stage of the Middle Paleolithic in the Main Chamber (layers 21–22) (Kozlikin 2016). It was also pointed out that the Paleolithic complexes from the lower part of the East Gallery and the Main Chamber of Denisova Cave are the oldest in the region after the Lower Paleolithic Karama pebble industry (Kozlikin 2016). Given the absence of Middle Pleistocene small mammals in the sediments of the lower part of the Main Chamber and East Gallery (see Shunkov and Agadjanian 2000), as well as the disputable quality of luminescent ages (RTL, OSL and post-IRSL), it is possible to conclude that the deposits of layers 14–15 were formed not earlier than the beginning of the Upper Pleistocene, ca. 130,000 years ago (see below).

The lithic industry of layer 11 of the South Gallery is characterized by a combination of Mousterian and Upper Paleolithic tool types, as well as by a developed technique of parallel primary flaking. This layer contains a small series of Levallois products. Side-scrapers on elongated blanks, an end-scraper with a high working edge, and a knife on a prismatic blade are among the Upper Paleolithic artifacts (Derevianko et al. 2000a). The appearance of the layer 11 assemblage, in our opinion, indicates a significant mixture of archaeological materials from different Paleolithic periods.

The presence of several fossil hominids in Denisova Cave and of adornments, including possible grave goods, for example, at least eight deer and fox tooth pendants, tubular beads, eggshell beads, and two perforated mollusk shells (Derevianko and Shunkov 2004; Shunkov et al. 2020a; see also Douka et al. 2019; Keates, personal observation 2002), may indicate that the cave also served as a place for hominin burial. The very fragmentary condition of hominin remains could be directly related to carnivore action. The direct ^{14}C dates of three pendants suggest three different episodes at ca. 32,400, ca. 39,900, and ca. 45,400 years ago (see Table S2).

Okladnikov, Strashnaya, and Chagyrskaya Caves

The lithic assemblages of Okladnikov Cave differ from those found at Denisova Cave, first of all by the presence of a Levallois component of the Sibiryachikha type (Fig. S10). The Levallois artifacts are represented by points and flakes with *chapeau de gendarme* striking platforms; they are dominant in layer 7 but not numerous in layers 6, 3, 2, and 1 (Derevianko and Markin 1992, p. 209). These artifacts are suggestive of short visits to the cave by Neanderthals who used the Levallois technique. The rare occurrence of these artifacts in strata above layer 7 can be explained by redeposition (see below). The disturbed nature of sediments in Okladnikov Cave can also explain the “younger” age of its artifacts compared to those of Chagyrskaya.

The archaeological materials from layers 5 (I–III)–10 in Strashnaya Cave belong to the Middle Paleolithic, and those from layers 3_1a–4 (I–II) belong to the Upper Paleolithic according to Derevianko et al. (2015a, b). Zubova et al. (2017b) and Krivoshapkin et al. (2018) distinguish three types of Upper Paleolithic stone industries: Denisovan phase (layer 3_3), with its origin related to the Middle Paleolithic; the Kara-Bom blade-based Initial Upper Paleolithic tradition (layer 3_1b); and late (advanced) Upper Paleolithic (layer 3_1a). Krivoshapkin et al. (2018) classify the layer 4 assemblage as Middle Paleolithic. In Chagyrskaya Cave, archaeological materials from layers 6a, 6b, and 6c/1–6c/2 (mainly from the two latter layers) are representative of the Middle Paleolithic (Mousterian) complex of Sibiryachikha type (Derevianko et al. 2013a; Kolobova et al. 2020).

General Characteristics of the Lithic Assemblages from the Altai Paleolithic Sites with Hominin Fossils

We suggest that by taking into account a high degree of mixture of the cultural sediments of Denisova Cave, as described below, and the stratigraphy and types of lithic industry of the open-air Paleolithic sites in the Altai, the main stages of development of the Paleolithic in the region (the Middle Paleolithic and the beginning of the Upper Paleolithic) are represented by five specific industries, including those present at Denisova Cave.

The Middle Paleolithic simple flake technique consists of parallel and radial primary flaking, with scrapers and denticulate-notched tools (Kozlikin 2016; Shunkov et al. 2020b) (Fig. 2). This complex is represented without admixture in layer 15 and probably in layer 14 of the East Gallery, in layer 22 of the South Gallery, and in layers 22.1–22.2 of the Main Chamber of Denisova Cave. It has also been documented in smaller amounts (as admixture) in the upper layers of all the cave’s sediments (except the Entrance zone). The timing for this complex is ca. 73,000–130,000 years ago (MIS 5). The upper boundary is not well determined; it could be ca. 55,000–60,000 years ago and can conceivably be estimated at the border of MIS 5 and MIS 4 and at the beginning of MIS 3. Considering the timeframe for Denisovans (see below), these hominins are possibly responsible for this Middle Paleolithic complex.

The Middle Paleolithic Levallois convergent technique for making points can be found without admixture in some parts of the Kara-Bom site (Mousterian or MP2) (Derevianko and Markin 1998; Slavinsky et al. 2016) and the Ust-Karakol 1 site (layer 18) (Derevianko et al. 2003a; Rybin and Slavinsky 2015) (Fig. S9). It is also present with admixtures at the Ust-Kan Cave (Lesage et al. 2020; Rudenko 1961), to lesser degrees at the Strashnaya and Okladnikov Caves (Derevianko and Zenin 1997; Krivoshapkin et al. 2016; Okladnikov et al. 1973), and at Denisova Cave with a gradual decrease beginning in layers 12–13 of the East Gallery, layer 21 of the South Gallery and Main Chamber, and layer 10 of the Entrance zone. The age of this complex is ca. 50,000–59,000 years ago, i.e., early MIS 3. The potential manufacturer of this Middle Paleolithic industry is Neanderthal.

The Middle Paleolithic radial Sibiryachikha technique was used to manufacture flakes that were often used as blanks for *déjeté* tools (Fig. S10). It occurs without admixture in Chagyrskaya Cave (Derevianko et al. 2013b) and with admixtures in Okladnikov Cave and possibly at Strashnaya and Denisova Caves. Kolobova et al. (2020) define the Chagyrskaya Cave assemblages as Micoquian, similar to those from eastern Europe. The timing for this complex is ca. 50,000–59,000 years ago, and the hominins associated with it were conceivably Neanderthals.

The Initial Upper Paleolithic bidirectional Kara-Bom technique for blade manufacture is found without admixture in some parts of the Kara-Bom site (Derevianko et al. 1998; Rybin 2014; Slavinsky and Rybin 2015; Slavinsky et al. 2016; Zwyns 2012; Zwyns et al. 2012) and the Maly Yaloman Cave (Derevianko and Petrin 1989;

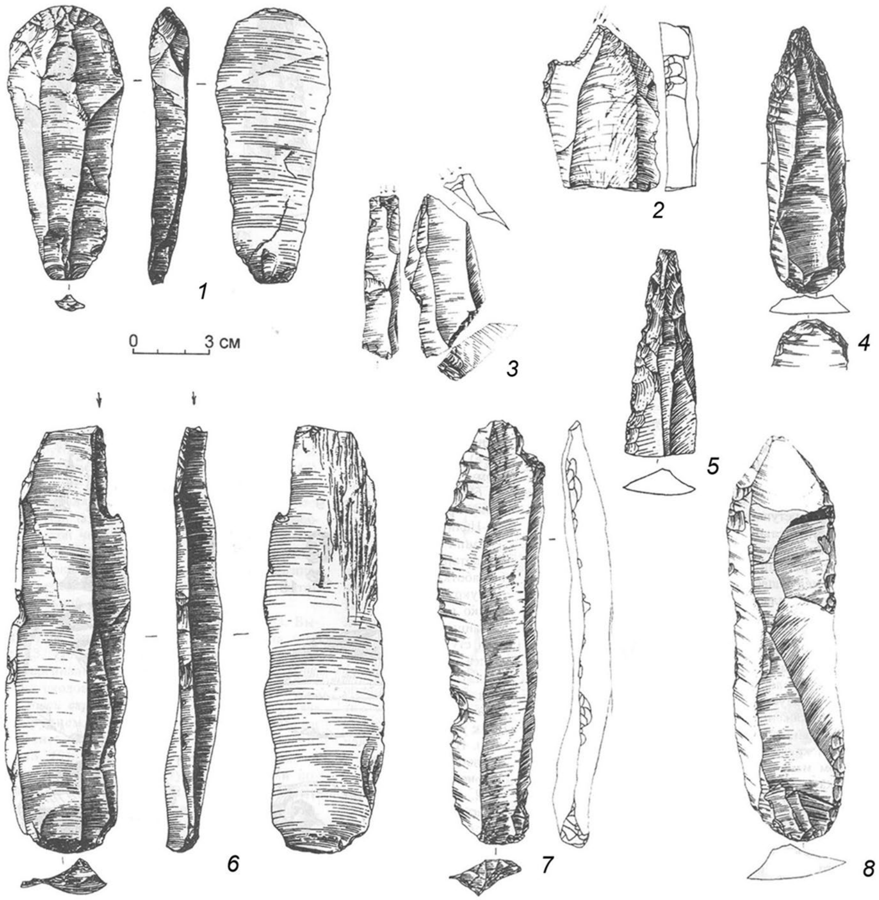


Fig. 3 Initial Upper Paleolithic industry of the Kara-Bom site (after Derevianko et al. 1998; Slavinsky et al. 2016; modified by Y. V. Kuzmin): 1—end-scraper; 2, 3, 6—burins; 4, 5—points; 7, 8—blades

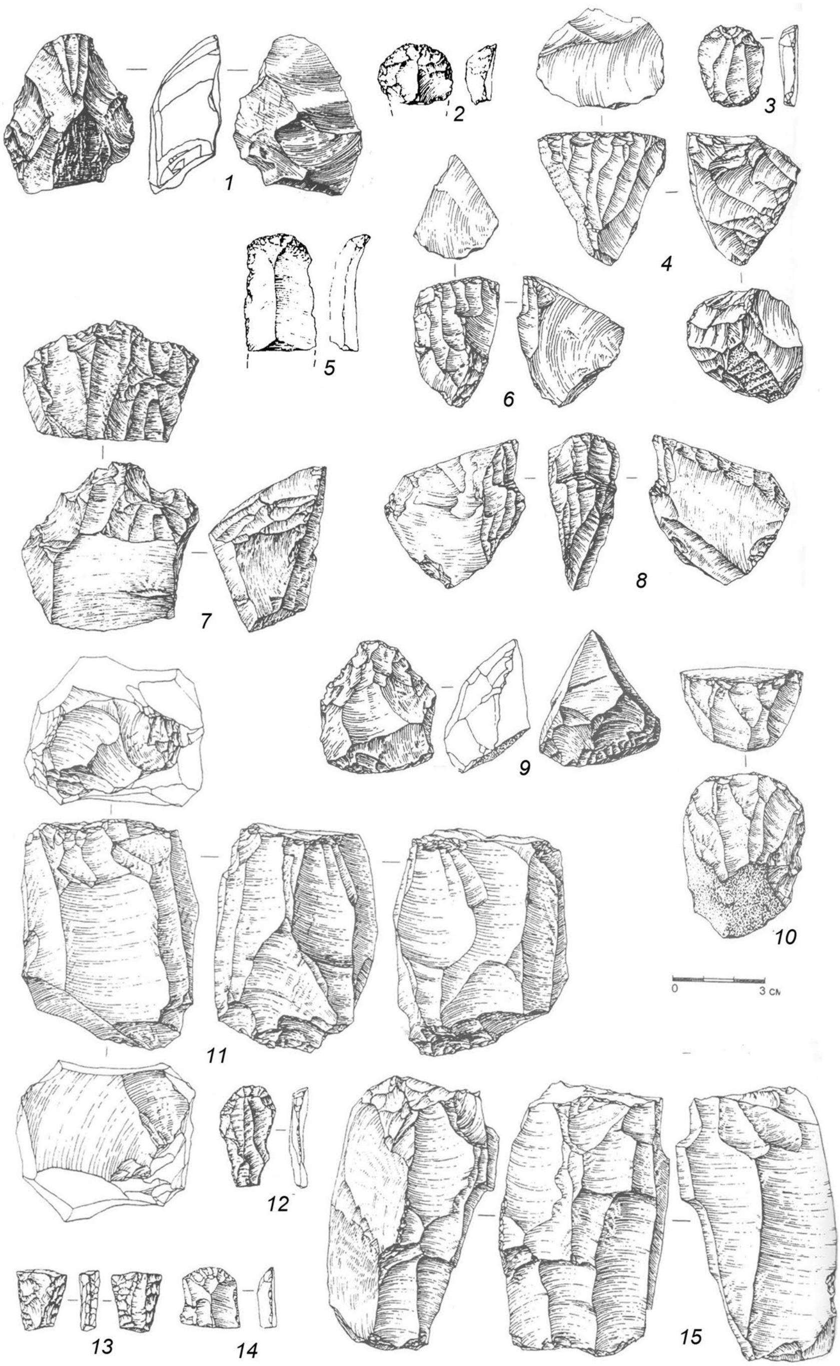


Fig. 4 Early Upper Paleolithic industry of the Karakol variant, Ust-Karakol 1 site (after Derevianko et al. 1998, 2000a, 2003a; modified by Y. V. Kuzmin): 1–3, 5, 7, 9–10, 12, 14—end-scrapers; 4, 6, 8, 11, 15—cores; 13—biface

Derevianko et al. 1998) (Figs. 3, S11). With admixture of both Early Upper Paleolithic and Late Upper Paleolithic, this industry is present in Denisova Cave (beginning with layer 12 of the East Gallery, layer 14 of the Main Chamber and South Gallery, and layer 9 of the Entrance zone), and in Strashnaya Cave, Anui 1, Anui 3, Kara-Tenesh, and Tumechin 4 sites. The time period of this complex is estimated as ca. 35,000–48,000 years ago, i.e., the middle of MIS 3. This industry could have been manufactured by anatomically modern humans.

The Early Upper Paleolithic unidirectional subprismatic technique for making blades uses carenoid cores for the production of small blades and bladelets (Fig. 4). It is represented without admixture at the Ust-Karakol 1 site (layers 8–11) (Belousova 2018; Derevianko et al. 2003a) and Anui 3 (Derevianko et al. 1998, 1999, 2000b). With admixture of later Upper Paleolithic assemblages, this complex has been documented at Denisova Cave (layer 11.4 and above of the East Gallery, layer 11 of the Main Chamber and South Gallery, and layer 8 of the Entrance zone), and at some other sites like Strashnaya Cave and Tumechin 4. The timing for this assemblage is preliminarily estimated as ca. 29,000–33,000 years ago, i.e., the end of MIS 3, although it is difficult to establish when this industry ceased considering the development and gradual changes in the late Upper Paleolithic and Mesolithic until the beginning of the Holocene. This industry is possibly solely linked to anatomically modern humans.

Stratigraphic Context, Taphonomy, and Chronology of the Altai Cave Sites with Pleistocene Hominin Fossils

Denisova Cave

The overall stratigraphy of Denisova Cave is quite complex, with frequent disturbances and deformations of the cultural layers caused by both natural and biogenic (animal and hominin induced) factors (Figs. 5, 6). Layer 11.3 in Fig. 5 is not depicted because it was not recognized in the test pit of 1995 (see Derevianko et al. 2003a, p. 74). The main body of the deposits was formed under influence of several earthquakes and, possibly, as a result of frost weathering; the latter is represented by clastic limestone material of the arch and walls of the cave. Numerous blocks of limestone, found everywhere, significantly deformed the stratigraphic units due to their weight. The complex profiles of the cave walls prevented a well-stratified formation of sediments. The parts near the walls with the greatest deformation of layers, caused by the contraction of deposits next to the limestone and an opening of a "crack" where artifacts of later times could have dropped down, and also by the burrowing activity of rodents in these spaces, sometimes constitute the main volume of the excavated areas.

It is important to remember that the cultural layers here do not always have clear boundaries (Derevianko et al. 2003a, p. 69). It is also necessary to keep in mind that Pleistocene lithological and cultural layers from different parts of the cave are not connected to each other stratigraphically, even though they have the same enumeration (e.g., Jacobs et al. 2019, p. 595). For example, the existence of a rock threshold

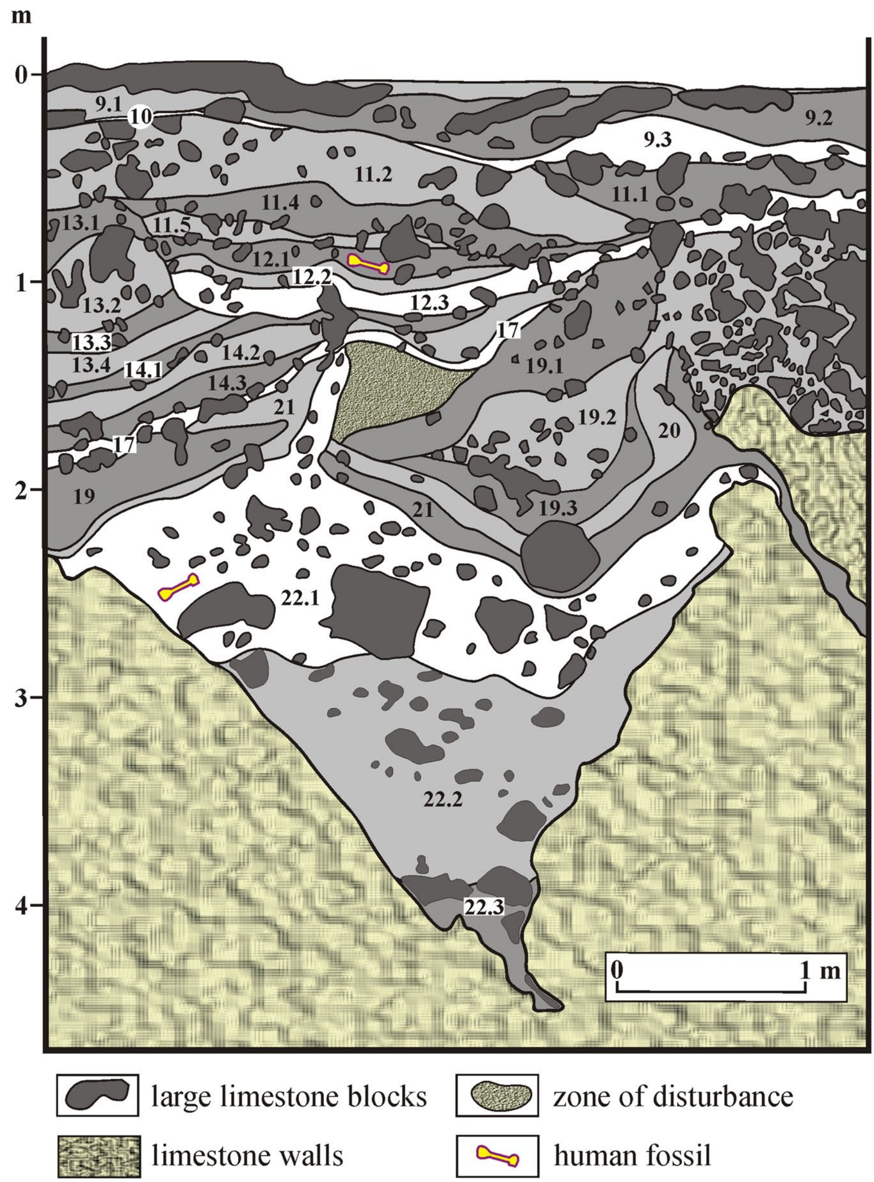
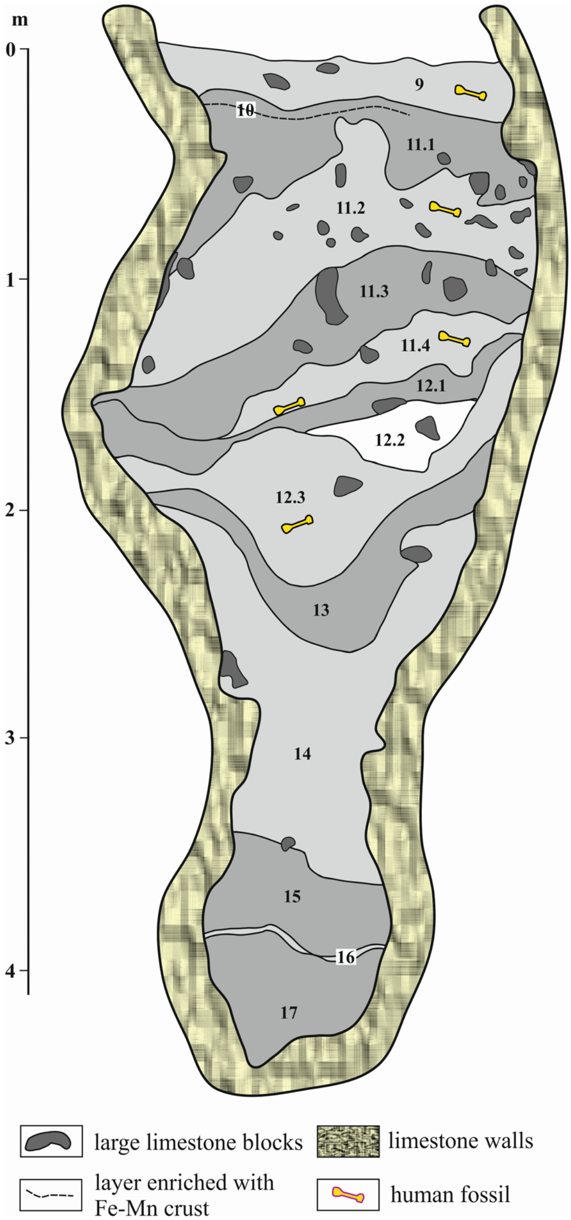


Fig. 5 Stratigraphy of the Pleistocene layers in the Main Chamber of Denisova Cave, 1995 test pit (after Derevianko et al. 2003a; modified by Y. V. Kuzmin); note that the horizontal and vertical scales are different

between layer 11 of the East Gallery and layer 11 of the Main Chamber makes it impossible to correlate the archaeological and chronological data from different parts of the cave directly, as was often done before (e.g., Derevianko et al. 2014, pp. 72–73). It seems that the excavators followed some *a priori* scheme for numbering

Fig. 6 Stratigraphy of the Pleistocene layers in the East Gallery of Denisova Cave (after Jacobs et al. 2019; modified by Y. V. Kuzmin)



the strata in different parts of Denisova Cave, without solid evidence of a stratigraphic connection between them.

Sedimentation in the Main Chamber was discontinuous, as a result of natural processes—episodes of rock fall, desquamation, and the flow of viscous loams under pressure of the above lying deposits; and biogenic processes—disturbance caused by the activity of cave hyenas and Paleolithic hominins. No channels were found. The sedimentation hiatus between layers 22 and 21 and denudation of the cave deposits are noteworthy (see Fig. 5). Turner et al. (2013, p. 89) warned about the existence of sedimentation gaps and disturbances in the Main Chamber, recently confirmed by Jacobs et al. (2019). It was also noted "… it is clear that there has been major post-depositional mixing in this part of the cave" (Reich et al. 2010, supplementary information, p. 85).

The deformation of sediments in the lower part of the Main Chamber (Derevianko et al. 2003a, p. 85), at the contact of layer 22 and the strata above it, is connected to the process of intra-mass differentiation of viscous and plastic loams and was caused by pressure of loose deposits situated above layer 22. In the East Gallery, several episodes of sediment subsidence are documented for layers 12.3–17 and 11.1–12.1 (Jacobs et al. 2019). Ulianov et al. (2015) found that the largest subsiding deformations in the sediments of layers 12.3–17.1 correspond to the axial line of the gallery. The most substantial amplitudes of subsidence in layers 11.1–12.1 shifted to the eastern corner of the section, to the area with negative angles (more than 90°) near the northeast wall of the East Gallery.

Derevianko et al. (2009) tried to downplay the conditions of sedimentation in the East Gallery by not mentioning traces of catastrophic events (blocks of disintegrated rocks), which in this case were periodic earthquakes that resulted in the weight of the limestone placing pressure on the deposits. Thus, the stratigraphy of layer 11.4 with the Denisova 8 fossil was not less affected by post-depositional deformations than layer 11.2 with the Denisova 3 fossil.

Layer 15 of the East Gallery has no noticeable post-depositional disturbances, and traces of cave hyenas are minimal (Fig. 6). Despite a lack of reliable radiometric dates for this layer (see below), its archaeological material is homogenous and is represented by a lithic tool assemblage without explicit evidence of admixture with later materials. All these factors point to the relatively in situ nature of layer 15.

We include here more specific data on the find locations of three fossils, since more detailed information is available for them. There is also the issue concerning the exact stratigraphic and planigraphic positions of some of the hominin fossils at Denisova Cave. The Denisova 3 bone was found in the 5-mm-mesh sieve from the sediments of grid D-2 in layer 11.2. Excavations were conducted using a trowel and removing the deposit in 3–5-cm-thick arbitrary levels, strictly within the boundaries of the grid; large artifacts and animal remains were recorded on a plan (without taking into account small lithic debitage and small fragmented bones). Afterwards, as a rule, all the sieved small mammal material from a certain grid and stratigraphic unit was put together. As a result, the material was analyzed as a single specimen. Thus, Denisova 3 in fact does not have a clear stratigraphic and planigraphic reference, and its location should be determined as grid D-2, layer 11.2, excavations of 2008. Grid D-2 covers almost 1 m^2 of space; the thickness of layer 11.2 within the boundaries of the 2008 excavations varies from 35 to 95 cm.

The Denisova 2 fossil was found in layer 22.1 of the Main Chamber during the first major excavation campaign in 1984. Similar to Denisova 3, the exact location of Denisova 2 is unknown. According to the major sources (Derevianko et al. 2003a, pp. 112, 364; Shpakova 2001; Shpakova and Derevianko 2000; Turner et al. 2013, pp. 87–89), the entire layer 22.1 is treated as a part of layer 22 within the 1984 excavation area and should be considered the place of discovery. The layer 22 deposit was discovered in 1977, and a test pit was excavated in that year. The main excavation campaign was in 1984, while work in 1993–1995, 1997, and 2016 focused on cleaning the 1984 excavation walls. The total area of the layer 22 deposits is about 15–18 m^2, with an average thickness of ca. 1.5–2 m.

The Denisova 4 fossil derives from the South Gallery, in grid G-2, layer 11.1, recovered during excavations in 2000 (e.g., Sawyer et al. 2015) (Fig. S3). Information about the discovery, however, was not published until aDNA research was conducted, because it was not identified as human until nine years after it had been found. The description of the stratigraphy of the deposits is presented in fragmentary fashion in several short publications (e.g., Derevianko et al. 2003b). Grid G-2 belongs to the southwestern part of the South Gallery. This area is separated from the northeastern part by a large block of limestone. Considering the large amount of limestone rubble in layer 11, up to 50–60% of the studied area as indicated in the description, we cannot exclude a neotectonic seismic cause of the appearance of this limestone block that "moved" layer 11 to one side of the underlying layers when it collapsed from the roof of the gallery. If we take into account that layer 10 lies on top of this block, and the base of the rock lies between layers 11 and 14, the hypothetical earthquake occurred at some time during the formation of layer 11 or of layers 11–14 as a whole; layers 12–14 contain an equally large share of rubble of slide-scree genesis. Layer 14 consists of intercalated layers of blocks and gravel of the same age. The considerable share of clastic limestone is an indicator of the strong gravitational disturbance of the sediments and, as a consequence, this process could have displaced the sediments and possibly mixed the archaeological materials in the South Gallery.

Taphonomic studies in Denisova Cave (see Derevianko et al. 2003a, pp. 178–196; Turner et al. 2013, p. 89) concluded that for most of the Pleistocene the cave was occupied by carnivores like cave bears and hyenas, who dug dens and, therefore, significantly disturbed the original stratigraphy. According to Derevianko et al. (2003a, pp. 196, 232–233), people periodically occupied the Main Chamber, especially during the accumulation of layers 11–14. On the other hand, Turner et al. (2013, p. 89) argued that hominins were hardly present in the cave (e.g., Baryshnikov 1999), and large mammal bones were transported into the cave by hyenas. This was recently confirmed by micromorphological studies of the Main Chamber and East Gallery (Morley et al. 2019); the large amount of hyena coprolites is an indicator of their frequent presence in the cave sediments, while the charcoal and ash as traces of hominin activities are found only in some layers.

The presence of bones with traces of acid erosion caused by carnivore digestion—up to 26% of all large mammal bones in the Main Chamber (Derevianko et al. 2003a, p. 191)—is another argument attesting to the predominant animal occupation of the cave. The amount of carnivore remains at Denisova Cave is very high: 50.9% in the Main Chamber, 36.3% in the South Gallery, and 31.7% in the East Gallery. The bone material is very fragmented. There are also several bones with traces of

Table 2 Radiometric age ranges for Main Chamber of Denisova Cave[a]

Layer and sublayer no.	^{14}C dates, cal BP[b]	Luminescent dates	
		RTL method[c]	OSL methods[d]
9	7960–8170[e]	–	22,600–36,800[f]
11	>41,980	–	45,700
11A	39,940–43,270	–	–
11G	42,430–49,790	–	–
11.2	37,030–40,560	–	41,300–58,200
11.2–3	39,620–41,280	–	–
11.3	37,040–42,260	–	39,400–49,700
11.4	37,050–>54,000	–	38,200
11.5	–	–	45,700
12.1	>54,000	–	56,600
12.2	–	–	67,800
12.3–4	>54,000	–	63,100[g]
13	–	–	114,500–157,400
14	–	69,000[h]	98,000–111,200
17	–	–	137,800
19	–	–	128,600–161,500
20	–	–	179,800–226,000
21	39,200–45,450	155,000	254,600[i]
22	–	171,000–282,000[j]	301,000–356,100

[a]All dates are in calendar scale (years ago), unless otherwise indicated. Standard deviations are not indicated (see Table S2; Derevianko et al. 2003a; Jacobs et al. 2019; Douka et al. 2019). Calibration of radiocarbon dates in Tables 2, 3, 4, 5, 6, 7 was performed using Calib Rev 7.0.4 software (available at http://calib.org/calib/), with ± 2σ; in some cases, with CalPal Online software (available at http://www.calpal-online.de), with ± 1σ; and by a rough estimate based on the Lake Suigetsu records (Bronk Ramsey et al. 2012)

[b]For the complete list, see Table S2

[c]See details in Derevianko et al. (2003a)

[d]See details in Jacobs et al. (2019). OSL and pIRSL techniques were used

[e]Sublayer 9.2

[f]For the east profile, the dates for this layer are 8600–46,900 years (Jacobs et al. 2019, Supplementary Information, p. 42)

[g]Sublayer 12.3

[h]Sublayer 14.1

[i]For the east profile, the date for this layer is 196,900 years (Jacobs et al. 2019, supplementary information, p. 42)

[j]For sublayer 22.1, the dates are 171,000–182,000 years, and for sublayer 22.2 – 223,000–282,000 years

burning, and some are cut marked (Derevianko et al. 2003a, p. 193; Turner et al. 2013, p. 89) and chop marked (Turner et al. 2013, p. 89).

Table 3 Radiometric age ranges for East Gallery of Denisova Cave[a]

Layer and sublayer no.	^{14}C dates, cal BP[b]	U-series dates[c]	Luminescent dates[d]
9	46,410–52,360[e]	–	10,300–13,800
11	18,830–34,570	–	–
11.1	31,100–57,230	–	43,100–46,200
11.2	38,080–>54,000	–	55,700–77,900
11.3	51,560–60,640	–	73,400–76,200
11.4	>51,780-54,400	–	103,500–123,000
12	–	67,500	–
12.1	–	–	113,000
12.2	–	–	143,300
12.3	–	–	128,200–139,000
13	–	–	147,400
14	–	–	194,700[f]
15	–	–	191,100
16	–	–	238,300[g]
17	–	–	294,100–351,300[h]

[a]All dates are in calendar scale (years ago), unless otherwise indicated. Standard deviations are not indicated (see Table S2; Jacobs et al. 2019)

[b]For a complete list, see Table S2

[c]See details in Douka et al. (2019)

[d]OSL, pIRSL and pIRIR techniques were used (see Jacobs et al. 2019)

[e]Sublayer 9.2

[f]For the northwest profile, the dates are 195,800–222,100 years ago

[g]For the northwest profile, the date is 247,500 years ago

[h]For the northwest profile, the dates are 256,900–508,100 years ago

The ^{14}C dates show that the chronology of Denisova Cave is not straightforward (Tables 2, 3, 4, S2; Fig. 7). For example, the ^{14}C age of layer 11.4 in the Main Chamber is older than that of layer 21. Similarly, layer 11 in the East Gallery has a wide range of ^{14}C dates produced on hominin-modified animal bones, ca. 19,000–34,200 years ago, some of which come from a disturbed context (Reich et al. 2010, supplementary information, p. 84). The "blurred" nature of the East Gallery layers is not surprising given the disturbed stratigraphy. This is also shown by the distribution of ^{14}C dates (Fig. 7b), where the age of layers 9.2–9.3 is older than the majority of ^{14}C values from the underlying layers 11.1–11.2. The South Gallery has a relatively consistent chronology, with the top layer ^{14}C-dated to ca. 33,500 years ago and the bottom of the sequence to ca. 53,000 years ago.

New ^{14}C dates (Douka et al. 2019) have only confirmed the severely distorted nature of the stratigraphic sequence of both the Main Chamber and the East Gallery. Douka et al. (2019) ignore previously published ^{14}C dates for layer 21 (see Tables 2, S2; Fig. 7a), which do not correspond to their age model. One can

Table 4 Radiometric age ranges for South Gallery and Entrance of Denisova Cave[a]

Cave	Layer no.	^{14}C dates, cal BP[b]	Luminescent dates	
			RTL method[c]	OSL methods[d]
Denisova Cave, South Gallery	10/11	32,890–34,060	–	–
	11.2	49,870–56,750	–	–
	12	–	–	49,200–58,900
	14	–	–	106,200–120,800
	19	–	–	125,500
	22	–	–	338,300–366,400
Denisova Cave, Entrance	9	46,820–53,020	50,000	–
	10	–	66,000	–
	12	–	101,000	–
	14	–	163,000	–

[a]All dates are in calendar scale (years ago), unless otherwise indicated. Standard deviations are not indicated (see Table S2; Derevianko et al. 2003a; Jacobs et al. 2019)

[b]For the complete list, see Table S2

[c]See details in Derevianko et al. (2003a)

[d]See details in Jacobs et al. (2019). OSL, pIRSL and pIRIR techniques were used

easily see that the new ^{14}C ages from the Main Chamber do not change with depth (Fig. 7a). This is a consequence of redeposition and was suggested by Turner et al. (2013, pp. 366–367), a source omitted by Douka et al. (2019), Jacobs et al. (2019), and Morley et al. (2019). The situation in the East Gallery (Fig. 7b) is also very unclear, with numerous age inversions.

Another aspect of the Denisova Cave chronology is the application of the RTL method, one of the luminescent dating techniques. According to RTL, the age of the layers is much older than the ^{14}C dates (Table 2). For example, while the ^{14}C values for layer 21 of the Main Chamber are ca. 39,700–43,400 years ago, the RTL date is ca. 155,000 years ago, with a large standard deviation of 20% of the RTL value (Table 2).

While the RTL dates are still accepted by some of the Denisova Cave researchers (e.g., Derevianko and Shunkov 2009; see also Jacobs et al. 2019), these dates are not compatible with the paleontological findings. According to Agadjanian (2001), Agadjanian and Serdyuk (2005), Baryshnikov (1999), Borodin et al. (2013), and Shunkov and Agadjanian (2000), the relative age of layer 22 based on the morphology and species composition of small mammals from the Main Chamber is not older than the beginning of the Upper Pleistocene, Eemian (Kazantsevo in Siberia) interglacial (MIS 5e). This conclusion was supported previously by Derevianko et al. (1998, p. 38). Similar views were expressed by Wrinn (2010) and Zwyns (2012, p. 303). This very warm period is dated to ca. 115,000–130,000 years ago (e.g., Berger et al. 2016). In contrast, at ca. 220,000–280,000 years ago, the RTL dates from layer 22 exceed the faunal chronology estimate, a discrepancy that has not been addressed by those favoring the RTL interpretation. The small mammals (water voles, *Arvicola* sp.) from layers 9-20 are representative of the Upper Pleistocene (Agadjanian

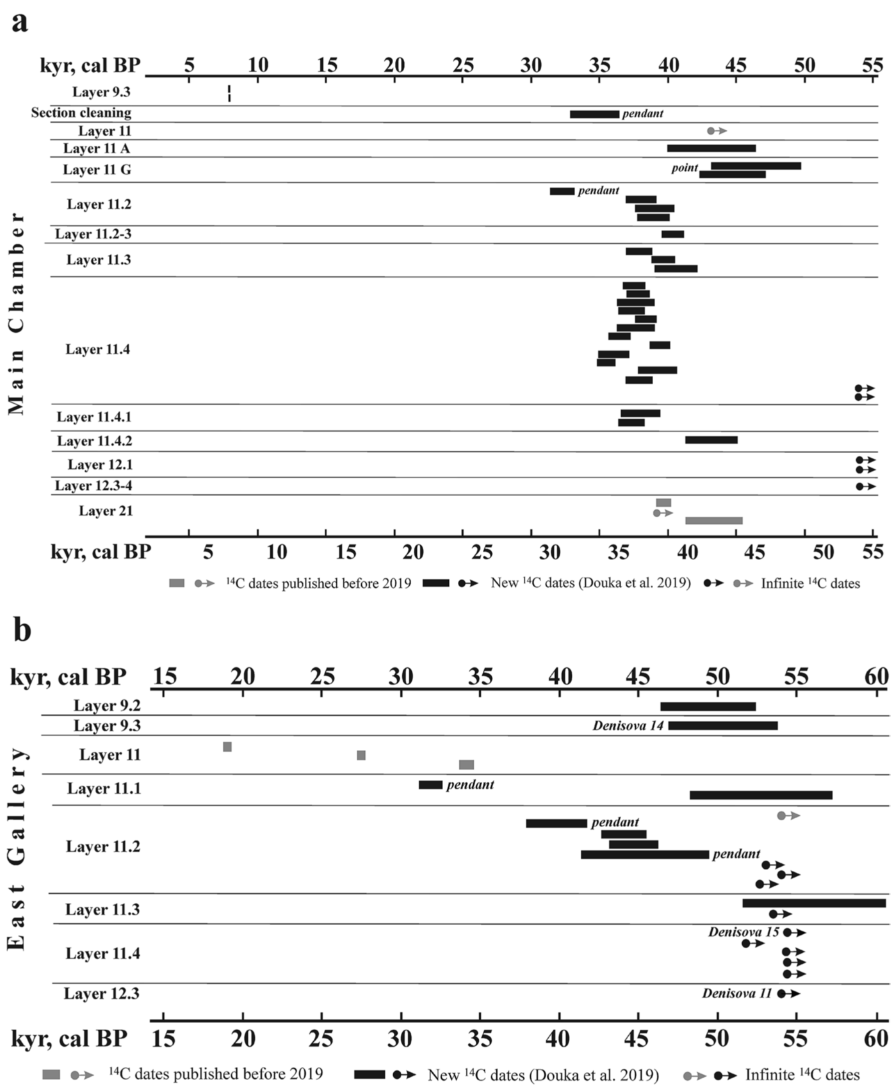


Fig. 7 a—Chronology of the Main Chamber of Denisova Cave (^{14}C dates are after Douka et al. 2019 and other sources; see Table S2), b—chronology of the East Gallery of Denisova Cave (^{14}C dates are after Douka et al. 2019 and other sources; see Table S2)

2001; Shunkov and Agadjanian 2000; see also Borodin et al. 2013). These studies are not mentioned by Derevianko and Shunkov (2009) and Jacobs et al. (2019). The recent application of OSL luminescent method (see Jacobs et al. 2019) resulted in ages of ca. 24,000–300,000 years. The ca. 300,000-year OSL age estimate for layer 22 contradicts the paleontological data (e.g., Shunkov and Agadjanian 2000).

In consideration of the redeposited and severely disturbed nature of the Denisova Cave sediments, the results obtained by Jacobs et al. (2019) are not surprising. Jacobs et al. (2019) accept the fact of post-depositional disturbance of the sediments in the cave, but they believe that the distortion of the stratigraphy does not affect their age model. However, this selective approach contradicts one of the basic principles of stratigraphic analysis: if a site is badly disturbed, it is impossible to construct a reliable chronology.

Okladnikov Cave

The stratigraphy of this cave is quite complex, with several disturbances attributable to natural factors (such as water erosion and large limestone blocks that fell from the roof of the cave) and by animal and hominin activities (Figs. S6b, c). Baryshnikov and Maloletko (1998, p. 19) point out that the stratigraphic units (layers) were to some extent determined provisionally, as the layers were illustrated with reference to the color of sediments and not according to the type of deposit. For example, in the Entrance area the older layer 3 intrudes into the younger layer 2 (Figs. S6b, c). According to Baryshnikov and Maloletko's (1998, pp. 53–55) geomorphological and Quaternary studies, the accumulation of layer 3 can be reconstructed. At ca. 40,000 years ago, the level of the Anui River rose, and a water current washed colluvial deposits from the cave entrance area into the galleries and deposited them there. The flow was quite strong, and in some places, it partially destroyed layer 7 and moved some of its stone material (including artifacts) into layer 3 of the galleries.

Maloletko's (1990) analysis of the stratigraphy of Okladnikov Cave concluded that only layer 7 is in a partially non-redeposited state, which survived only as fragments of the original sediments. Layer 7 (thickness is mainly 0.2–0.4 m, in some places up to 0.7 m) contains artifacts of two distinct Middle Paleolithic traditions—Levallois and Sibiryachikha (see above). This, in our opinion, reflects visits of the cave by two different groups of Neanderthals. We suggest that the stone artifacts of the two Middle Paleolithic variants, found above layer 7, were originally deposited in layer 7; they were moved into layers 6 and 1–3 after a series of strong redeposition events. The bottom of layer 3, containing angular rock fragments, was created as a result of a large earthquake (Maloletko 1990, p. 56); it corresponds to the end of hominin occupation of Okladnikov Cave.

This event corresponds well to similar phenomena observed in the sediments of Strashnaya and Chagyrskaya Caves (see below). We assume that this earthquake occurred during the early MIS 3 cooling. The presence of limestone fragments with traces of weathering in layer 3 of Okladnikov Cave (Derevianko and Markin 1992, pp. 53, 55) is an additional argument that supports a similar timing for a large earthquake in the Altai in the early MIS 3 cooling phase.

It, thus, appears that the process of sediment formation in Okladnikov Cave was far from a slow and continuous accumulation of sediments, rocks, animal bones, and artifacts. Beside the natural processes described above, the major contribution to redeposition was the activity of cave hyenas, as is clear from a meticulous study by Turner et al. (2013, p. 211): "… the perimortem taphonomy leads us to believe that hyena use of Okladnikov Cave far exceeded that of humans." There are 921 hyena bones (of 7679 medium and large-sized mammal bones, i.e., 12% of the total), of which teeth are the most numerous skeletal part (870, i.e., 94.5% of the total) (Ovodov and Martynovich 2004). It is worth mentioning that in Okladnikov Cave teeth constitute 90.7% of mammalian skeletal elements, which is much closer in frequency to hyena dens in the Altai Mountains such as Logovo Gieny [Hyena's Den] site (77.5%) than to open-air sites intensively occupied by hominins such as Ust-Kova in the Angara River basin (14.7%) (Ovodov and Martynovich 2004; see also Turner et al. 2013, pp. 303–311).

The chronology of Okladnikov Cave is based on ^{14}C dates and U-series values (Tables 5, S3). Most of the dates were obtained from layer 3 of the Entrance with the ^{14}C values in the range of ca. 36,600 to ca. 47,200 years ago. The ^{14}C age of layer 3 in Gallery 1 is ca. 32,600 years ago. The U-series value of ca. 38,700 years ago is from the bottom of the cave deposits in Gallery 1 (see Turner et al. 2013, p. 202) and is associated with layer 3 (Derevianko and Markin 1992; Derevianko et al. 2005). Two other U-series dates from layer 7 of Gallery 1 are ca. 44,600–44,800 years ago (Derevianko et al. 2005; Krause et al. 2007, supplementary information, p. 2).

Derevianko et al. (2003a, pp. 90–91) consider the U-series dates from layer 7 of Gallery 1 as the most reliable age estimates because this part of the cave was not disturbed by hyenas. The differences in ^{14}C dates from layer 3 of the Entrance are attributed to various contaminants by Derevianko et al. (2013a). None of these arguments is, however, convincing. First, the disturbance of sediments by hyenas is clear, and there is no "intact" stratigraphy in the entire cave. Second, contamination cannot make a ^{14}C age older than it is, because contaminants are very unlikely to be older than the dated bones. Careful cleaning of the samples and dating of the collagen, the most resistant part of the bone (e.g., Brock et al. 2010a, 2012), successfully eliminates contamination by modern carbon (e.g., Brock et al. 2010a, b).

The statement by Derevianko et al. (2013a, p. 91) that "… all the culture-bearing lithological strata in the cave date to 45–40 ka BP …" is not supported by the evidence, i.e., the ^{14}C and U-series values from Okladnikov Cave. The most probable reason for the wide variation and several age inversions (when the overlying layer

Table 5 Radiometric age ranges for Okladnikov Cave[a]

Site	Layer No.	^{14}C dates, cal BP[b]	U-series dates[c]
Okladnikov Cave, Entrance	1	36,070–39,410	–
	2	40,780–43,090	–
	3	36,560–47,220	–
Okladnikov Cave, Gallery	3	35,210–49,550	38,725
	7	–	44,600–44,800

[a]All dates are in calendar scale (years ago), unless otherwise indicated. Standard deviations are not indicated (see Table S3; Derevianko and Markin 1992)

[b]For the complete list, see Table S3

[c]See details in Derevianko and Markin (1992)

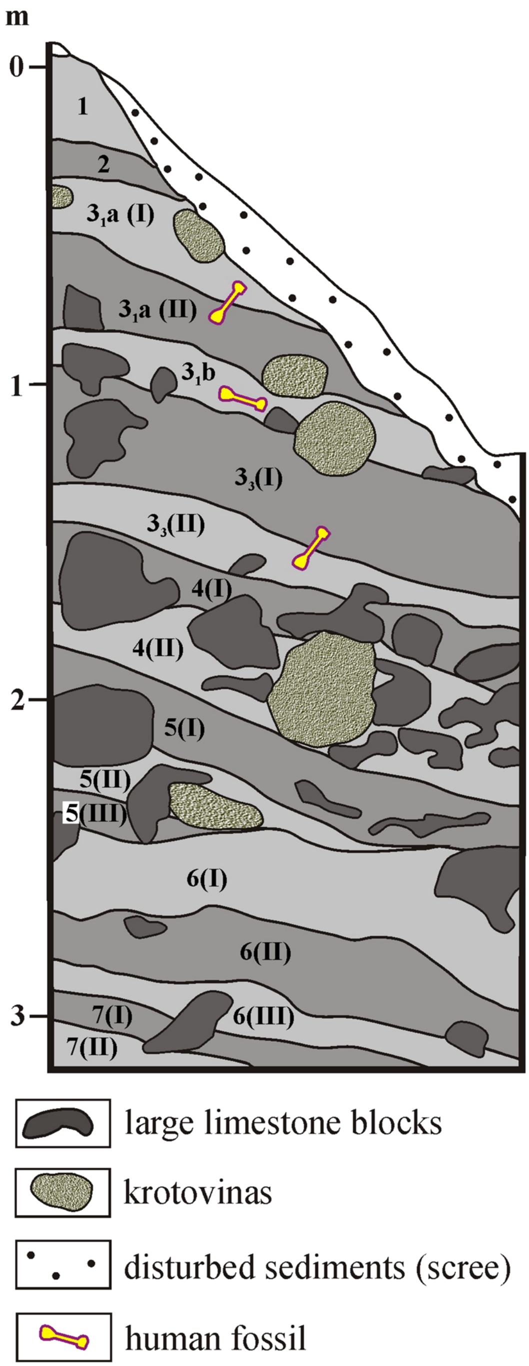


Fig. 8 Stratigraphy of Strashnaya Cave (after Derevianko et al. 2015; Krivoshapkin et al. 2018; modified by Y. V. Kuzmin)

has older dates compared to the underlying one) is significant disturbance of the site by hyenas (see Turner et al. 2013, p. 220).

Strashnaya Cave

The cave stratigraphy is very complex (Fig. 8). Since the 2006 campaign, particular attention has been given to the bioturbated layers that sometimes constitute half of the excavation area (Vasiliev and Zenin 2009). The largest contribution of this disturbance can be associated with the burrowing of gray marmots (*Marmota baibacina*). The activity of this rodent in Strashnaya Cave is unprecedented among the Altai cave sites, and its burrows (krotovinas) penetrate the cultural sequence (e.g., Krivoshapkin et al. 2013). A large number of carnivore remains (35.2% of all large mammal bones), mainly hyenas, was identified in all layers of the cave (Vasiliev and Zenin 2009, 2010). Vasiliev and Zenin (2010) concluded that hyenas and wolves played a major role in the accumulation of large mammal bones in the cave, while the activity of Paleolithic hominins was secondary in this respect. Another indicator of hyena activities is that 28.3% of the bones bear traces of acid erosion, which has led Turner et al. (2013, p. 273) to conclude that hyenas were probably the principal occupants of the cave. Another factor complicating the stratigraphic situation is the presence of large limestone blocks; these are often surrounded by artifacts and animal bones that penetrated from above (see Derev'anko and Markin 1998, p. 100), causing some of the redeposition. The stratigraphy near the walls is also disturbed (e.g., Zubova et al. 2017b). Overall, the cave deposits are quite mixed (Vasiliev and Zenin 2009, p. 60).

The first ^{14}C dates from Strashnaya Cave, published before 2013 (e.g., Vasil'ev et al. 2002; see Table S4), have a poor stratigraphic correspondence; thus, the

Table 6 Radiocarbon age ranges for Strashnaya Cave[a]

Layer and sublayer no.	^{14}C dates, cal BP[b]
3_1a	22,820–>44,630
3_1b	45,570–>53,000
3-3	>29,040
3 (III)	>44,630
4	>44,630–>49,210
4 (I)	>53,000
4 (II)	>44,630–>53,000
5 (I)	35,640–>44,630
5 (II)	>44,630–>53,000
5 (III)	30,780–>53,000
6 (III)	36,620–42,010

[a]All dates are in calendar scale (years ago), unless otherwise indicated. Standard deviations are not indicated (see Table S4; Krivoshapkin et al. 2013; Kuzmin et al. 2017; Vasil'ev et al. 2002; Zubova et al. 2017b)

[b]For the complete list, see Table S4

association of these dates with the stone tool assemblages is vague. The current set of ^{14}C values also does not fit the stratigraphy (Table 6). A good illustration for this is layer 3_1a with two ^{14}C dates, ca. 23,100 (average value) and > 44,600 years ago. The large difference between these ages and lack of correspondence to the ^{14}C chronology of the underlying layers are obvious. Another example is layer 5(I) with its three ^{14}C dates—ca. 39,300 to > 44,600 years ago—which are quite different from each other. In the lower part of the site's profile, the ^{14}C value from layer 6(III), ca. 39,300 years ago (average age), is considerably younger than the ^{14}C ages of the overlying layers.

All these examples may well be related to the disturbance of initially stratified cultural layers by hyenas (Turner et al. 2013, p. 273) and marmots (Vasiliev and Zenin 2009, 2010). The site's excavators accept that the chronology of Strashnaya

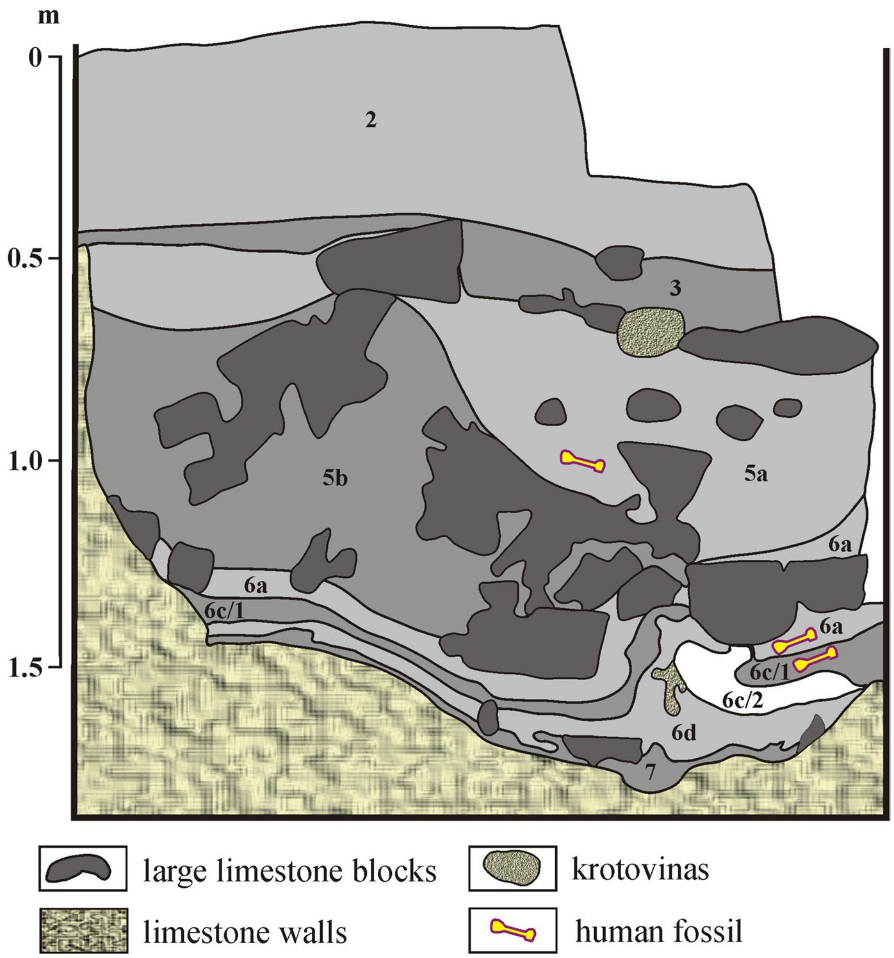


Fig. 9 Stratigraphy of Chagyrskaya Cave (after Kolobova et al. 2017; modified by Y. V. Kuzmin)

Cave is complex and ambiguous (e.g., Derevianko et al. 2015a, b; Krivoshapkin et al. 2018).

Chagyrskaya Cave

The stratigraphy of this cave (Fig. 9) is similar to the other cave sites in the Altai (especially Denisova and Strashnaya), with large limestone blocks and krotovinas that distort the sequence of layers. According to zooarchaeological data (Rudaya et al. 2017; Vasiliev 2013), many animal bones and teeth from layers 5 and 6 have traces of acid corrosion, a sign that they went through the digestive system of carnivores, mainly cave hyena and wolf. The ratio of carnivores in the large mammal assemblage is high, from 18.5% (layer 6) to 23.9% (layer 5) (Vasiliev 2013); the average value is 21.5% (Derevianko et al. 2018, p. 76). Chagyrskaya Cave was used

Table 7 Radiometric age ranges for Chagyrskaya Cave[a]

Layer and sublayer no.	^{14}C dates, cal BP[b]	Luminescent dates[c]
5.1	37,660–38,680	48,300–58,900[d]
5.2	>53,000	–
5.5	5050–5290	–
6a/1	>44,630–>53,000	47,700–53,300[e]
6b/3	>53,000	51,100–53,100[f]
6b/4	>53,000	–
6c/1,1	45,460–>53,000	52,300–60,300[g]
6c/1,2	48,740–56,860	–
6c/1,3	>53,000	–
6c/1,4	>53,000	–
6c/1,5	21,060–>53,000	–
6c/2	>53,000	52,900–54,600
6d	–	59,300–63,200
7[h]	–	309,000–347,000

[a]All dates are in calendar scale (years ago), unless otherwise indicated. Standard deviations are not indicated (see Table S5; Kolobova et al. 2020)

[b]For the complete list, see Table S5

[c]OSL, pIRSL, and pIRIR techniques were used (see Kolobova et al. 2020)

[d]Layer 5 (Kolobova et al. 2020, supplementary information, p. 63)

[e]Subunit 6a (Kolobova et al. 2020, supplementary information, p. 63)

[f]Subunit 6b (Kolobova et al. 2020, supplementary information, p. 63)

[g]Sublayer 6c/1 (Kolobova et al. 2020, supplementary information, p. 63)

[h]This layer does not contain any artifacts (Kolobova et al. 2020)

mainly by predatory animals (cave hyenas and wolves) as a den and/or shelter. Stratum 6c/1, horizons 1–5, yielded 13 cut-marked bone fragments, including ribs and long bones, some of which have several cut marks (Vasiliev 2013, p. 29). The cut marks were found mainly on Pleistocene bison, *Bison priscus* (Rudaya et al. 2017). It has been suggested that during the accumulation of layers 6b and 6c hominins periodically occupied the cave (Derevianko et al. 2018; Rudaya et al. 2017).

The sequence of ^{14}C dates is far less ambiguous at Chagyrskaya Cave (Tables 7, S5). For layers 5 and 6, most of the ^{14}C values are infinite, beyond the limit of detection by the radiocarbon method, from >46,600 to >53,000 years ago (Table 7). From layer 6c/1, some ^{14}C dates are finite, ca. 48,900 year ago (average value), while the 50,500 BP date is possibly infinite (Table S5). The youngest ^{14}C value, ca. 37,700–38,700 years ago, is from layer 5. With the exception of the youngest ^{14}C value, the age of the cave sediments is around 48,000 years ago and older. It is possible that cave hyena burrowing to some extent distorted the chronological picture (see Fig. 9 with deformed layers, especially 6c/1 and 6c/2), but in the absence of large age inversions the general situation looks quite homogenous.

The OSL ages for layers 5–6 are in the order of ca. 53,000 years ago (Derevianko et al. 2018, pp. 121–150; Kolobova et al. 2020) (Table 7), while layer 7 is significantly older at ca. 290,000–305,000 years ago. The latter age range, as in Denisova Cave (see above), is not in line with the paleontological data, which shows that only extant small mammals existed around the cave during the formation of layer 7 (Derevianko et al. 2018, pp. 104–108). If the OSL dates are correct, the age of layer 7 is in the Middle Pleistocene range, and the Altai, along with other regions of western Siberia at that time, was populated by quite different species of rodents (e.g., Borodin 1996). The site's excavators (Derevianko et al. 2018; Kolobova et al. 2020) do not explain this discrepancy.

As a result of the analysis of the stratigraphic and lithological features of the Denisova, Okladnikov, Strashnaya, and Chagyrskaya Caves as presented above, including our first-hand knowledge, we conclude that the stratigraphy of these sites was greatly affected by both natural and biotic factors. Especially important is the activity of animals that dig large depressions (hyenas, bears, and wolves) and burrows (rodents, especially gray marmots), initially established by Turner et al. (2013). The impact of the severe distortion of cave sediments resulted in the disturbance of the cultural strata, which is reflected in the contradictions of the sites' chronology. Therefore, these caves cannot serve as reference objects for understanding the differences between the lithic assemblages and the chronology of hominin fossils.

Discussion: Critical Evaluation of Results

The Direct ^{14}C Ages of Pleistocene Hominin Fossils from the Altai

The key to establishing valid dates of hominin fossils is, in our opinion, their direct age determination, as indirect dating on associated material can result in inaccurate age estimates (e.g., Conard et al. 2004; Keates et al. 2007; Kuzmin and Keates 2014; Street et al. 2006). For example, during excavation of a small rock shelter called

Sibiryachikha 6 (Fig. S5), about 100 m from Okladnikov Cave, Ovodov retrieved a child's humerus along with animal bones of extinct Pleistocene species (woolly rhinoceros and cave hyena) (see Turner et al. 2013, pp. 199, 218). Ovodov submitted this hominin fossil to us for direct AMS ^{14}C dating. The age of the bone was determined as 2370 ± 55 BP (AA-83721), thus, showing that it belongs to the Late Holocene despite associated Pleistocene-age animal finds in the same layer. Another recent example comes from the famous Sungir (a.k.a. Sunghir) site in central Russia. Here the human mandible of Sungir 6 was found near the Sungir 2 skeleton, ^{14}C-dated to ca. 26,200–27,200 BP (e.g., Kuzmin 2019; Kuzmin et al. 2014). The direct ^{14}C age of Sungir 6 turned out to be only ca. 880–930 BP (Sikora et al. 2017). These are clear cases of how easily the relative age of human fossils can be misidentified. Therefore, there is a need to date the Altai Paleolithic hominins directly. There are presently four direct dates generated for Denisova Cave (three ^{14}C dates and a U-series date) and four ^{14}C dates from Okladnikov Cave (Table 8) (Douka et al. 2019). Some of these values require comments.

The ^{14}C age of the Denisova 14 individual of an uncertain species from layer 9.3 (e.g., Douka et al. 2019) is at odds with the chronology of the underlying layers (Fig. 7b), perhaps due to redeposition; this was ignored by Douka et al. (2019). As for the two hominin humeri from the Entrance of Okladnikov Cave, the age of an adult humerus from layer 2 is ca. 28,300 years ago, and the juvenile humerus from

Table 8 Direct ^{14}C dates of Paleolithic hominins from the Altai (after Douka et al. 2019; Krause et al. 2007)

Site and layer	^{14}C date (BP)	Lab code	Species[a]	Skeletal part
Denisova Cave, layer 9.3[b,c]	46,300 ± 2600	OxA-36011[d]	Hominin indet.	Long bone
Denisova Cave, layer 11.4[b,e]	>50,200	OxA-36012[d]	N	Long bone
Denisova Cave, layer 12.3[b,f,g]	>49,900	OxA-32241[d]	N/D	Long bone
Okladnikov Cave, layer 3[h,i]	29,990 ± 500	KIA-27011[d]	N	Juvenile humerus
	34,860 ± 360	Beta-186881	N	Juvenile humerus
	37,800 ± 450	OxA-15481[d]	N	Juvenile humerus
Okladnikov Cave, layer 2	24,260 ± 180	KIA-27010[d]	Hominin indet. (AMH?)	Adult humerus

[a]N = Neanderthal; N/D = Neanderthal–Denisovan offspring; AMH = anatomically modern human

[b]East Gallery

[c]Denisova 14 individual

[d]Ultrafiltered collagen (e.g., Higham et al. 2006) was dated

[e]Denisova 15 individual

[f]Denisova 11 individual

[g]U-series dating gave a minimum age of the Denisova 11 individual of 67,500 ± 2500 years (Douka et al. 2019)

[h]OK1 individual

[i]In Krause et al. (2007, supplementary information 1, p. 1), the average value of 34,190 ± 760 BP is given for these three dates. Now, all of them are highly debatable (see Higham 2019, p. 1073)

layer 3 was dated to ca. 34,000–42,100 years ago (see Kuzmin and Keates 2020, table 1). The lack of DNA (Krause et al. 2007) in the adult humerus makes species assignation very difficult, although the ^{14}C date may indicate a representative of modern humans, also suggested by the presence of this species at that time and before in Siberia (Kuzmin and Keates 2014; see also Mednikova 2011, p. 88). The direct ages of early modern humans in Siberia are ca. 16,900–45,000 years ago (e.g., Fu et al. 2014; Kuzmin and Keates 2014, 2020). The ^{14}C date of the layer 2 humerus is much younger than the ca. 41,900-years-old animal bone from the same layer; another animal bone from layer 1 dates to ca. 37,700 years ago.

The wide variation of ^{14}C ages of the same juvenile humerus from layer 3, within around 7800 ^{14}C years (see Table 8), makes all these values less reliable, despite the collagen being of seemingly satisfactory quality (see Krause et al. 2007, supplementary information, p. 3). The issue of the age for this bone has so far not been resolved (e.g., Kuzmin 2019; Kuzmin and Keates 2014). It has now been indicated by Higham (2019, p. 1073) that this hominin (presumably the juvenile humerus from layer 3) has been redated to greater than ca. 53,000 years ago, that is, outside the detection limit of the radiocarbon method. This makes the issue of the direct age of hominin fossils from Okladnikov Cave even more confusing, because all the other ^{14}C and U-series dates are finite, i.e., less than ca. 53,000 years ago.

Chronological Framework for Hominin Fossils from the Altai Mountains

One of the main issues for the Altai Paleolithic sites with hominin remains is their chronology. Unfortunately, in most of cases it is not satisfactory, and here we point out the major discrepancies. The overall chronology of Denisova Cave is puzzling. The ^{14}C dates presented by Douka et al. (2019) (Fig. 7) have substantiated the very disturbed stratigraphy of both the Main Chamber and the East Gallery. The application of Bayesian modeling to an unsatisfactory stratigraphic sequence (Douka et al. 2019) is difficult to reconcile with the concept of stratigraphic integrity, a precondition for the use of Bayesian statistics (Bayliss 2009).

Nevertheless, the age of layer 11 at Denisova Cave (including the Main Chamber and galleries) of ca. 44,000–53,000 years ago is accepted by Derevianko et al. (2014) to accommodate the chronology of several important innovations in the early Upper Paleolithic—adornments, eyed needles, a stone bracelet, and a “diadem” (or “bracelet”) of mammoth ivory (Derevianko et al. 2016; Shunkov et al. 2020a, pp. 9–17). Some researchers (e.g., d’Errico et al. 2018; Gilligan 2019; Hoffecker 2017; see also Pitulko and Pavlova 2019, p. 159) are not convinced of such an early appearance of eyed needles at Denisova and Strashnaya Caves. The dated layer 11 context ranges from >53,000 to ca. 19,000–36,000 years ago, while eyed needles in other layers have indirect ages of ca. 29,000 and ca. 20,500 years ago (d’Errico et al. 2018). According to d’Errico et al. (2018), using all of the information discussed here, it is impossible to establish the age of these artifacts with any degree of certainty. Directly ^{14}C-dated pendants from Denisova Cave are in the age range of ca. 32,000-45,000 years ago (Fig. 7).

The chronology of Okladnikov Cave is also confusing and unresolved. Currently, one can assume the age of its layers as up to ca. 57,000 years ago, without a reliable estimate of the minimum age. A similar situation can be observed for Strashnaya Cave, with a wide variation of ^{14}C values.

Along with the ^{14}C method, sediments of Denisova and Chagyrskaya caves were dated by luminescent techniques. The use of the RTL method in Siberian archaeology has shown that the results obtained by this technique are not reliable. For example, the ages of >1,000,000 years ago and 2,900,000 ± 950,000 years ago for the Diring Yuriakh site in Yakutia (Mochanov and Fedoseeva 2008) are significantly older than the non-RTL luminescent dates of ca. 267,000–366,000 years ago (Waters et al. 1999). At the open-air site of Ust-Karakol 1 in the Altai, the RTL age for layer 9C is ca. 50,000 years, while the ^{14}C dates are ca. 33,900–37,600 years ago (Kuzmin 2000).

According to Slon et al. (2017a, p. 3), the Denisova 2 fossil was found in layer 22.1 of the Main Chamber of Denisova Cave, with a RTL date of between 128,000 and 227,000 years. However, the RTL ages from this layer are ca. 171,000–182,000 years (Table 2; see Derevianko et al. 2003a, p. 110). Also, Slon et al. (2017a, pp. 3–4) state that the Denisova 2 individual lived at least 100,000 years ago. Both of these conclusions are incompatible even with the site's RTL chronology as accepted by Derevianko et al. (2014).

Huntley (1992) criticizes the RTL methodology used by Vlasov and Kulikov (1989). When compared to other dating methods at Denisova, the results of RTL dating do not fit. In cave sediments, the history of bleaching is not known. In the case of Denisova Cave, the proportions of Silurian limestone from the cave itself and washed-in sediments from outside of the cave are unknown (see Agadjanian and Serdyuk 2005, p. S651). Other factors that complicate matters in evaluating the validity of the RTL dates are animal and hominin disturbance of the deposits (see above). Therefore, it is not possible to use RTL dates to determine the age of Denisova Cave and other sites, as some researchers still do (e.g., Jacobs et al. 2019).

The application of OSL method (see Jacobs et al. 2019) resulted in ages that are at variance with the paleontological record of small mammals (e.g., Derevianko et al. 2018, pp. 104–108; Shunkov and Agadjanian 2000; see above). Therefore, different kinds of luminescent dating have failed to produce reliable ages for Denisova Cave. Further, the dated mineral grains were redeposited a number of times.

The use of the Bayesian approach to the sequence of age determinations at Denisova Cave as employed by Douka et al. (2019, p. 643) shows clearly that at least two key hominin fossils were redeposited, and their "modelled age estimates" are not in accord with the site's stratigraphy. By moving the key fossils of Denisova 2 and Denisova 11 farther up in the section, Douka et al. (2019) have built a more coherent model. This, however, contradicts the supposed site's integrity (sensu Jacobs et al. 2019) and also demonstrates severe disturbance of the layers. In our opinion, Bayesian modeling should not be used in such insecure cases.

The uncritical acceptance of luminescent dates for Denisova Cave (sensu Douka et al. 2019) do not bring scholars any certainty in estimating the age of Denisovans and Neanderthals at this locality. This is quite similar, in our opinion, to the situation in East Africa in the 1970s when the argon–argon (Ar–Ar) dates of ca. 2.6 million years ago associated with artifacts at the Koobi Fora site conflicted with the paleontological information (see Lewin 1987). Only careful redating of the key KBS Tuff made it possible to conclude that the initial age was too old. Another example is the ^{14}C dates of animal bones at Kent's Cavern (UK) and their projection on modern human fossils from supposedly the same layer (Higham et al. 2011); it was shown to be invalid (White and Pettitt 2012). It is clear that only a nonbiased approach that takes into account all lines of evidence can generate reliable ages. This approach was not taken by the Denosiva Cave excavators (e.g., Douka et al. 2019).

In light of this analysis, it is necessary to evaluate the latest data generated for Denisova Cave (Douka et al. 2019; Jacobs et al. 2019). Jacobs et al. (2019) determined the age of hominin fossils in the cave as ca. 48,000–217,000 years ago, and perhaps slightly younger, for Denisovans, and as ca. 86,000–205,000 years ago for Neanderthals. Douka et al. (2019) estimated the age of Denisovans as ca. 52,000–195,000 years and of Neanderthals and Neanderthal/Denisovan offspring as ca. 80,000–140,000 years ago. These results are based on a few direct ^{14}C dates for Neanderthals and one direct U-series date for Denisovan/Neanderthal hybrid, but mainly they derive from associated ^{14}C and luminescent dates and subsequent modeling of the age for the cave's layers.

A closer view revealed several major problems that allow us to challenge these results (see above). In our opinion, a preliminary chronology of the Pleistocene hominin fossils from the Altai is that the remains of Denisovans can be dated to ca. 73,000–130,000 years ago, and the age of Neanderthals can be assumed to date to at least ca. 50,000–59,000 years ago, with a reservation that this is still quite uncertain. Early modern humans in the Altai can tentatively be dated to ca. 12,000–48,000 years ago.

Relationship Between Hominin Fossils and Archaeological Assemblages in the Pleistocene Altai Records

The issue of correspondence between hominin species and archaeological assemblages from the Pleistocene Altai sites has been a focus of discussion in the last decade (Derevianko 2009, 2011a, b; Derevianko et al. 2014). Initially, Derevianko (2009, p. 116) associated the Upper Paleolithic in the Altai with anatomically modern humans; later he linked the Initial Upper Paleolithic industry with Denisovans (Derevianko 2011a, pp. 194–195, 465; see also Derevianko et al. 2014, pp. 94, 200; Douka et al. 2019). On the other hand, DNA of Denisovans was detected in several hominin fossils from layers associated with the Middle Paleolithic and Initial Upper Paleolithic at Denisova Cave, and Neanderthal fossils were found along with Middle Paleolithic assemblages at Denisova, Okladnikov, and Chagyrskaya Caves (see Table 1). Anatomically modern human fossils and Upper Paleolithic stone tools were recorded in layer 3_1a of Strashnaya Cave (Table 1). The question arises: did Denisovans create the Upper Paleolithic tools?

In consideration of the available data, it is difficult to associate the lithic assemblage from layer 11.2 of the East Gallery with the Initial Upper Paleolithic (contra Jacobs et al. 2019). This suggests that there is no reliable connection between the Denisovan fossils and the Upper Paleolithic (sensu Derevianko et al. 2014, p. 189). The direct ages for Denisovan/Neanderthal hybrid, determined by both ^{14}C and U-series (Table 8; Fig. 7), also indicate that they are not associated with the Upper Paleolithic. The oldest pendant is from layer 11.2 in the East Gallery and is dated to ca. 46,100 years ago (with a large standard deviation) (Table S2; Fig. 7b). Remains of Denisovans (Denisova 3 individual, see Table 1) were also found in the East Gallery, layer 11.2. The "modeled" age of Denisova 3 is 51,600–76,200 years ago (Douka et al. 2019, p. 643), thus, older than the adornments. The chronology of other Denisovan fossils also contradicts the results of direct ^{14}C dates of the adornments at ca. 32,000-45,000 years ago (Fig. 7). Furthermore, Douka et al. (2019, p. 644) are not certain about the association of personal adornments and bone points. In respect of the bone points, before these can be accepted as hominin-modified specimens, we suggest that they are carefully analyzed, including by scanning electron microscopy (see Villa and d'Errico 2001).

Thus, if we consider together the hominin genetic material from the samples of layer 15 in the East Gallery of Denisova Cave (Slon et al. 2017a), the lithic industry of this layer, and the apparently overwhelming majority of artifacts from layer 14, we should accept that all these artifacts are the products of Denisovans, the most ancient hominin species in the Altai up to now and possibly the creators of the oldest stone industry in this region. The assemblages of layers 14–15 are characterized by primary flaking methods used by the Denisovans and correspond to the Middle Paleolithic technology without the Levallois technique and Upper Paleolithic innovations (such as bone tools and adornments). Statements that the Denisovans knew Levallois Middle Paleolithic and prismatic Upper Paleolithic technologies (e.g., Derevianko et al. 2014) are not proven and are speculative at best. The remains of Denisovans found in the overlying layers 11.2–11.4, along with artifacts of later periods (produced most probably by other species of *Homo*, either *Homo sapiens* or *Homo neanderthalensis*), including nonutilitarian objects, do not prove that these artifacts are the result of the technological development of Denisovans, or their close and "amicable" coexistence with other species of *Homo* (Derevianko et al. 2014); rather they were caused by strong post-depositional disturbances of the deposits in the East Gallery.

Thus, the Denisova 2 individual inhabited the cave at the beginning of MIS 5 (ca. 100,000–130,000 years ago), and Denisovans lived in the Altai throughout several dozens of millennia, visiting Denisova Cave from time to time. According to osteological and aDNA studies, Neanderthals appeared in the Altai at Okladnikov, Chagyrskaya, and Denisova Caves at ca. 40,000–55,000 years ago (e.g., Krause et al. 2007; Prüfer et al. 2014; Slon et al. 2017b). Cases of contacts between Denisovans and Neanderthals are now proven (Slon et al. 2018); previously, Buzhilova et al. (2017, p. S500) suggested that a small group of Neanderthals who appeared in the Altai at about 45,000–55,000 years ago "… was possibly assimilated, and their arrival did not result in long-lasting changes in the material culture of the local Denisovan population" and that the presence of Denisovans was interrupted by the settling of Neanderthals.

Apparently, these scenarios were created based on aDNA data; Neanderthal DNA was retrieved from a bone found in the East Gallery, but the possibility that the sediments are mixed is not considered by Buzhilova et al. (2017). Stratigraphic units (layers) 11.3, 11.4, and 12 in the East Gallery have the most "Neanderthal" artifacts (Shunkov and Kozlikin 2016), represented by Mousterian scrapers (including a *déjeté* type) (Chagyrsky variant; Fig. S10) and Levallois points (Kara-Bom variant; Fig. S9). The proportion of these types of artifacts belonging to two of the varieties of the Middle Paleolithic of the Altai gradually decreases below and above these layers. Furthermore, layers 11.1–11.4 and, probably, layers 9–11.2 in the East Gallery are the conditional "end points" where two kinds of Upper Paleolithic industries, represented by the Kara-Bom and Karakol variants, respectively, predominate.

Solid evidence of contact between the assumed creators of the different lithic industries based on the materials of Denisova Cave and other cave and open-air sites in the Altai has not been identified to date. Middle-to-Upper Paleolithic "transitional" industries, which could serve as a bridge for "interspecies" linear development in the Paleolithic, have not been found yet in the Altai region. Given the new data that point to the hybridization between Neanderthals and Denisovans (Slon et al. 2018), one can assume that during a certain period of time the existence of a "mixed" stone industry of the Middle Paleolithic in the Altai that was created by this hybrid cannot be completely excluded. However, the archaeological materials of layers 11 and 12 of Denisova Cave, where the remains of the late Denisovans and Neanderthals (as well as their hybrid) are found together, as shown above, are situated in a disturbed stratigraphic context and cannot be used as examples of genuine Middle Paleolithic complexes.

It is necessary to recall that early modern humans from the Levant and Arabia, dated to ca. 85,000–180,000 years ago, are found along with Middle Paleolithic (Levallois) assemblages (e.g., Groucutt et al. 2018; Hershkovitz et al. 2018). The Châtelperronian industry of the transitional Middle-to-Upper Paleolithic type at the Grotte du Renne site in France was created by Neanderthals (Ruebens et al. 2015; Welker et al. 2016). It can, therefore, be misleading to derive information about a hominin species from stone tool assemblages, as was done by Derevianko (2009, 2011a).

The Evolutionary Model of the Development of Paleolithic Stone Assemblages in the Altai: An Evaluation

The development of Paleolithic technologies in southern Siberia, in general, and in the Altai Mountains, in particular, has been studied for a long time by a team of scholars under the leadership of Derevianko, in accordance with the concept of continuous evolutionary development, which assumes smooth and gradual technological transitions between the Paleolithic periods and the emergence of Upper Paleolithic complexes from underlying Middle Paleolithic assemblages, with the Denisova Cave as a key site (Derevianko 2009, 2011a; see also Buzhilova et al. 2017; Derevianko et al. 2014; Shunkov et al. 2020b).

In our opinion, Buzhilova et al. (2017), without clear evidence, argued that the Altai Paleolithic technologies continuously (i.e., evolutionary) developed from the

Lower to the Upper Paleolithic within the time interval of ca. 10,000–800,000 years ago. At the same time, they use unproven data and suggestions and do not take into account the hominin species factor. In their paper, they offer the latest version of their model for the development of ancient hominins and determine the place and contribution of the Denisovans (Buzhilova et al. 2017).

Alternatively, Turner et al. (2013, p. 89) argued that the disturbed stratigraphy at Denisova, Okladnikov, and Strashnaya Caves makes it impossible to separate different cultural complexes in redeposited contexts: "… blurring (bioturbation) of stratigraphic horizons due to hyena digging should be considered when issues of cultural and hominin population continuity are being considered" (see also Turner et al. 2013, p. 367). Evidence of hyena occupation and bioturbation needs to be taken into account "… when making inferences about cultural continuity or discontinuity …" (Turner et al. 2013, p. 383). Therefore, it is impossible to see the development of Upper Paleolithic technologies as a gradual evolution of the underlying Middle Paleolithic complexes in the Altai (Turner et al. 2013, p. 385). Unfortunately, these conclusions were ignored by Derevianko et al. (2014), Douka et al. (2019), and Jacobs et al. (2019).

In consideration of the lithic typology of the East Gallery in Denisova Cave, the assemblages of layers 11.4 (Middle Paleolithic) and 11.2 (Initial Upper Paleolithic) are very similar (Kozlikin 2017). This is an additional argument against the association of layer 11.2 with the Upper Paleolithic. Also, Rybin (2015, p. 476) highlighted that for the Altai the relationship between Middle Paleolithic (MP) and Upper Paleolithic complexes is: "… a direct replacement of MP industries with Levallois points and blades … by Upper Paleolithic complexes focused on subprismatic blade production with stable and standardized Upper Paleolithic tool types."

Three Middle Paleolithic industries (one related to Denisovans and two to Neanderthals) and two Upper Paleolithic industries (Kara-Bom and Karakol, possibly related to *H. sapiens*) are documented in the sediments of the East Gallery, in particular, and in the rest of Denisova Cave, in general, including the Entrance. Taking into account the data of refitted artifacts at open-air Paleolithic sites in the Altai Mountains (Slavinsky et al. 2016), there were no evolutionary changes and gradual transitions from the Middle to the Upper Paleolithic (sensu Derevianko 2001, 2009, 2012). On the contrary, all factors indicate a sharp change in industries, without intermediate so-called transitional techniques and technologies.

Suggestions that the appearance of Neanderthals in Okladnikov Cave at ca. 45,000–55,000 years ago was the result of migration from either the Near East or central Asia (modern Uzbekistan; see Derevianko et al. 2014, p. 103), or even eastern Europe (Kolobova et al. 2020), fail to consider why this should not have been possible for early modern humans with Upper Paleolithic technologies, who replaced or assimilated the "native" Neanderthals and Denisovans. We know that at ca. 45,000 years ago modern humans existed in the central West Siberian Plain, at the Ust-Ishim locality (Fu et al. 2014), ca. 1100 km northwest of the Altai sites.

However, we believe that the conclusions reached by Derevianko et al. (2014) and Shunkov et al. (2020b) are far from what happened in the Altai throughout the Paleolithic. The evolutionary model of Derevianko (2009, 2011a) appears to be the continuation of an autochthonous development paradigm for prehistoric cultural complexes and hominin populations, which was common in Soviet archaeology in the 1930s–1950s (Klejn 2012, pp. 106–114; see also Klejn 2017, pp. 69–77).

Conclusions

From our critical analysis of the Altai sites with Pleistocene hominin fossils, we summarize here a number of key points to be considered in interpretations of this material. It is clear that all four caves—Denisova, Okladnikov, Strashnaya, and Chagyrskaya—have disturbed stratigraphy. Caves were used mostly by animals, especially hyenas, which was one of the most significant factors that caused displacement of sediments. This has a direct impact on all related issues, especially the chronology of hominin fossils and lithic assemblages, as initially pointed out by Turner et al. (2013) but largely ignored by other researchers (e.g., Douka et al. 2019; Jacobs et al. 2019; Morley et al. 2019).

As a result, at the current stage of research, it is not possible to build a reliable chronology using the mainly disturbed stratigraphy of the Altai caves of Denisova, Okladnikov, and Strashnaya. However, some preliminary conclusions can be made. The Middle Paleolithic lithic assemblages can be dated from ca. 130,000 years ago at Denisova Cave to ca. 50,000 years ago at Okladnikov Cave. The Upper Paleolithic complexes can be tentatively dated to ca. 12,000–48,000 years ago. The age of Denisovans is ca. 73,000–130,000 years ago, of Neanderthals—more than ca. 50,000–59,000 years ago (with a large uncertainty), and of early modern humans—ca. 12,000–45,000 years ago.

Luminescent dating techniques (RTL, OSL, and post-IRSL) have failed to produce reliable results because of either ambiguities in the basic principles (RTL) or the complicated history of sediment formation and repeated redeposition of the cave deposits (OSL and post-IRSL). The attempt to apply a Bayesian approach to the poorly stratified sequence of Denisova Cave runs counter to the principle of stratigraphic integrity that is necessary for the use of Bayesian statistics.

Hominin presence in the Altai was discontinuous. This is conceivable if we take into account the distinct differences between the warm (MIS 5 and MIS 3) and cold (MIS 4 and MIS 2) intervals in the Upper Pleistocene and also between favorable climatic intervals for hominin occupations (MIS 5e and 5c, and the warmest phase of MIS 3) and sharp cooling periods called Heinrich (H) events (e.g., Heinrich 1988), dated to ca. 75,000 (H7), 70,000 (H6), 50,000 (H5), 35,000 (H4), and 27,000 (H3) years ago (Prokopenko et al. 2001; Swann et al. 2005). The H5 event (ca. 50,000 years ago) at the peak of early MIS 3 cooling can be considered as a border between the Middle Paleolithic and Upper Paleolithic lithic industries. The boundary between the Initial Upper Paleolithic of Kara-Bom type and Early Upper Paleolithic of Karakol type can be associated with the H4 event (ca. 35,000 years ago). In this case, the Middle Paleolithic complexes and assemblages with Neanderthal fossils are contemporaneous with the late Denisovans as supported by the fact of their hybridization (Slon et al. 2018), and they are widely distributed in the Altai in early MIS 3 times. The hybridization event indicates that either Neanderthals were present before ca. 73,000 years ago or that Denisovans are older than so far determined.

Alternatively, hybridization in the wider region may not have occurred at Denisova. The Initial Upper Paleolithic is related to the Malaya Kheta warming (middle of MIS 3), and the Early Upper Paleolithic is connected with the Lipovka–Novoselovo warming (late MIS 3). The ages for these complexes can be determined (with ± 1000–2000 years uncertainties) as ca. 35,000–48,000 and 29,000–33,000 years ago, respectively.

Both Denisovan and Neanderthal fossils are associated with Middle Paleolithic stone artifacts. Denisovan fossils have not been found with the Initial Upper Paleolithic complexes. Only at Strashnaya Cave were early modern humans possibly found together with the Upper Paleolithic assemblage. The lack of modern human fossils at Denisova Cave does not in itself preclude this species as the manufacturer of the Initial Upper Paleolithic in southern Siberia, including the Altai. It is unhelpful to use archaeology (lithic typology) as a proxy for anthropology, particularly the determination of hominin species.

The evolutionary model of the development of Paleolithic stone assemblages in the Altai contradicts the chronology and stratigraphy of the cave sites with hominin fossils. According to Derevianko et al. (2014) and Jacobs et al. (2019), Denisovans created both Middle Paleolithic and Initial Upper Paleolithic assemblages, but they preceded Neanderthals who are also assumed to have been the manufacturers of the Middle Paleolithic. In other words, Denisovan fossils are too old to be associated with the relatively young Initial Upper Paleolithic assemblages of Denisova Cave.

Despite the importance of Denisovans for human evolution in the Pleistocene of Eurasia, our knowledge of their anthropology, chronology, and environment, as well as their relationship to other hominins, is still limited. The heavily disturbed deposits and the lack of stratigraphic integrity of Denisova Cave are major obstacles for understanding the age and type of lithic assemblage associated with the Denisovans. Their diagnostic morphology and, thus, taxonomic position remain to be determined (species or subspecies?), with no holotype announced so far. Future research should help clarify these issues with more complete fossils and a better-preserved and recorded stratigraphy compared to what is now known. This is all the more relevant because of the evidence of Denisovan and Neanderthal hybrids. The relationship of early modern humans in terms of Upper Paleolithic technology can provisionally be assumed considering the chronology and Middle Paleolithic technology of the older hominins, even though at one site there is possibly associated evidence of *H. sapiens* and Upper Paleolithic artifacts (Strashnaya Cave).

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