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LARGE MAMMALS AND NEANDERTHAL PALEOECOLOGY IN THE ALTAI MOUNTAINS (CENTRAL ASIA, RUSSIA)

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ABSTRACT

Analysis of large mammal bone assemblages from the Mousterian sites of Denisova Cave and the Ust-Karakol 1 open-air locality in the Altai region of central Asia revealed that they were accumulated both by ancient people and nonhuman predators. The latter appear to have played a greater role in accumulating bones in the cave than at the open-air site. The results indicate that Mousterian humans probably were capable of actively hunting large and medium mammals.

INTRODUCTION

One of the most interesting problems in hominid evolutionary ecology is the initial colonization of the boreal latitudes of northern Eurasia with their low plant biomass, lengthy winters, and strong seasonal fluctuations. Colonization of these environments required new survival strategies, which may have included changes in the tool technology, foraging tactics, and social organization (HOFFECKER, 1997). Information concerning human diet and ecology related to these new adaptations is derived from the fossil remains of the large mammals found in Lower, and especially Middle, Paleolithic sites in boreal latitudes, including southern Siberia.

The northwestern Altai Mountains are particularly rich in Middle Paleolithic sites containing faunal remains. The stratified sites of Denisova Cave and the Ust-Karakol 1 open-air locality are situated along the upper course of the Anui River, near the village Cherny Anui, at an elevation of 700 m above sea level. Both sites were excavated by the Institute of Archaeology and Ethnography, Siberian Branch of the Russian Academy of Sciences at Novosibirsk under the general leadership of Academician Prof. A. Derevianko.

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Analysis of the site stratigraphy and chronology indicate that these sites were initially occupied no later than the Kasantsevo Interglacial (= Eem in Europe), and that their occupation history spans the entire first half of the late Pleistocene (DEREVIANKO *et al.*,1998). The lengthy duration of the accumulation of the bone material, its abundance and good preservation, and diversity of represented mammal species all contribute to the importance of these sites for reconstructing the paleoecology of the earliest known inhabitants of the Altai Mountains.

DENISOVA CAVE

This cave is horizontal in form and situated 28 m above the modern level of the Anui River (Fig. 1). The excavations were focused on two parts of the cave: the central chamber and entrance area. In the central chamber, the Mousterian industry occurred in layers 12-22, and in the entrance area it was found in layers 9-10; layer 8 contains an industry that is transitional to the Upper Paleolithic (DEREVIANKO *et al.*, 1998). Although a radiothermoluminescence date of 282,000 ± 56,000 years ago (RTL-548) was obtained from the lower part of layer 22 in the central chamber, and additional dates from the upper part of this layer fall within a range of 171,000 - 224,000 years (DEREVIANKO *et al.*, 1992), the morphological and evolutionary indices of the small mammals from layer 22 are not consistent with a late Middle Pleistocene age (DEREVIANKO *et al.*, 1998).

Identifiable bones and teeth constitute only a small portion of the entire large mammal assemblage recovered from the cave. Twenty-four species were identified from the Pleistocene layers in the central chamber, and seventeen species from the same layers of the entrance area (Table 1). The representation of species is very similar for both areas of the cave, although the remains from the central chamber contain more carnivores.

Mammals characteristic of open landscapes dominate, but forest-steppe and forest inhabitants are also present. Tundra-taiga species (e.g., *Alopex lagopus*) occur in layers 22, 19 and 12 in the central chamber. Mammoth (*Mammuthus primigenius*) is represented only by very small fragments of the cheek teeth, and may or may not have been an inhabitant of the Anui River valley. It is possible that mammoth teeth were brought from the foothill plains to the cave by its human occupants or carnivores. The absence of reindeer (*Rangifer tarandus*) in the Mousterian fauna is surprising, as this species now inhabits the same latitude in Siberia (Sayany Mountains). The presence of mammoth and reindeer in river valleys like the Anui during the earlier Late Pleistocene may have been discouraged by extremely arid conditions in the steppe zone north of the Altai.

The bones and the teeth from Denisova Cave are heavily fragmented (Fig. 2). Among a total of 110,000 fragments, only 1% represent pieces over 5 cm in length. Such heavy fragmentation may have been caused in part by sediment compression and frost action. However, a more significant factor appears to be the destructive effects of human occupation and carnivore activity (i.e., bear, hyena, wolf, lion).

In African dens of the recent spotted hyena (*Crocuta crocuta*), bones split and gnawed by this animal comprise many small fragments (SUTCLIFFE, 1970; RICHARDSON, 1980). The size of the fragments is rather evenly distributed between 2 and 12 cm (BRAIN, 1981). Therefore, GERMONPRE (1993), who studied the taphonomy of Denisova Cave, concluded that much of the bone fragmentation at the site had been caused by the cracking of long bones for marrow extraction by humans.

I believe, however, that carnivores probably played a more significant role in fragmentation, as indicated by traces of gnawing on the surfaces of the bones and the presence of hyena coprolites and regurgitated fragments (Fig. 3, 4). The presence of the latter reflects regurgitation by the cave hyena (*Crocuta spelaea*), as well as its modern relatives, of bones, teeth and other heavily digested prey parts, for stomach cleaning. Denisova Cave was clearly used by various carnivores during the Pleistocene, as predators and scavengers usually transport and store their prey in different places (HAYNES, 1980; BRAIN, 1981).

The degree of bone fragmentation increases as a function of distance from the entrance of the cave. The proportion of bones less 2 cm in length grows from 58% at the entrance area to 72% in the central chamber. This is characteristic of the behavior of carnivores that drag prey carcasses into the interior of the den for safety.

Taphonomic comparison of hyena localities in Africa and in Europe illustrates differences that may be due to variations in the behavior of modern and fossil forms of hyena (BRUGAL *et al.*, 1997). It has been suggested that the Pleistocene cave hyena lived in larger groups than the recent *Crocuta crocuta* (BARYSHNIKOV, VERESCHAGIN, 1996). The effects of a large number of hyenas might explain the extraordinarily high degree of bone fragmentation in Denisova Cave. A bone fragment of 2 cm in length is observable in a fractured hyena coprolite (Fig. 5); fragments of this size predominate in the assemblage.

In the lowermost layer of the central chamber (layer 22), bones of *Ursus arctos/rossicus* are common, and constitute 70% of all bear remains in Denisova Cave. The remains include teeth, long bones, and small bones, fragments of ribs and vertebrae, and os penis. The predominance of heavily worn cheek teeth from old individuals and deciduous teeth from bear cubs indicates natural mortality. During this period (i.e., initial occupation by humans), the cave appears to have been primarily a carnivore den in which were accumulated the remains of weakened animals that died from starvation or predators (e.g., lion, wolf, other bears) in the spring. In the overlying layers, remains of bear decrease significantly.

Stone artifacts were also found in layer 22 (DEREVIANKO *et al.*, 1998), indicating that at the time that humans first occupied Denisova Cave it was inhabited by bears. An analogous pattern is apparent at several other Paleolithic cave sites, including Kudaro Cave and Mezmaiskaya in the Caucasus, and Prolom 2 in the Crimea (BARYSHNIKOV, 1987; BARYSHNIKOV, HOFFECKER, BURGESS, 1996). Evidently, bears and humans competed for use of the cave at this time and the latter eventually displaced the animals.

In layer 22, bear bones constitute 45% of the total assemblage, while large ungulates represent only 7%. In layers 12-19, these proportions are reversed, and bears compose 2-7 %, while large ungulates compose 43-45%, of the assemblages, respectively. The percentages of bear and large ungulate remains in the Upper Mousterian layers reflect both carnivore activity and human occupation.

Remains of *Crocuta spelaea* are scarce in layer 22, but more common in layers 12-19. In these levels, between 26% and 47% of bone fragments exhibit traces of acidic corrosion evidently caused by hyena digestion. In the entrance area, such fragments comprise only 8% of the assemblage. Acidic corrosion was found on the teeth and bones of "wild ass," horses, and large and medium bovids, and was more common among the remains of young animals. Juveniles were most probably easier prey for cave hyenas. At the same time, bear bones with acidic corrosion are extremely rare.

It should be noted that the most intensive use of the cave by hyenas seems to coincide with periods of heavy human occupation. For example, layer 12 yielded 41% of all Mousterian tools from the cave, and here the proportion of the bones with acidic corrosion is 34%. There may have been a symbiotic relationship between Mousterian humans and hyenas during this period – a phenomenon previously suggested by Bunak (1980).

Evidence of human activity in Denisova Cave in the form of burned bone and cut-marks on bone are generally not common. Approximately 15 examples of cutmarks were observed on bones recovered from the central chamber, beginning with layer 19 (Fig. 6). Bones that were exposed to moderately high or high temperatures occur in all Mousterian layers in the central chamber, although almost half of them were recovered from layer 12. Burned bones are more common in the Upper Paleolithic layers. No burned bones or bones with cut-marks were found in Mousterian layers at the cave entrance area.

Denisova Cave was apparently occupied for brief periods -- perhaps sometimes in response to poor weather conditions – for overnight shelter or defense against specific threats from predators. A similar taphonomic pattern is evident at Barakaevskaya Cave in the Northern Caucasus (LIUBIN, 1994). Both sites may have been used as places for storage of stone tools intended for the processing of carcasses and other functions, and as occasional shelters and locations for observing the migration of ungulates along river valleys.

UST-KARAKOL 1 OPEN-AIR SITE

This site is located 2 km upstream from Denisova Cave along Anui River, at the confluence of the Karakol River. Radiothermoluminescence dates from the lower part of deposits include estimates of 133,000 ± 33,000 years ago (RTL-661) for layer 19A (containing stone artifacts), and 90,000 ± 18,000 years ago (RTL-658) for layer 18A (containing large mammals remains) (DEREVIANKO *et al.*, 1998). Eleven species of large mammals were identified from the Mousterian deposits (Table 2). Most of them are characteristic of open landscapes with steppe and meadow-steppe vegetation, with the exception of *Cervus elaphus* and *Capreolus pygargus*, which prefer forest and bush, and *Capra sibirica*, which is found in rocky terrain.

With respect to taphonomy, Ust-Karakol 1 differs significantly from Denisova Cave, both in terms of the relative scarcity of carnivore remains and substantially reduced degree of bone fragmentation. Several complete large bones were found here, including metacarpals of yak and sheep, and the pelvis of a horse. The preservation of bone fragments is good, but their surfaces exhibit traces of etching by plant roots.

The lowest cultural layer (layer 18A) of Ust-Karakol 1 yielded the cervical vertebrae of a large bovid in anatomical sequence, the skull fragment of a deer with antler, fragments of ribs, complete bones, and several carnivore bones. This pattern reveals information about the position of bones *in situ*, and is typical of the natural accumulations of vertebrate fossil bones.

However, even in the earliest levels at the site there are traces of human activity. All skeletal parts from the distal forelimb of a Siberian ibex (*Capra sibirica*)—metacarpus fragment, all phalanges, and two sesamoid bones -- were found in the lowest level (Fig. 7). Stone tool cut-marks were observed on the dorsal and volar side of the metacarpus, evidently caused by careful cutting of the tendons and hide (Fig. 8, 9). The animal had apparently been skinned and butchered immediately after it was killed by one or more ancient hunters. This bone complex differs from other remains from Ust-Karakol 1 in the absence of traces of plant roots. This indicates that the bones may have been buried in mud; the site could have been located on the river floodplain at this time. During the butchering of a *Capra sibirica*, a distal limb part with hoof was perhaps cut and discarded as of little food value.

In the upper Mousterian levels (layers 13-17), bone remains are not numerous. They are chiefly represented by fragments of long bones and isolated teeth. The degree of fragmentation is higher than in layer 18A. The number of bones regurgitated by hyenas increases; however, their percentage among the total assemblage from Ust-Karakol 1 is considerably lower than in Denisova Cave (not exceeding 12%). Undoubtedly, the role of carnivores in this open-air site bone accumulation was considerably lower than in the cave.

ECOLOGICAL ANALYSIS OF FAUNA

Twenty-two species of large mammals were identified in the Mousterian layers at Denisova Cave and Ust-Karakol 1. They may be divided into five trophic groups for the reconstruction of the ecological structure of the Pleistocene medium and large mammal community of the Anui River valley: (1) predators (eight species: *Alopex lagopus, Vulpes corsac, Vulpes vulpes, Cuon alpinus, Canis lupus, Crocuta spelaea, Panthera spelaea, Lynx lynx*); (2) omnivorous carnivores (two species: *Ursus arctos, Ursus rossicus*); (3) megafauna (one or two species: *Coelodonta antiquitatis* and possibly *Mammuthus primigenius*); (4) folivorous ungulates (two species: *Capreolus pygargus, Cervus elaphus*); (5) herbivorous ungulates (eight species: *Equus hydruntinus, Equus ferus, Poephagus mutus, Bison priscus, Procapra gutturosa, Saiga tatarica, Capra sibirica, Ovis ammon*).

The trophic structure of the Mousterian fauna of the Altai is surprisingly similar to that of the Crimea, which has been reconstructed from Prolom 2 (BARYSHNIKOV, 1995): (1) predators - six species; (2) omnivores - one species; (3) megafauna - two species; (4) folivorous ungulates - two species; and (5) herbivores - seven species. Especially characteristic of both faunas is the presence of the species association *Equus hydruntinus/Saiga tatarica,* which does not occur at higher latitudes in Eastern Europe and Siberia. The resemblance of the faunal structure of the Altai and the Crimea indicates the integration of Mousterian people in both regions with similar ecological systems.

The diversity of the large mammal species in the Altai indicates a high level of interspecific competition in the Pleistocene ecosystem. Humans must have had to define their own ecological niche in order to minimize competition for food resources with other members of the medium and large mammal community. Colonization of the environment of the northwest Altai region during the early Late Pleistocene was probably facilitated by a mosaic landscape. In addition, the social organization and foraging strategy of Mousterian people must have been specifically adapted to the local habitat.

FORAGING STRATEGY

The colonization of boreal latitudes required humans to adapt to the differential availability of food due to seasonal fluctuations. These conditions demanded a foraging strategy that addressed the environmental variations of warm and cold seasons.

Assumptions about human diet during the warm season are based on uniform associations. During the summer and autumn, groups in the Altai may have exploited a variety of plant foods, honey, small vertebrates, and invertebrates, and may have competed to a minor degree with herbivorous and omnivorous large mammals in the region. Such competition would have been minimized by the fact that the herbivorous ungulates occupied large territories and consumed foods low in calories - grass and leaves.

In all layers of Denisova Cave (with the exception of layer 22), deciduous teeth of "wild ass", horse, deer, bison, sheep, and other ungulates were found. The degree of crown wear indicates death of several of these immature animals in summer, and they may represent the prey of hyenas and other carnivores. Several newborns, which would have been concealed in grass during the first days of life, might have been killed by ancient hunters. However, such hunting was probably rare and opportunistic, as equid and bovid newborns are capable of following the female almost immediately after birth (SOBANSKY, 1992).

During the winter, Mousterian people probably had to consume more high quality food obtained from the killing of medium and large mammals, or from stealing their carcasses from other predators or scavengers. In this context, humans and carnivores are likely to have competed for the same resources. There is evidence of cannibalism among the hyenas, which presumably reflects severe winter food shortages, in the form of an adult hyena cheek tooth from Denisova Cave with acidic corrosion. Competition between the two would have been mitigated to some degree by differential diurnal activity, occasional food abundances due to mass ungulate deaths, and immigration to other areas.

The bone material from Denisova Cave is too fragmented to determine the medium ungulate sex ratio. However, the large size of cheek teeth suggest that the *Saiga tatarica* and *Ovis ammon* remains found in cave are primarily males, which apparently reflects the fact that mating in these taxa occurs in the late autumn or early winter, and males weakened during this event would have been easy prey for both carnivores and Mousterian hunters. A similar pattern is evident for *Saiga tatarica* from Paleolithic sites in the Crimea (BARYSHNIKOV *et al.*, 1994). Among recent *Ovis ammon*, old and mature males that actively participate in mating usually become the prey of carnivores (SOBANSKY, 1992).

In summary, seasonal fluctuations in environment probably elicited seasonal differences in human behavior. A flexible foraging strategy provided Mousterian people with food, and reduced competition with other members of the Pleistocene ecosystem. In summer, humans probably foraged widely, gathering a variety of plants and small animals. In winter they may have been more sedentary, with small hunting groups retrieving meat for the other members of the group. In the cold season, meat may have been easier to obtain from hunting weakened medium, and possibly large, ungulates, and from scavenging frozen carrion.

CONCLUSIONS

The Pleistocene layers of Denisova Cave yielded two isolated human teeth: a deciduous lower molar from layer 22, and an adult incisor from layer 12, which according to Turner (1990), are similar to the Neanderthal teeth from Shanidar 2. Thus, it appears that Neanderthals occupied these sites.

There are two points of view regarding the adaptive strategy of Neanderthals. The first holds that the Neanderthals occupied a different ecological niche from that of their modern human successors. According to this view, Neanderthal foraging strategy was flexible and reflected an emphasis on gathering and consuming carrion, invertebrates and smaller vertebrates, and plant foods, but not on the hunting of medium and large mammals (BINFORD, 1984; STINER, 1994). The second point of view holds that the foraging strategy of the Neanderthals was similar to that of modern humans (CHASE, 1989; HOFFECKER, BARYSHNIKOV, 1998), and that the two hominid taxa had analogous and overlapping ecological niches and would have competed for the same resources.

The traces of a skinned *Capra sibirica* found in the lowest cultural level (layer 18A) of Ust-Karakol 1 site represents evidence of an animal that had been skinned and butchered immediately after it was killed. Such careful processing of an animal that has died from natural causes is less likely to occur, as the skin rapidly loses its economic value. Mammal hides may have been used by Mousterian people for cold protection in the form of clothing or covering for an artificial shelter.

Thus, the earliest known human inhabitants of the Altai Mountains may have planned and executed the hunting of medium ungulates, varying their hunting tactics on the basis of the behavioral characteristics of their potential victims. They may have also scavenged meat and consumed plant foods like omnivorous carnivores. Their foraging strategy was probably a flexible one, reflecting seasonal shifts in available resources, and designed for efficient use of these resources. The adaptive strategy of the Neanderthals seems to have been similar to that of their modern human successors.

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Fig. 1. View to Denisova Cave.

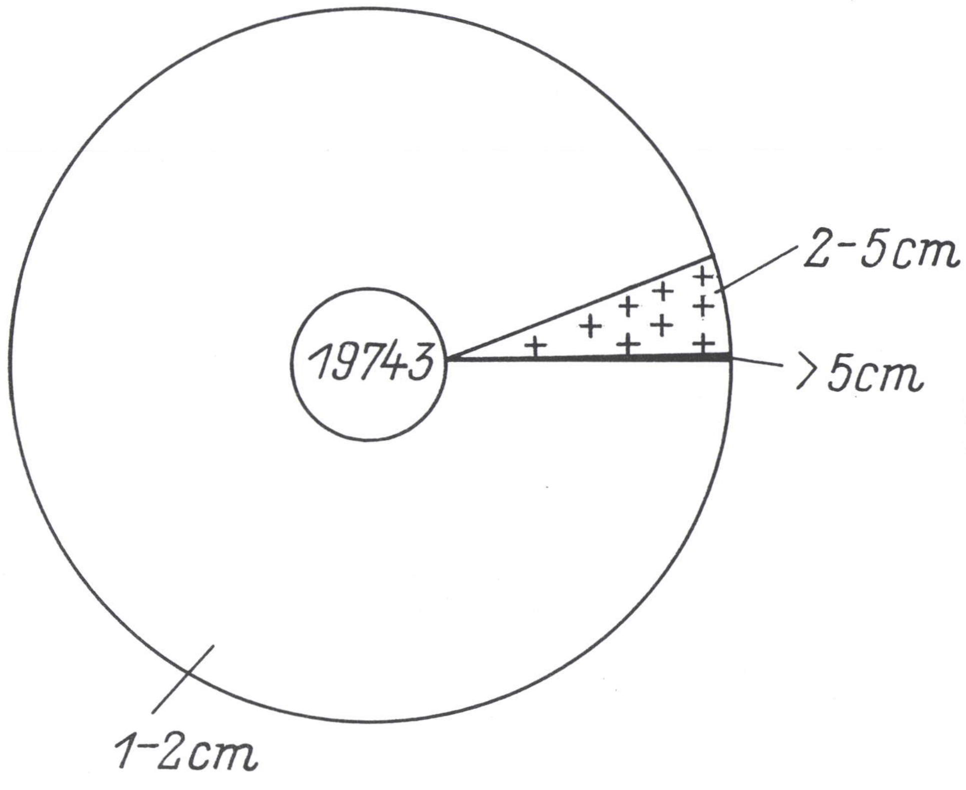

Fig. 2. Ratio (persentage) of size groups of bone in Denisova Cave.

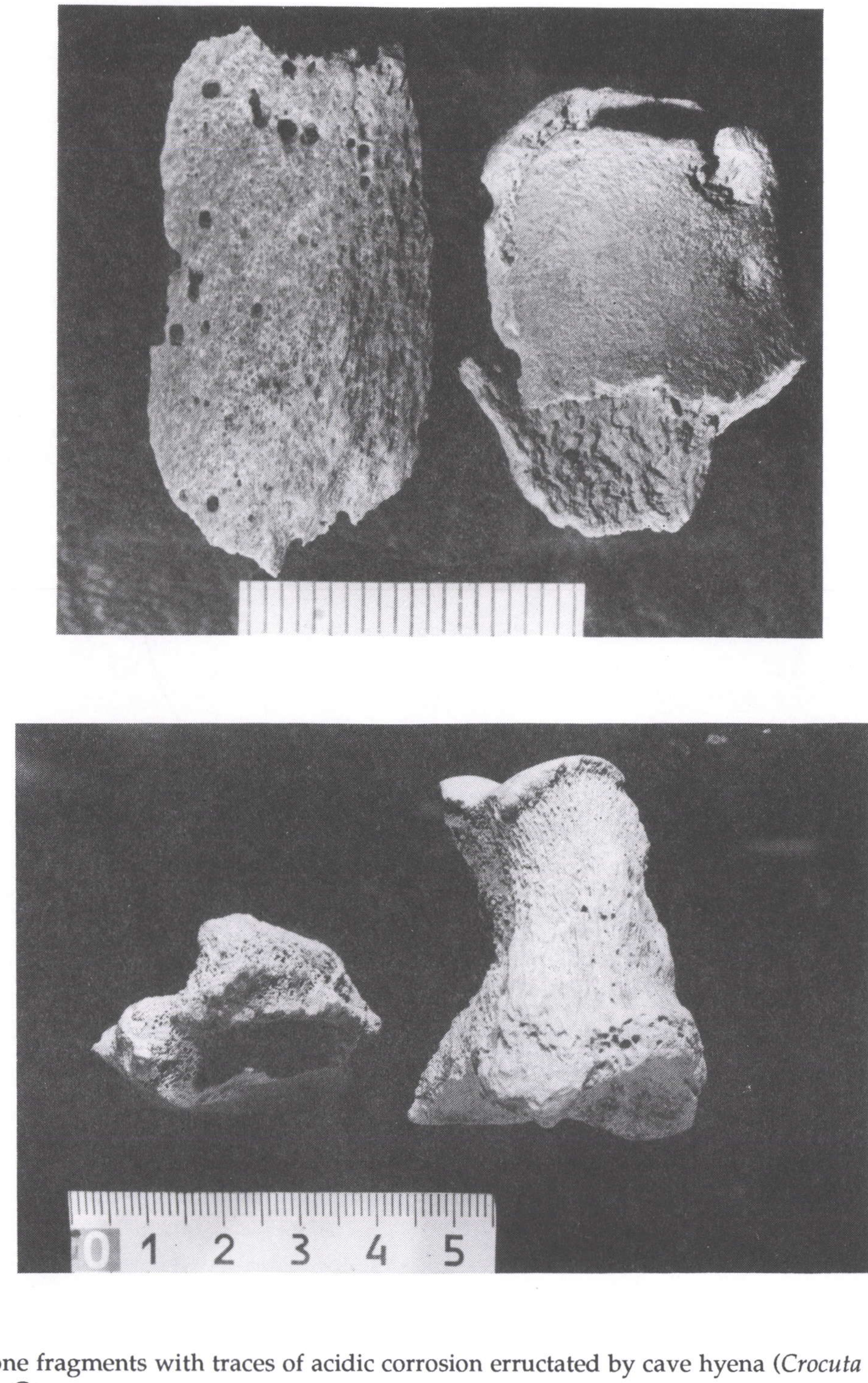

Fig. 3. Bone fragments with traces of acidic corrosion erructated by cave hyena (*Crocuta spelaea*) in Denisova Cave.

Fig. 4. Coprolites of cave hyena (*Crocuta spelaea*) from Denisova Cave.

Fig. 5. Hyena coprolite with bone fragment from layer 14 in the central chamber of Denisova Cave.

Fig. 6. Cut marks at the base of neural spine of vertebrae of small ungulate in Denisova Cave.

Fig. 7. Skeletal parts from the distal forelimb of the Siberian ibex (*Capra sibirica*) from layer 18A in the Ust-Karakol 1 open-air locality.

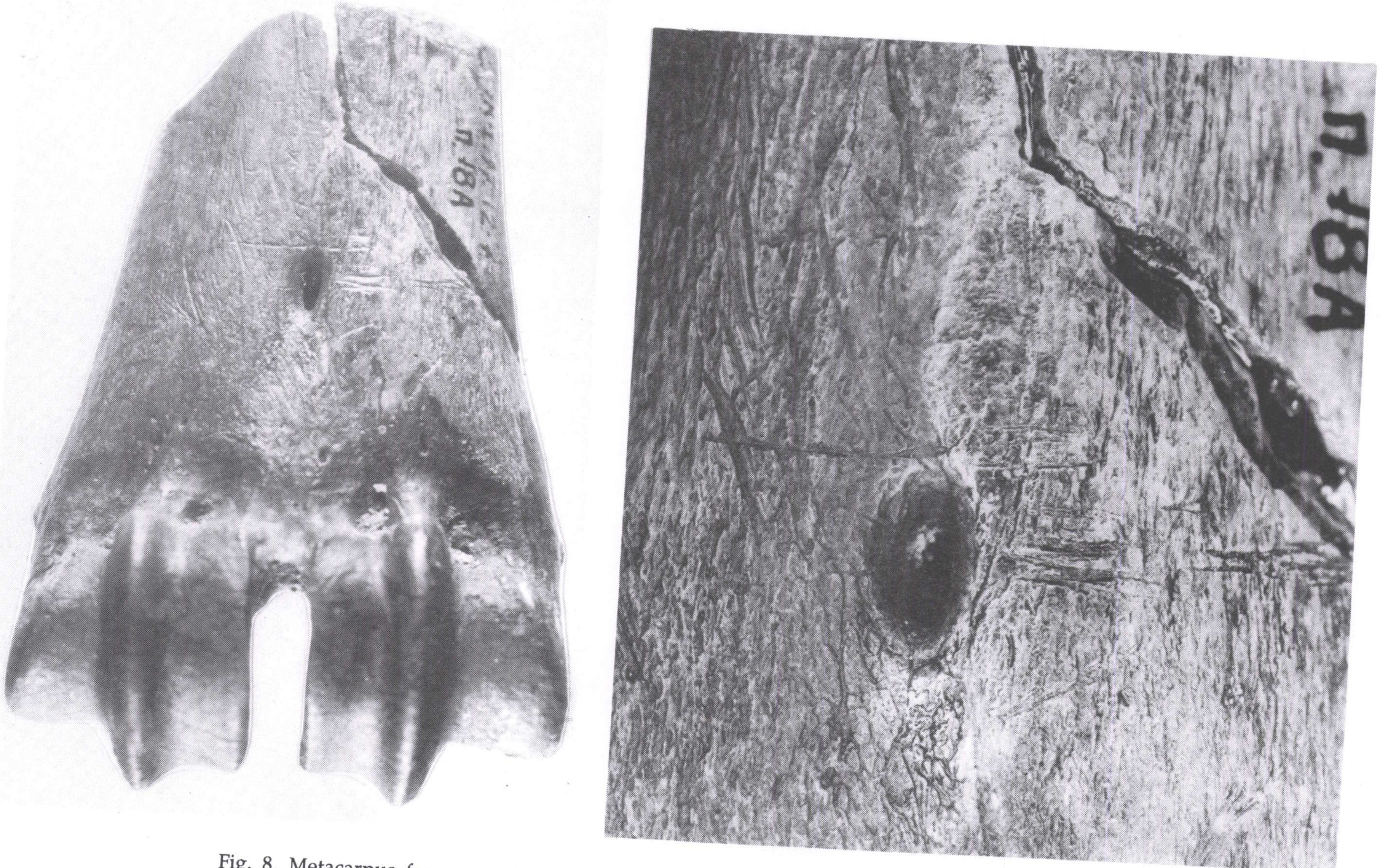

Fig. 8. Metacarpus fragment of *Capra sibirica* with cut marks in the Ust-Karakol 1 open-air locality. Dorsal view.

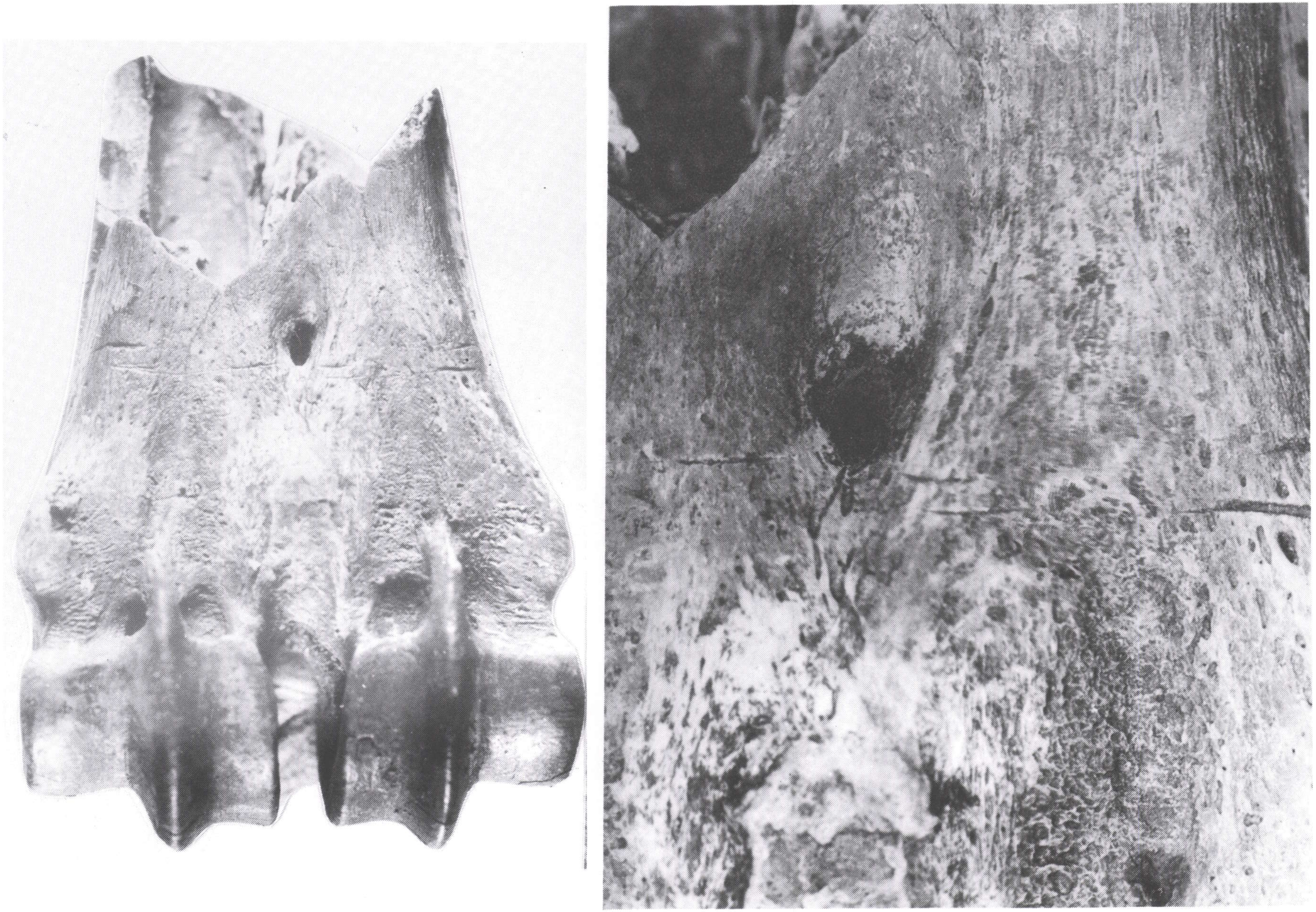

Fig. 9. Metacarpus fragment of *Capra sibirica* with cut marks in the Ust-Karakol 1 open-air-locality. Volar (palmar) view.

Table 1. Large and medium mammals and number of identified specimens from Denisova Cave (1984, 1991-1996 excavations)

Species	Mousterian layers								
	Central chamber						Entrance area		
	12	13-14	16-17	19	20-21	22	8	9	10
Carnivora									
Alopex lagopus	2			1		7			
Vulpes corsac	1	1		3	1	5			
Vulpes vulpes	12	10	1	12	11	42	3	2	1
Cuon alpinus	2	3		4	2	6			
Canis lupus	25	24	1	30	16	41		1	1
Ursus arctos		3		2	1	5		1	1
Ursus rossicus	2	1			1	15		2	
Ursus arctos/rossicus	6	12	4	14	10	159		7	16
Martes zibellina		1		1	2	1			
Mustela eversmannii		3		1	1	3			
Crocuta spelaea	16	22	2	28	12	15	6	3	
Panthera spelaea						1			
Lynx lynx				2		1			
Proboscidea									
Mammuthus primigenius	4	12		4	2		1	1	
Perissodactyla									
Coelodonta antiquuitatis	3	6	2	6	1	3	3	7	
Equus hydruntinus	5	4		5	1	2	1	1	
Equus ferus	4			3		1			2
Equus hydruntinus/ferus	19	12	3	9	5	4	13	9	16
Artyodactyla									
Capreolus pygargus	2	6	2	1	1	7	2	1	
Cervus elaphus	8	7	2	2		1	1	2	2
Poephagus mutus	1								
Bison priscus	8	6	1	5	1	1			
Poephagus/Bison	14	21		4	4	10	6	4	1
Procapra gutturosa	5	3	2	5	2	1		2	
Saiga tatarica	11	1		1	1		3		
Procapra/Saiga	5	5			3	4	3	5	
Capra sibirica	10	10	2	7	2	11	1	1	2
Ovis ammon	6	15	2	6	2	1	3		1
Capra/Ovis	23	19		10	6	18	19	7	7

Table 2. Large mammals and number of identified bone fragments from Ust-Karakol open-air site (1993-1997 excavations)

Species	Mousterian layers		
	13-16	17	18à
Carnivora			
Canis lupus			1
Crocuta spelaea			1
Perissodactyla			
Equus ferus/przewalskii	1		1
Artiodactyla			
Capreolus pygargus			1
Megaloceros giganteus			1
Cervus elaphus	1	12	
Poephagus mutus			5
Bison priscus	6	1	1
Capra sibirica			10
Ovis ammon		2	