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The first record of “spelaeoid” bears in Arctic Siberia

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ABSTRACT

For a long time, “spelaeoid” (cave-bear-like) bears, *Ursus* (*Spelearctos*) spp., were believed to be almost purely European animals. Their geographic range has recently been extended to the east, in southern Siberia, Transbaikalia, Kirghizia, Mongolia and Korea. Two unexpected new findings, presented here in detail, significantly change existing views on the distribution of cave bears; both were found in North-Eastern Siberia, far beyond the Arctic Circle, more than 1500 km to the north-east of the previously accepted range.

One of the fossils is a mandible, found near the town of Cherskiy at 68.73°N, 161.38°E. The analysis of local geology and accompanying mammal fossils suggests that it comes from the Olyorian Fauna (Early to early Middle Pleistocene). Morphologically, the Cherskiy mandible is closest to *Ursus savini*, a small middle Pleistocene cave bear from the British Cromer Forest-bed Formation, but differs in having a slightly more advanced dentition, and thus it is described as a new subspecies *Ursus savini nordostensis*. Another newly recognized fossil of the “spelaeoid” bear is an astragalus found at the Oskhordokh site at 67.54°N, 135.67°E, on a large gravel bar on the right bank of the Adycha River. This specimen is attributed to *Ursus* cf. *deningeri*.

The paper also presents an interesting example of the interaction between classical and “molecular” palaeontology.

The new finds significantly change existing ideas on the ecology and evolution of cave bears, some of the most remarkable members of the extinct Pleistocene megafauna.

1. Introduction

Cave bears *sensu lato*, or “spelaeoid bears”, *Ursus* (*Spelearctos*) spp., were some of the most remarkable members of the extinct Pleistocene megafauna. This subgenus comprises at least three species, *Ursus spelaeus* Rosenmüller, 1794, *Ursus deningeri* Reichenau, 1904, and *Ursus savini* Andrews, 1922 (=*Ursus rossicus* Borissiak, 1930, =*Ursus uralensis* Verestchagin, 1973)[1], with many subspecies (Kurtén, 1976; Musil, 1980–1981; Torres et al., 1991; García, 2003; Baryshnikov, 2007). There are two informal groups of cave bears – large-sized (*U. deningeri* and *U. spelaeus*) and small-sized (*U. savini*). The morphology of all of these species is “spelaeoid” (cave-bear-like) rather than “arctoid” (brown-bear-like). For a long time, spelaeoid bears were believed to be almost entirely European animals (Kurtén, 1976; Musil, 1980–1981). The Urals and the Caucasus were thought to be, respectively, the easternmost and the south-easternmost areas of their distribution. Fossils of both big and small cave bears have recently been found east of the Urals, mostly in southern Siberia. In addition to finds in the south of European Russia and middle Urals, small cave bear fossils have been recovered from a number of localities in south-western Siberia and also in Transbaikalia (Vereshchagin and Baryshnikov, 2000). Large cave bears, similar to *U. deningeri*, have been found in Israel, the Southern Caucasus, Kirghizia, as far east as Transbaikalia, and possibly in Mongolia and Korea (Baryshnikov

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[1] The recently-defined species *Ursus ingressus* Rabeder et al., 2004, should probably be added to this list of cave bear species.

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and Kalmykov, 2005; Baryshnikov, 2007). Until now, the northernmost records of *U. spelaeus* are from caves in the northern Urals, almost up to 64°N.

A bear astragalus was found by AVS in 1976 at the Arctic Siberian Oskhordokh site on the Adycha River, a tributary of Yana, the latter being one of the great rivers beyond the Verkhoyansk Ridge (Fig. 1). The specimen was originally identified as *Ursus* sp. since, at that time, the accepted paradigm was that cave bears never reached this region of Arctic Siberia. The bone was stored in the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN) under no. PIN 3723-496, until 2002 when it was sampled by AVS, along with other bear fossils, and sent to the Ancient Biomolecules Centre (ABC) at Oxford University for ancient DNA analysis. From the sample of PIN 3723-496 JW, then at the ABC, obtained a "spelaeoid" sequence for a segment of the D-loop of mitochondrial DNA (mtDNA). After double-checking for possible laboratory error (mislabeling the sample), independent replication of another subsample of the same bone at the Max Planck Institute for Evolutionary Anthropology (Leipzig) yielded a longer DNA fragment that confirmed the "spelaeoid" affinity of the sequence. The astragalus was also studied in detail by GFB who, after detailed investigation of its morphological characteristics, confirmed that it belonged to a cave bear.

A manuscript reporting these results was in preparation when, in September 2007, AVS and SPD found a bear mandible near Cherskiy, along the lower course of the Kolyma River at 68.73°N (Fig. 1). Spelaeoid characteristics are rather more apparent in cave bear mandibles than in the astragalus, and thus the palaeontologists recognized it almost immediately as a cave bear. First, GGB and AVS examined the specimen in Yakutsk, and concluded that it did not belong to a brown bear. Subsequent examination by GFB revealed a strong morphological resemblance between the Cherskiy mandible and the small ancestral form of cave bear *U. savini*. Molecular studies on this specimen were conducted in Leipzig, but unfortunately the biomolecular preservation allowed only fragmentary information to be retrieved.

The discovery of a "spelaeoid" mitochondrial DNA sequence (Knapp et al., 2009) from a bear bone found in North-Eastern Siberia, far beyond the Arctic Circle, was completely unexpected. Nevertheless, morphological study confirms the genetic results. Even more surprising was the find of a cave bear mandible near the town of Cherskiy. Although the mandible was not found *in situ*, the source horizon of the canine, found separately, but belonging to the same individual, is more certain, so we have strong reasons to believe that these rare fossils come from the Olyorian Fauna (Early to early Middle Pleistocene: Sher, 1987).

The two new findings, described here, significantly change existing views on the distribution, evolution and ecological adaptations of cave bears.

2. Description of the cave bear finds from Arctic Siberia

2.1. Geographical position and geological settings of new cave bear sites in Arctic Siberia

2.1.1. The Cherskiy ("Ovrag") find of a cave bear mandible

The Cherskiy site is named after the town that is located on the right bank of the lower course of the Kolyma River at 68.73°N, 161.38°E. Situated ca 250 km north of the Arctic Circle, this area has a severe continental climate and thick permafrost. Vegetation is sparse larch forest only about 60 km south from treeless tundra. A short review of the climate and vegetation of the region can be

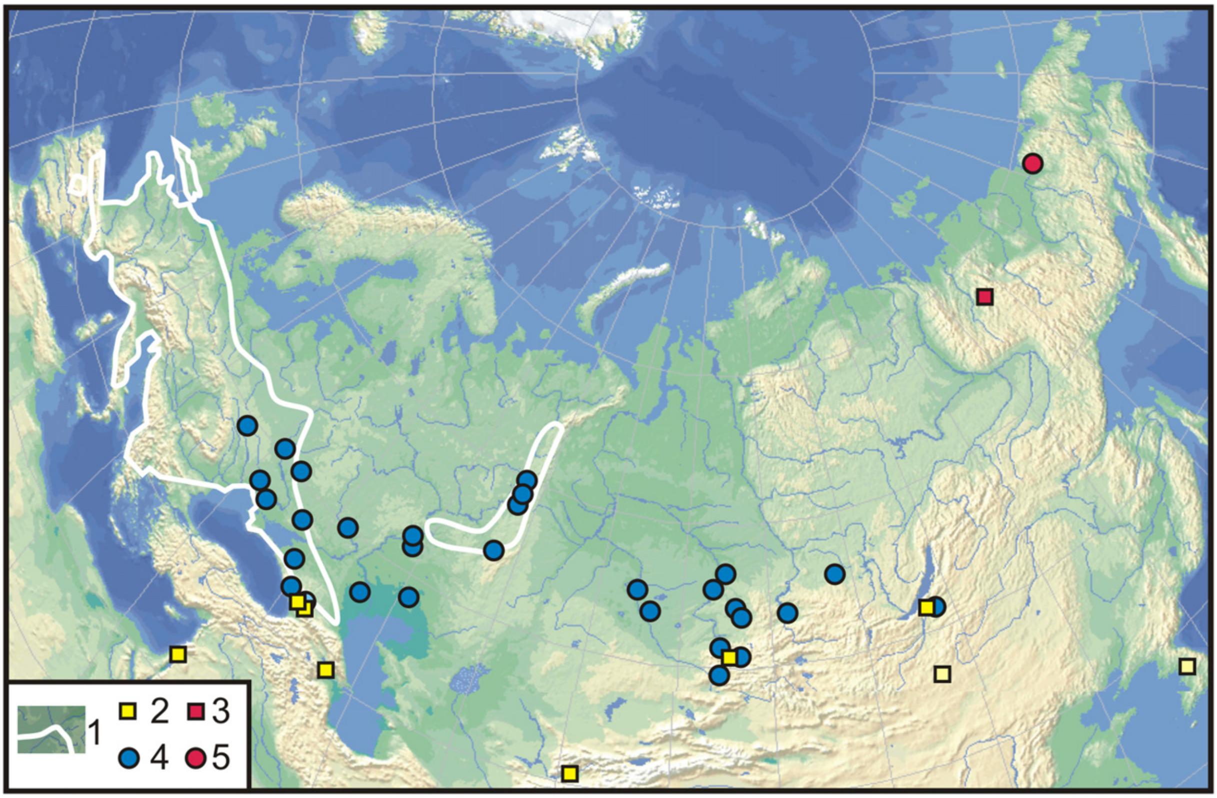
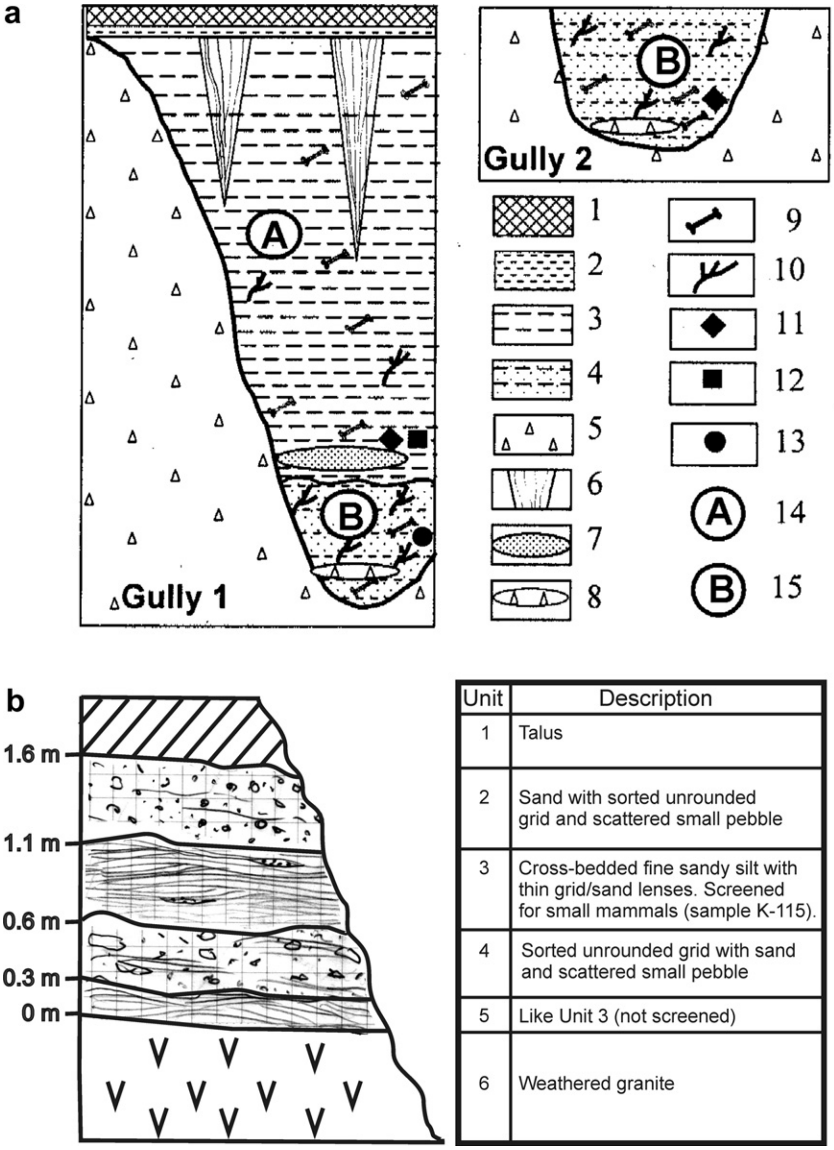


Fig. 1. Map with currently accepted distributions of various cave bears and the position of new findings (Adycha and Cherskiy). 1 – the European range of *Ursus spelaeus* and *Ursus deningeri* (after Kahlke, 1994); 2 – Asian findings of *U. deningeri* (after Baryshnikov and Kalmykov, 2005 and Baryshnikov, 2007); 3 – new find of *U.* cf. *deningeri* in northeastern Siberia (Adycha); 4 – findings of *U. savini rossicus* and *U. savini uralensis* (after Vereshchagin and Baryshnikov, 2000; Baryshnikov, 2007); 5 – Lower Kolyma River, Cherskiy locality of *Ursus savini nordostensis* subsp. nov.

found in Sher et al. (1979). The North-East Scientific Station of the Pacific Institute for Geography, a significant research centre in this remote area, is positioned 4 km east from downtown Cherskiy, on the high right bank of the Panteleikha River, a tributary of the Kolyma. Industrial extraction of rock debris for airstrip reconstruction started in 2000 1 km west of the Station, between it and Cherskiy Airport, which resulted in the exposure of the underlying bedrock and overlying loose permafrost sediments. Between then and 2007, SPD, a member of the Station staff, has studied the opened sections and collected numerous fossil bones. This report is based on his activities (Davydov, 2007).

The right banks of the Panteleikha and Kolyma Rivers near Cherskiy are built of Jurassic granites exposed at the junction of the Kolyma Lowland and the NW branches of the Northern Anyuisk Ridge. Rock hills 300–600 m high, such as Rodinka and Panteleikha Mountains, are only 5–20 km from the site. The granites are strongly eroded at the river banks, overlain by loose Pleistocene sediments, and cut through by gullies filled with currently refrozen Pleistocene sediments; for this reason, the site was called "Ovrag" ("The Gully"). After the bulldozer opened these ancient gullies, they were further eroded down to the bottom – the Paleogene eluvial deposits and underlying rocks – but only some of their parts (sections) were opened at any one time, while others were already covered by debris.

The larger of two gullies (Gully 1, Fig. 2a) was about 7 m deep and cut into the eluvial deposits; its maximum length was 20 m. Several years of observation allowed the compilation of a complete section of its infilling. The upper part (Unit A), up to 6 m in thickness, was formed of loess-like silty loams with polygonal ice wedges. This type of sediment is very common in North-Eastern Siberia, and is usually called "Yedoma" or "Ice Complex" (see Sher et al., 1979 for details). A twig from the lower part of Unit A (Fig. 2a) was ^{14}C dated to 55 900 ± 6170 BP at the Keck Carbon Cycle AMS Facility in the Earth Science Department of the University of California, Irvine, USA (sample 7A D2).



Unit	Description
1	Talus
2	Sand with sorted unrounded grid and scattered small pebble
3	Cross-bedded fine sandy silt with thin grid/sand lenses. Screened for small mammals (sample K-115).
4	Sorted unrounded grid with sand and scattered small pebble
5	Like Unit 3 (not screened)
6	Weathered granite

Fig. 2. Locality "Ovrag" near town of Cherskiy. (a) Sections of two filled gullies 1 km W of the North-East Station, Cherskiy. The sections are reconstructed from several years' observations by SPD. 1 – sod and soil; 2 – loams of transitional layer; 3 – silty loams; 4 – sandy silt; 5 – eluvial deposits; 6 – ice wedges; 7 – ice lens; 8 – lens enriched with grass material; 9 – fossil mammal bones; 10 – plant remains; 11 – sampling for ^{14}C dating; 12 – sampling for beetle fossils; 13 – sampling for small mammals; 14 – Unit A, presumably of Late Pleistocene age; 15 – Unit B, presumably of Olyorian age (Early Pleistocene – early Middle Pleistocene). (b) The site in the lower part of Gully 1 (Unit B), where Olyorian rodents were screened. Field sketch by PAN, edited.

With an erosional unconformity, Unit A overlies Unit B, 1–2.5 m thick (Fig. 2a). Unit B is a stratified body of sandy silt with lenses and layers of non-rounded granite gruss with single inclusions of rounded pebbles. In some places, the upper part of Unit B is highly enriched with plant detritus (fragments of shrub branches and logs of thin trees); the sandy silt here is dark, almost black, in colour.

The smaller gully (Gully 2, Fig. 2a) was less than 2 m deep, and in different years was exposed in two sections – the lower one, 12 m long (2002), and the upper one, 5–7 m long (spring 2007). Both exposures revealed sediments identical to Unit B in the larger gully. By September 2007, the upper part of the Gully 2 was partially destroyed by bulldozers, which pushed the sediments upward along the slope. The cave bear mandible was found by AVS on the surface of such a dump in the upper part of the Gully 2. About 5 m away from the mandible, and a little down the slope, the shallow upper part of the gully was still open (not covered by debris). Inside the sediments at its bottom, at a depth of about 20 cm, SPD found a canine tooth of bear. Since it fitted the mandible in size and preservation, we assume that the canine belonged to the same individual, and suggest the following scenario. The mandible and canine were originally buried in the gully filling, together or not far from each other; then the bulldozer pushed up part of the infill including the mandible, while the canine remained in its original position in the sediment. It was a very lucky chance to find two separated pieces of the same fossil during 10 min. Thus, we can be sure that the original position of the mandible was in the Unit B sediments in the upper part of Gully 2.

The fillings of both gullies included a large number of mammal bones. For 8 years SPD regularly collected bones that appeared during the course of technical activities and/or erosion of the gullies, documenting the position of new finds in relation to the periodically exposed outcrops. Approximately 100 fossil bones have been collected from this locality.

The ice-rich silty loams of Unit A yielded fossils of such common Late Pleistocene animals as mammoth, *Mammuthus primigenius*, horse, *Equus* sp., reindeer, *Rangifer tarandus* and bison, *Bison priscus*. The bones of an incomplete mammoth skeleton, including skull fragments, cervical and thoracic vertebras, costae, scapula, humerus, and pelvis fragments were thawing out of permafrost of Unit A at Gully 1 for a long period of time.

Mammal fossils presumably coming from Unit B are much more unusual. Firstly, the list of bones recovered from this unit in Gully 1, and at both exposures of Gully 2, includes almost 25% musk-oxen (Ovibovini). By contrast, the percentage of musk-oxen in late Middle and Late Pleistocene assemblages is usually less than 1%. It has been shown that in the Olyorian faunas of North-Eastern Siberia (late Early and early Middle Pleistocene) the relative abundance of Ovibovini fossils is much higher, mostly at the expense of bison, one of the dominant elements of the later faunas (Sher, 1971). Moreover, most of musk-ox fossils found at the Cherskiy site are referred to the extinct genus *Praeovibos*. This site has provided very good specimens (neurocrania with horn cores) of an extinct musk-ox referred by Sher (1971) to *Praeovibos* cf. *priscus*. However, the morphology of the large sample of NE Siberian fossils, assigned until now to *Praeovibos priscus* Staudinger, suggests that a description of a new taxon, related but not identical to the European *P. priscus*, is due. The Cherskiy collection includes one male and three female cranial fragments of *Praeovibos* cf. *priscus*, several limb bones confidently identified as *Praeovibos* sp., and a few musk-ox horn fragments, almost certainly not belonging to *Ovibos*.

Another element of the Unit B fauna is a gigantic horse. Unfortunately, fossils that would allow an unambiguous specific determination are lacking, but this form seems very similar to the huge archaic horses, *Equus (Plesippus)* sp., that dominated the Olyorian fauna. Other horse teeth found here belong to the extant subgenus, *Equus (Equus)* sp., but to a very large form, registered in the Late Olyorian. A few fossils of mammoth and bison (limb bones) also belonged to very large varieties, uncommon in the Late Pleistocene. Finally, a deer, identified as *Cervus* ex gr. *elaphus*, is another taxon found in Unit B.

The preservation of most of the bones from Unit B is very different from those from Unit A. Most of them look more mineralized and have a dark brown or almost black colour. This kind of preservation is also characteristic of the cave bear mandible.

In 2005, PAN screened small mammal fossils from the sediments of Unit B in Gully 1 (sample K-115, Figs. 2B and 3). According to VSZ, they include such typical Early Olyorian species as primitive collared lemming *Predicrostonyx compitalis* Zazhigin, 1976 (one upper M2 and lower m1 and m3). Two collared lemming teeth (lower m1 and upper M2) appear to be somewhat derived and were identified as *P. compitalis* or *Dicrostonyx renidens* Zazhigin, 1976; the latter species is typical for the Late Olyorian. Another Early Olyorian species in this sample is the extinct vole *Allophaiomys reservatus* Zazhigin, 1998 (one upper M1). Seven teeth belong to brown lemming (*Lemmus*). The Early Olyorian species of this genus, *Lemmus sheri* Abramson, 1992 was based mostly on cranial and mandibular features, so its identification from isolated teeth is problematic. For this reason the teeth from Cherskiy are referred to *Lemmus* cf. *sibiricus* Kerr.

Thus, the fossils of both large and small mammals clearly indicate an Early Olyorian age for the assemblage, but with possible admixture of Late Olyorian elements due to the later reworking of the sediment.

It should be noted that the occurrence of Olyorian fossil mammals near Cherskiy has been known since almost 40 years ago. In 1970s AVS and colleagues discovered, and in 1976 excavated, a similar locality 1 km west of Cherskiy, between the town and the port of Zeleniy Mys. At this locality, called “Tretiy Ruchey” (the “Third Creek” downstream from Cherskiy), the Kolyma River eroded the sediments of slopes and gully infillings inserted into the weathering crust – bright yellow and orange clays with rock debris. The frozen Pleistocene sediments – silts with fine gruss – yielded about a hundred bones of animals such as a very large archaic horse *Equus* (*Plesippus*) sp. (dominant), giant moose *Cervalces* sp., extinct musk-oxen (*Praeovibos* cf. *priscus, Praeovibos* sp., *Ovibovini* gen.), bison *Bison* sp. and mammoth *Mammuthus* sp. The Olyorian bones, excavated at “Tretiy Ruchey” from permafrost with a water jet, were of lighter colour than those found at “Ovrag” and in general had a fresher appearance and excellent preservation. However, attempts to extract ancient DNA from horse and musk-ox

Fig. 3. Photo of the section of Unit B, where rodents were screened (SPD).

Fig. 4. The left mandible of *Ursus savini nordostensis* ssp. nov. from the "Ovrag" locality near Cherskiy, Lower Kolyma; collection of the Ice Age Museum, Moscow, No. IAM F-2365. Labial (a), lingual (b) and upper (c) views; *h* – depression (pit).

bones from this locality were not successful (Alan Cooper, Paula Campos, pers comms.). The screening of bone-bearing layers for rodents yielded teeth of *Sorex* sp., *Ochotona* sp., *Lepus* sp., *Lemmus* cf. *sibiricus, Predicrostonyx compitalis* or *Dicrostonyx renidens, Allophaiomys reservatus, Microtus* ex gr. *oeconomus* and *Microtus* sp.

Just as the small mammals clearly represent a mixed assemblage of various ages, some large mammal fossils excavated at "Tretiy Ruchey" seem to be post-Olyorian, e.g. small caballine horses and bison. Paleomagnetic analysis of the sediment showed the presence of some reversely magnetized samples, but the general conclusion is that the faunal horizon is a mixture of sediments of Matuyama and Brunhes magnetic epochs (Elena Virina, unpublished data)[2].

With regard to the find of cave bear mandible east of Cherskiy, we can conclude that its provenance from the Olyorian sediments of the Unit B is almost certain, thanks to the definite location of the fitting canine. Furthermore, its preservation is very different from that of bones from Unit A and from all Late Pleistocene bones in this region. Its colour and visible degree of mineralization are similar to fossils of extinct taxa of musk-oxen and horses found here and known from the Olyorian. Although the sediments of ancient gullies and slopes here have probably been re-deposited, with incorporation of some younger fossils, the age of the vast majority of samples is clearly Olyorian. However, due to the complicated circumstances of the find described above, we cannot be sure whether it belongs to the Early or Late Olyorian (late Early and early Middle Pleistocene respectively).

2.1.2. The Adycha (Oskhordokh) find of a cave bear astragalus

The Oskhordokh site lies above the Arctic Circle at 67.54°N, 135.67°E. It is a large gravel bar on the right bank of the Adycha River, where thousands of mammal bones have been collected by professionals and amateurs. They belong to animals of different geological ages – from the Early to the Late Pleistocene. There are no open exposures near or upstream of the Oskhordokh Bar,

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[2] The Early Olyorian is dated to the later part of the Matuyama Chron, while the Late Olyorian is in the early Brunhes (Sher et al., 1979).

Fig. 5. The same mandible as Fig. 4, occlusal view of p4-m2.

except for a low and presumably quite young terrace, so the original source of fossils remains unclear, and the geological age of the bear astragalus can be hypothesized from indirect evidence only. Downstream of Oskhordokh several high bluffs are exposed, which are formed from Quaternary deposits of various ages and are rich with mammal fossils. The best-studied bluff is Ulakhan-Sullar, 20 km north from Oskhordokh and about 60 m high. The main part of the section (upper 50 m) is formed from well-washed sands of fluvial origin (the Ulakhan-Sullar Suite) referred to the latest Middle Pleistocene to early Late Pleistocene. The base of the section (the lower unit, ca 8 m thick) is represented by a very complex geological formation (silts, gravels and rock debris with large accumulations of tree trunks) – the Adychan Suite. The age of this unit is uncertain; it was believed to date somewhere between Late Pliocene and early Middle Pleistocene (Kaplina et al., 1983; Shilo, 1987). Recent study by PAN has shown, however, that the upper part of the Adychan Suite is of late Middle Pleistocene age. The uncertainty is explained by the fact that numerous bones found *in situ* in the lower unit (both of large and small mammals) belong to a mixed assemblage of various ages. The Adychan Suite includes numerous bones of such extinct taxa as the canid *Canis (Xenocyon) lycaonoides* (Sotnikova, 1978, 2007), an early form of *Mammuthus trogontherii*, huge archaic horses *Equus* (*Plesippus*) *verae* and *Equus* (*Plesippus*) sp., a giant moose *Cervalces* aff. *latifrons*, and various extinct musk-oxen such as *Praeovibos* cf. *priscus*, *Praeovibos beringiensis* and *Soergelia* sp. A mandible of the most primitive wolverine *Gulo minor,* a possible ancestor of later wolverines (*Gulo*) (Sotnikova, 1982), and a saber-tooth cat *Homotherium* sp. (Sotnikova, 1978, 2007), were found on the bar adjacent to Ulakhan-Sullar. Thus, there is a very strong ancient component in the Adychan fauna. However, the occurrence of rather advanced microtines, and the normal magnetic polarity of the lower unit of Ulakhan-Sullar (Brunhes Chron: Minyuk, 2004), suggest a later (late Middle Pleistocene) age, with the admixture of more ancient fossils by re-deposition. All bones found in the upper unit are light-coloured (white or yellowish). The preservation of bones from the lower unit is variable but the colour on their surface is usually darker, and the internal colour more intense, than those from the upper unit.

The bear astragalus has a dark-brown colour; moreover, during the sampling process it was observed that the bone was uniformly brown inside as well. Bones of such coloration have never been found in the upper unit of the Adychan sections, but are rather common in the lower unit. Hence, we can assume that the age of the bear astragalus is older than late Middle Pleistocene; its age is early Middle Pleistocene (Late Olyorian) or even earlier.

Baryshnikov and Boeskorov (1998) described a number of bear fossils from the Adycha River (Ulakhan-Sullar and neighbouring sites); their collection, however, included only brown bear specimens. After the recognition of the Oskhordokh astragalus as a cave bear, GFB examined other bear specimens from Adycha, recently collected there by PAN, but failed to find any cave bear material.

2.2. Comparative characteristics of new cave bear fossils from North-Eastern Siberia

2.2.1. The cave bear mandible from Cherskiy

The specimen, a left mandible from Cherskiy ("Ovrag") site (IAM F-2365), is relatively well preserved (Figs. 4 and 5). The ascending ramus is broken off. Of the cheek teeth, p4, m1 and m2 are preserved; there is an empty alveolus of m3. The canine, found about 5 m aside from the mandible, by its size, shape and preservation fits the mandible quite well, so it very likely belongs to the same individual.

The fossil seems to be rather deeply mineralized; it has a dark brown colour, and the dental enamel is brownish with an opal shade. There are no traces of rounding. The dimensions of IAM F-2365 are given in Table 1.

The horizontal ramus of the mandible is very high, especially in relation to the crown height of the cheek teeth. Its depth decreases only slightly anteriorly. There are two large mental foramina, the posterior one positioned below the p4. The symphysis is strong and extending downwards, forming a pronounced "chin". The preserved small fragment of the coronoid process of the mandible strongly suggests that its anterior edge rose steeply. The lower border of the horizontal ramus is straight.

A very unusual feature of the mandible is a small depression behind the alveolus of m3 (*h,* Fig. 4c). Its anterior and lateral walls are steep (vertical), and the posterior wall flat. This depression is definitely not a tooth alveolus, and its function is still unclear. Most probably, it is an attachment area of a powerful chewing muscle (*m. temporalis* or *m. buccinator*).

Table 1
Size of mandible and dentition of small cave bears, *Ursus savini* ssp.

Measurements, mm	*U. savini nordostensis* ssp. nov.	*U. savini savini*					*U. savini rossicus*
	Cherskiy, lower Kolyma River	Bacton, Cromer Forest-Bed Formation, England					Bachatsk Quarry, Kuzbass, south-western Siberia
	IAM F-2365	NHM 6186	NHM 17912	NHM 17906	NHM 16448, holotype	NHM 6186 [1245]	IGG 328
Mandible							
Length, tooth row c1-m3	155.5	164.6		157.5	155.7	150.3	159.3
Length, tooth row p4-m3	85.6	89.0	95.0	91.3	90.4	84.1	94.5
Height of mandible behind m1	51.7	–	–	–	–	–	54.5
Height of mandible at diastema	49.8	58.3	63.8	53.8	53.3	52.4	52.1
Teeth							
c1 length	21.1	25.2			23.4	18.4	26.5
Width	15.9	17.6			17.7	15.0	18.4
p4 length	13.5	14.6	15.6	13.6	15.7	14.9	15.0
Width	9.1	8.5	9.1	8.4	10.2	7.9	9.5
m1 length	24.4	27.5		26.5	24.8		27.0
Width	11.8	12.7		13.2	12.2		13.5
m2 length	23.9		25.7	24.8	24.8	23.3	28.5
Width	14.8		16.3	16.6	16.0	15.8	17.0

Abbreviations: IAM – Ice Age Museum, Moscow; IGG – Institute of Geology and Geophysics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk; NHM – Natural History Museum, London.

The lower canine has the common structure for bears. The height of the enamel crown is 33.5 mm. According to the length and width of the canine, the jaw belonged to a female.

The cheek teeth are narrow, with worn occlusal surfaces, especially from the labial side (except for p4). The anterior premolars p1–3 are completely absent; the diastema between the canine and p4 is 44.8 mm long. Lower molars m1 and m2 adjoin, while p4 is separated from m1 by a short diastema.

The fourth lower premolar (p4) is small; its length only slightly exceeds half the length of m1. The tooth has two separated roots. The tooth crown expands posteriorly only slightly. The protoconid (principal or main cusp) is large and high (see Fig. 6 for explanation of terms). The tooth bears a strong but low antero-lingual cusp, which protrudes forward. There are three large accessory cone-shaped cusps situated on the lingual side of the crown of p4 at the protoconid base. There is a weak labial cingulid, stretching out to the back edge of the crown.

The first lower molar (m1) is slightly longer than m2. The minimum crown width in the area of contact between trigonid and talonid is only insignificantly smaller than the trigonid width. The metaconid is large, with two additional cone-shaped pre-metaconid cusps. Most of the talonid is occupied by the large hypoconid. There is a tubercle in front of the hypoconid. The talonid basin looks like a shallow horizontal groove. It separates lingual cusps from the group of entoconid tubercles, which consists of two cone-shaped cusps with a lower additional tubercle between them. A weak labial cingulid can be seen in the area of contact between the trigonid and talonid.

In the second lower molar (m2) the talonid is reduced, and notably smaller in its width than the trigonid. The metaconid is worn, being smaller than protoconid, and has a posterior cusp, which extends a little farther lingually than the main peak. Two small additional tubercles are present in front of the metaconid. The entoconid consists of two tubercles, almost equal in size.

We used the morphological analyses based on original and early published data (Rabeder, 1983, 1999; Baryshnikov, 1998; García, 2003; Grandal d'Anglade and López-Gonzáles, 2004) to compare the Cherskiy specimen with other fossil bears (Table 2).

The Cherskiy mandible has definite features of "spelaeoid" bears, clearly differentiating the specimen from "arctoid" bears: (1) lack of the anterior premolars p1–p3; (2) complicated structure of the lower check teeth, especially that of p4; (3) vertical position of the anterior edge of the coronoid process; (4) comparatively high ramus. Based on this morphology we should attribute the find to the *Ursus* (*Spelearctos*) subgenus.

The Cherskiy mandible (IAM F-2365) differs from that of both *U. deningeri* and *U. spelaeus* in smaller size, longer diastema

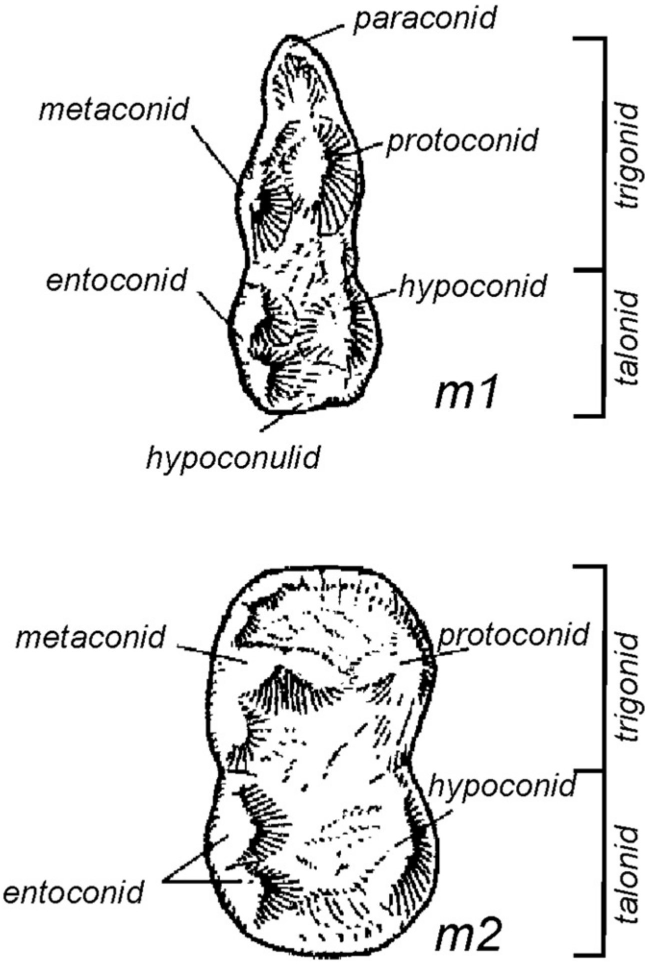

Fig. 6. The nomenclature of the elements of lower dentition of cave bear (*Ursus spelaeus*) used in this paper (after Baryshnikov, 2007).

Table 2
Comparative characteristics of mandible and lower check teeth in cave and brown bears.

Characters	*U. savini nordenstensis* ssp. n.	*U. s. savini*	*U. s. rossicus*	*U. deningeri*	*U. spelaeus*	*U. arctos*
Mandible						
Size	Small	Small	Small	Small to large	Large	Small to large
Lower border of mandible	Straight	Straight	Convex	Straight or convex	Convex	Straight
Upper border of mandible in front of p4	Concave	Straight	Straight	Concave or straight	Predominantly straight	Predominantly concave
Height of ramus (with regard to c1-m3 length)	Medium	High	High	Medium	Medium	Low
Anterior border of coronoid process	Steep (?)	Steep	Steep or gentle	Steep or gentle	Gentle	Gentle
Teeth						
First premolar p4	Absent	Absent	Absent	Usually absent	Absent	Present
Structure of p4 crown	Complicated	Simple or complicated	Complicated	Simple	Complicated	Simple
Paraconid-like cusp of p4	Simple, large	Simple or double	Simple or double	Simple, small	Simple or double	Absent or small
Metaconid-like cusp of p4	Double	Simple or double	Simple or double	Simple	Double	Absent
Length m1/Length m2	m1 > m2	m1 > m2	m1 < m2	m1 < m2	m1 = m2	m1 < m2
Width of m1 (with regard to half-length of m1)	Smaller	Equal	Equal	Smaller	Smaller	Smaller
Metaconid of m1	Triple	Double or triple	Double	Double	Double or triple	Double
Entoconid of m1	Double	Double	Double	Double	Double or triple	Single or double
Talonid of m2	Short	Short or medium	Medium	Medium	Long	Medium
Width of m2 trigonid as compared to width of m2 talonid	Trigonid wider than talonid	Trigonid narrower than talonid	Trigonid narrower than talonid	Trigonid narrower than talonid	Trigonid narrower than talonid	Trigonid narrower than talonid
Metaconid of m2	Triple	Triple	Double or triple	Double or triple	Triple	Double
Entoconid of m2	Double	Triple	Double	Double or triple	Double, triple or quaternary	Double

between the canine and p4 premolar, and a complex of primitive tooth morphology such as elongated m1 (compared to m2), small talonid in m2, and the presence of large accessory cone-shaped cusps situated on the lingual side of the crown of p4 at the protoconid base (Baryshnikov, 2007). All other features demonstrate a close resemblance to the *U. savini* species[3].

Principal components analysis of the 9 morphometric features in Table 1 (excluding the height of mandible behind m1, and canine dimensions) was applied to compare the “spelaeoid” bears with *Ursus arctos* and *Ursus etruscus*. *U. etruscus* is likely to be the common ancestor of the “spelaeoid” and “arctoid” lineages (Kurtén, 1976). In total we included 6 samples of “spelaeoid”, recent “arctoid” and Etruscan bears. Factor 1 accounted for 43.9% of the variance and was heavily weighted by p4-m3 length, m1 length, m1 width, m2 length and m2 width, while Factor 2 accounted for 20.8% of the variance and was heavily weighted by c1-m3 length and mandible height at diastema. A plot of Factor 1 vs. Factor 2 is shown in Fig. 7. The Cherskiy mandible is grouped with the smallest specimens of *U. savini savini* and *U. savini rossicus*. It is also placed close to *U. etruscus*. The new find is well distanced from *U. deningeri deningeri* and *U. deningeri kudarensis* on Factor 1 and from the recent *U. arctos* on Factor 2.

Thus, the morphological and the morphometric results suggest the close resemblance of the Cherskiy bear and *U. savini*, and of the Cherskiy bear and the ancestral species *U. etruscus*.

The following features, suggesting that *U. savini* and *U. etruscus* are closely related to each other: the steep front edge of the coronoid process, large m1, and relatively narrow talonid on m2. Our study of these characters in the Cherskiy mandible implies that the Cherskiy bear, *U. savini,* and *U. etruscus* are more closely related to each other than either is to the “arctoid” bears *Ursus dolinensis* and *Ursus rodei* from the Early Pleistocene of Europe discussed by García and Arsuaga (2001) and Musil (2001).

In dental morphology, size and proportions, the Cherskiy mandible is closest to *U. savini savini*. Other varieties of small cave bears, such as *U. savini rossicus* and *U. s. uralensis* (from the Kizel-Cave in the Middle Urals), do not have such a strongly pronounced “chin” which is the characteristic of our mandible. Moreover, they have m1 shorter than m2, and the ascending ramus of the jaw is

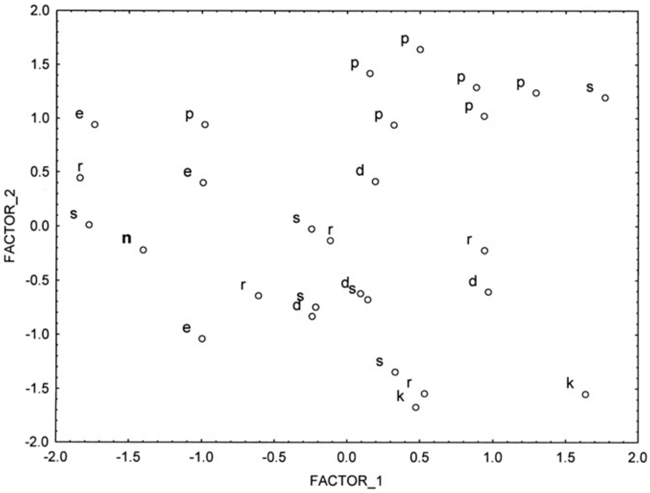

Fig. 7. Plot of factor scores of Factor 1 and Factor 2 from principal component analysis of bear mandibles. d – *Ursus deningeri deningeri*, Mosbach, Germany; e – *U. etruscus*; k – *U. deningeri kudarensis*, Kudaro 1 Cave (layers 3–4), Georgia; n- Cherskiy; p – *U. arctos pruinosus*, Tibet, China, recent; r – *U. savini rossicus*, Siberia, Russia; s – *U. savini savini*, Bacton Forest Bed, Britain.

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[3] The type specimen of *Ursus savini* was collected in 1840s by Rev. C. Green near Bacton, on the Norfolk Coast (United Kingdom), one of the localities of the Cromer Forest-bed Formation. Later, similar specimens found at Bacton and at other localities on the Norfolk coast (East Runton, Mundesley, Sidestrand and Overstrand) were assigned by different palaeontologists to the same species. Bacton itself, or more precisely Ostend, where most of Rev. C. Green's collections were made, includes sediments of Early Pleistocene and early Middle Pleistocene age (Stuart and West, 1976; Lister, 1993, 1996). So the exact age of *Ursus savini* remains uncertain, but within the mentioned time range.

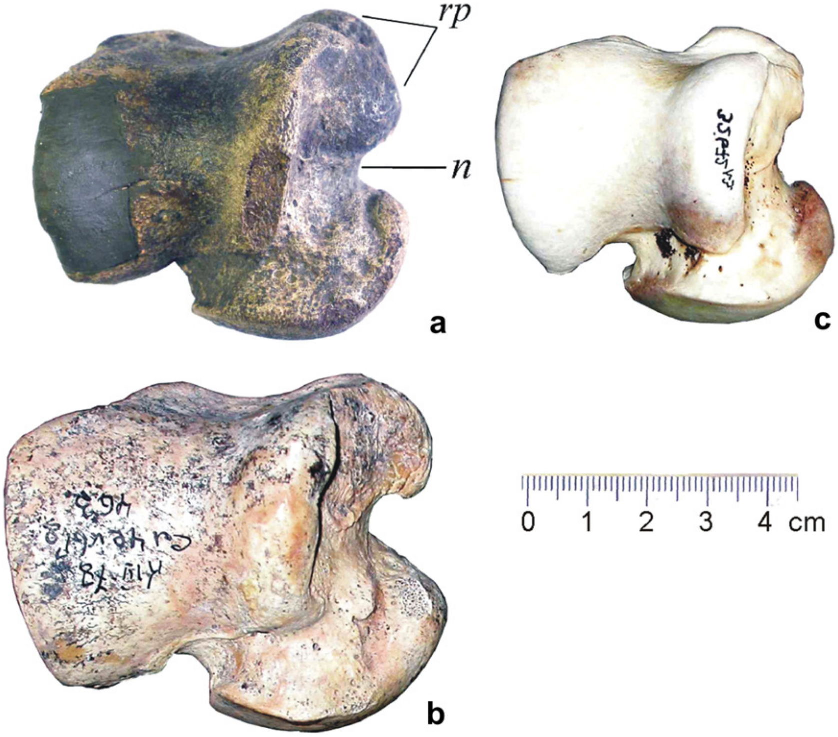

Fig. 8. Right astragali of cave bears (a, b) and brown bear (c), dorsal view. (a) *Ursus* cf. *deningeri*, Oskhordokh, Adycha River, Yakutia (black patch on the lateral side of articular block is a restored area from which the subsamples for DNA were cut); (b) *U. deningeri kudarensis*, Kudaro-3 Cave (layer 4), Georgia; (c) *U. arctos*, Kamchatka, Russia, recent. *rp* – rough platform, *n* – notch.

less steep than in the Cherskiy specimen (cf. Vereshchagin and Baryshnikov, 2000; Baryshnikov and Foronova, 2001).

On the other hand, our specimen differs from the nominative subspecies from the Cromer Forest-bed Formation in showing advanced features such as the more complicated structure of its fourth premolar. None of the 13 examined specimens of p4 from the type Formation[4] possesses more than two additional tubercles on the lingual side. Some other characters that discriminate these fossil bears are shown in the Table 2. Therefore, the new fossil is found to be beyond the limits of variability of *U. s. savini,* which suggests that it should be regarded as a distinct taxon of subspecies rank.

Family Ursidae Fisher, 1814
Genus ***Ursus*** Linnaeus, 1758
U. savini Andrews, 1922
Ursus savini nordostensis Baryshnikov subsp. nov.

Etymology. The most north-eastern record of cave bears in Eurasia known so far.

Type locality. Cherskiy Settlement, lower course of Kolyma River Basin, right bank of the Panteleikha River 1 km W of the Northern Geographic Station of the Pacific Institute of Geography, “Ovrag” site, the upper part of Gully 2.

Holotype. Left mandibular ramus with p4-m2 preserved and apparently fitting canine of the same individual, found separately, IAM F-2365, Ice Age Museum, Moscow, Russia.

Differential diagnosis. p4 has 3–4 small accessory lingual cusps and a weak labial cingulid stretching out to the back edge of the crown, while p4 of *U. savini savini* usually has only one, rarely two accessory cusps and no labial cingulid. p4 IAM F-2365 is similar to the teeth of *U. savini rossicus* from Siberia, e.g. from the Berezhekovo site on the Yenisei River. *U. s. nordostensis* subsp. nov. has m1 bigger than m2, while in *U. savini rossicus* and *Ursus savini uralensis* m1 is smaller than m2. The horizontal ramus is very high, especially in relation to the crown height of the cheek teeth, as in *U. savini savini*. The symphysis of the mandible extends downwards, forming a pronounced “chin” as in *U. savini savini* but not in *U. savini rossicus*. The anterior edge of the mandible rises steeply, as in *U. savini savini*.

Geological age. Although the mandible was not found *in situ*, it can be confidently stated that it belongs to the Olyorian Mammal Age, ca. 1.5–0.5 Ma (Sher, 1987), due to a more certain provenance of the fitting canine, the preservation of the fossils, and the accompanying fossil fauna.

Distribution. So far it is known from the type locality only.

Comment. In dental morphology, size and proportions, the Cherskiy mandible is very close to *U. savini savini*. Other small cave bears, *U. savini rossicus* and *U. savini uralensis*, do not have such a strongly pronounced “chin” as seen in our mandible. Moreover, they have m1 shorter than m2, and the ascending ramus of the jaw is less steep than in the Cherskiy specimen (cf. Vereshchagin and Baryshnikov, 2000; Baryshnikov and Foronova, 2001). On the other hand, our specimen differs from the nominative subspecies from Norfolk in having a more complicated structure of its fourth premolar, which is a derived trait for cave bears. *U. savini rossicus* and *U. savini uralensis* are more advanced than *U. savini nordostensis* subsp. nov., as their m1 are smaller than m2; the lower m1 of cave bears tends to enlarge during evolution.

2.2.2. The cave bear astragalus from the Adycha River

The bone in question is a bear right astragalus (talus) from the collection of the Paleontological Institute of the Russian Academy of

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[4] The Norfolk collection of *Ursus savini* was personally studied and measured by GFB (Table 1) using the methods described by Baryshnikov (2007)

Sciences, PIN 3723-496 (Fig. 8). The story of its finding, local geology and preservation are described above.

The greatest length of the bone is 53.8 mm, its greatest width 61.4 mm, which corresponds to the dimensions of female astragali of large cave bears and male astragali of small cave bears. The specimen has a "spelaeoid" morphology. It differs from brown bear (*Ursus arctos* L.) in the characters distinguishing the latter species from *U. deningeri* and *U. savini*, namely by a stronger rough platform bordering the articular area (*trochlea tali*) along the upper and interior (medial) sides (*rp,* Fig. 8), as well as by a deeper notch (*n,* Fig. 8) separating this platform from the head of the astragalus (*caput tali*). Importantly, the Adycha astragalus is clearly more robust than those of *U. savini rossicus*.

After a "spelaeoid" mtDNA sequence was retrieved from specimen PIN 3723-496 at Oxford, the second subsample of this specimen was analyzed in the Max Planck Institute for Evolutionary Anthropology (Leipzig), where a series of cave bear fossils had by that time been analyzed for aDNA. This independent replication not only confirmed that the Adycha astragalus belonged to cave bears (*s.l.*), but also showed a relatively close similarity of its mtDNA sequence to that of the bear from Kudaro-3 Cave in the Southern Caucasus (Knapp et al., 2009). The bear from Kudaro-3 (Late Pleistocene layers 3–4) was originally described as *Ursus spelaeus kudarensis* by Baryshnikov (in Lubine et al., 1985), but later study indicated a closer affinity to *U. deningeri* than to *U. spelaeus*; thus the Kudaro-3 bear was renamed *U. deningeri kudarensis* (Baryshnikov, 1998, 2007). However, the recent genetic study (Knapp et al., 2009) has demonstrated that the Southern Caucasus bears (and the Kudaro-3 bear in particular) represent an mtDNA lineage that had very early separated from all other cave bears; consequently, it was concluded that it should be considered as an independent species, *Ursus kudarensis* (Knapp et al., 2009).

Following these arguments, we should apply the same name to the Adycha astragalus, which belongs to the same mtDNA lineage. However, because the relatively low diagnostic value of the astragali compared to the mandibles, we would prefer at present to assign it to *Ursus* cf. *deningeri*.

3. Discussion

The two new fossils from north-eastern Siberia definitely belong to cave bears *sensu lato*, *Ursus* (*Spelearctos*), and fundamentally change accepted ideas about the range and ecological potential of these animals.

Of the two new cave bear fossils, the Cherskiy mandible is not only morphologically the more informative, but was also found in a more reliable geological context. It can be confidently assigned to the Olyorian *sensu lato*, i.e. 1.5–0.5 Ma.

The Adycha and Cherskiy sites are respectively about 100 and 250 km north of the Arctic Circle. Today this region has an extremely continental climate with winter temperatures approaching the lowest in the Northern Hemisphere, with continuous permafrost up to 400–700 m thick. The Pleistocene environmental history of the region is known rather well. It has been shown that permafrost appeared on the Yana-Kolyma Lowland not later than 2.5 million years ago (Sher et al., 1979). Extremely continental climate with low precipitation resulted in early development of the environment that we call tundra-steppe – mostly treeless dry grassland on permafrost. The paleobotanical evidence suggests that it was a complex, mosaic landscape: in addition to xeric tundra-steppe and meadow-steppe communities, typical mesic tundra biotopes existed in the areas with higher moisture supply, and larch and tree birch sporadically formed sparse and spatially restricted groves. Such an environment was definitely more severe than in the main (south-western) range of cave bears.

Thus, new findings in North-Eastern Siberia not only extend the previously known range of "spelaeoid" bears in Arctic Siberia (Fig. 1), but place these animals in a very different type of environment than that in which they were found before. Karst-susceptible rocks (limestone, etc.) are not very common in the whole Yana-Kolyma region; moreover, the ubiquitous presence of thick permafrost practically excludes karst development and formation of caves.

Such an environment would probably better suit the small cave bear *U. savini rossicus* and *U. savini uralensis*, which is believed to have been an inhabitant of open plains and low hills, although its remains have been identified in at least five caves in the Middle and Southern Urals, where they occur together with the bones of the large cave bear, *U. spelaeus* (Baryshnikov, 2007). Middle and Late Pleistocene sites with *U. savini uralensis* fossils are found in the south, in the present-day steppe zone, mostly south of 55°N; the northernmost localities (Middle Urals) are between 55 and 60°N (Fig. 1). There are very few ^{14}C dates on small cave bear fossils; most of them indicate MIS-3 interstadial or earlier age. The new find of a small cave bear in the lower Kolyma suggests that as early as the Olyorian, this population was already well adapted to life in Arctic tundra-steppe conditions.

The group of large cave bears, *U. deningeri* – *U. spelaeus*, also had a mostly southern distribution; this is especially true for the earlier known finds of *U. deningeri* in Asia (Fig. 1): Israel, Transcaucasia, Kirghizia, Altai, Transbaikalia and probably even Mongolia and Korea. *U. spelaeus,* however, at least in the Urals, were distributed further north than *U. savini uralensis*, and almost reached 64°N. If the Adycha astragalus really belongs to *U. deningeri*, the new ecological inferences made about *U. savini nordostensis* should be applied to the group of large cave bears as well (or at least to the *U. deningeri* representatives).

A point worth stressing concerning the present study is the synergy between molecular and morphological research. The current rapid advance in the study of ancient DNA will almost certainly lead to surprising new discoveries similar to those reported here. It is very important that these two lines of research are run as a cooperative enterprise between palaeontologists and geneticists; in particular, it is essential that for the purpose of aDNA analysis, specimens are selected that are morphologically diagnostic.

It is probably too early to discuss the problems of cave bear phylogeny and dispersal in the light of these new, unexpected findings, as they are based on very scant fossil material. However, some problems arising from these new results can be already delineated. First is the question of the assignation of the Adycha astragalus to *U. deningeri kudarensis*. Although it has some features in common with the latter (Fig. 8), we should remember that the relationships among *U. deningeri kudarensis*, other *U. deningeri*, and *U. spelaeus* were investigated on complete skulls, mandibles and dentition – much more informative and representative material than a single astragalus. Suggested predecessors of *U. kudarensis* in the Caucasus (*Ursus praekudarensis* Baryshnikov, 1998), or in Europe and Siberia (*U. deningeri*) are so far not studied genetically[5]. It should be noted, however, that the observed mtDNA difference between the Kudaro-3 and Adycha fossils (Knapp et al., 2009) suggests a relatively ancient divergence between clades, which would have been sufficient for developing different adaptations.

The finding of a cave bear mandible in Cherskiy raises another question – the relationship among the small cave bears (*U. savini*

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[5] Recently, DNA sequences from ~400 000 year old *U. deningeri* bones have been published (Valdiosera et al., 2006), but they were obtained on cytochrome *b*, and unfortunately are not comparable with the results by Knapp et al. (2009), who studied the control region.

savini, U. savini rossicus, U. savini uralensis). Baryshnikov (2007) considered these forms as subspecies of a single species *Ursus (Spelearctos) savini*, implying that the earliest form, *U. savini savini,* is the ancestor of *U. savini rossicus* and *U. savini uralensis*. Morphological features, size and the morphometric proportions show that the Cherskiy mandible clearly differs from large cave bears (*U. deningeri* – *U. spelaeus*) and belongs to the lineage of small cave bears, being most similar to the type of *U. savini*. On the other hand, the Cherskiy mandible, in comparison to the type of *U. savini,* has some more derived features, such as more complicated structure of the p4. At the same time, it is less advanced than *U. savini rossicus* and *U. savini uralensis*. As far as can be determined from a single fossil, therefore, an intermediate evolutionary position of the new subspecies, *U. savini nordostensis*, between *U. s. savini* and *U. s. rossicus*, seems possible. However, the chronological relationship between the British and NE Siberian forms remains unclear, since both are dated within a similar, but wide, time range.

North-Eastern Siberian faunas in general, and the Olyorian fauna in particular, have already delivered a number of surprises. It turned out to be the area where early stages of evolution of several groups of mammals took place, such as lemmings and some voles (Zazhigin, 1976, 1998; Abramson, 1992), mammoths (Lister and Sher, 2001), some horses, moose, saiga antelopes and musk-oxen (Sher, 1971; Baryshnikov et al., 1998), and others. The complex of Olyorian carnivores included such animals as extinct wolves and xenocyons, early Arctic foxes and wolverines, and large cats such as *Panthera* sp. and *Homotherium* sp. (Sotnikova, 1978, 2007). Thus, this region played an important role in mammalian speciation. Recent genetic studies, e.g. the discovery of extinct ancient haplotypes of woolly mammoth in North-Eastern Siberia (Barnes et al., 2007), corroborate this concept. The peculiar climate and environment of North-Eastern Siberia, with early development of the tundra-steppe biome, resulted in higher rates of evolution in some mammalian lineages; this has been particularly demonstrated for mammoths (Lister and Sher, 2001). The Olyorian Land Mammal Age (Sher, 1987), like the corresponding time in Europe (Early to Middle Pleistocene transition), was a period of important events in the development of mammalian faunas; some Olyorian taxa have been shown to have impacted the evolution of related lineages in the temperate latitudes of Eurasia (Sher, 1992). For these reasons, we should be cautious when comparing Beringian and European fossils. In our case, a slightly more advanced morphology of Cherskiy mandible compared with the type series of *U. savini* from England does not necessarily imply a later geological age.

The discovery of cave bears in this area, which was much closer to Alaska even than to the Urals, and is considered as the Western (Asiatic) part of the Beringian Land, also raises the question about their possible dispersal to the New World during the Pleistocene.

The solution of these problems, however, should wait until additional fossils of cave bears are found in North-Eastern Siberia.

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