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Short communication

The northernmost and latest occurrence of the fossil porcupine (*Hystrix brachyura vinogradovi* Argyropulo, 1941) in the Altai Mountains in the Late Pleistocene (ca. 32,000–41,000 cal BP)

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ABSTRACT

Several new finds of the Late Pleistocene porcupine (*Hystrix brachyura vinogradovi*) in the Altai Mountains of southern Siberia and the Urals occur far north of previously assigned range for porcupine. These finds have necessitated a renewed study of this species's chronology and spatial distribution. We conclude that the oldest records of this porcupine in the Ural Mountains date to MIS 5e, and its geographic range possibly included also the Altai at that time. Directly radiocarbon-dated porcupine bones in the Altai fall in MIS 3 (ca. 32,000–41,000 cal BP). It is the northernmost record of this species and the youngest find outside its current geographic range.

1. Introduction

In the last two decades (1990s–2010s), studies focusing on Late Pleistocene mammals have made advances using direct radiocarbon (^{14}C) dates on animal bone by Accelerator Mass Spectrometry (AMS) (e.g., Stuart and Lister, 2012, 2014; Stuart et al., 2002, 2004; Kuzmin, 2010). The technical availability of direct dating is a big advantage in comparison to previous indirect data for understanding the spatiotemporal patterns of species expansion or disappearance (e.g., Orlova et al., 2004; MacDonald et al., 2012). It has become clear that age estimates based on indirect data (i.e., ^{14}C dating of associated material, often loosely connected to fossils) may lead to unreliable conclusions which require additional studies (e.g., Turvey et al., 2013).

The presence of fossil remains far outside of main habitats for the extant species is another important issue in mammal palaeoecology and biogeography. The loss of habitats (most probably caused by palaeoenvironmental changes) is closely related to the process of extinction. It is known that the porcupine (*Hystrix brachyura vinogradovi*) occupied the Urals and Altai Mountains of Siberia in the Late Pleistocene, and the northern limit for habitats of fossil porcupine was almost at 60° N (Baryshnikov, 2001, 2003). The Altai Pleistocene porcupines occurred approximately 950 km north of today's habitat boundary for Malayan porcupine. In the Urals they were found 1300–2100 km north from the limit of their present-day distribution (Fig. 1).

Porcupine (genus *Hystrix*) remains have been found at more than 100 Pleistocene fossil localities in Europe and Asia (Baryshnikov, 2003; Tong, 2008); however, they are very rare in Siberia and the Urals (Fig. 1). Therefore, ^{14}C dates on these specimens are extremely important for palaeoecological

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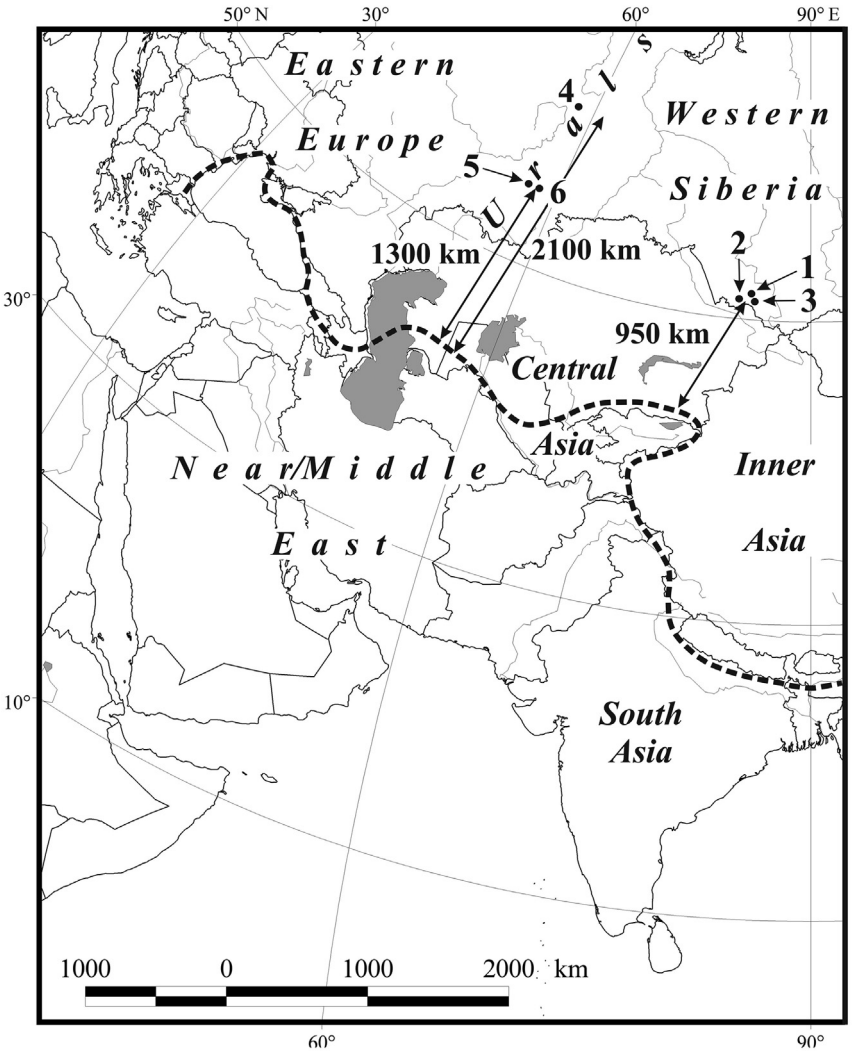

Fig. 1. Localities in the Altai Mountains and the Urals with records of *H. brachyura vinogradovi*: 1 – Razboinichya Cave; 2 – Strashnaya Cave; 3 – Ust-Kanskaya Cave; 4 – Makhnevskaya Ice and Viasher caves; 5 – Pallas and Barsuchii Dol caves; 6 – Idrisovskaya Cave. Dashed line is the northern limit of modern porcupine's habitat (after Gromov and Erbaeva, 1995).

reconstructions. Here we present palaeontological and chronological studies of Late Pleistocene porcupines from Siberia and the Urals.

2. Material and methods

Currently, the Pleistocene small porcupine is known from eight localities in the Altai Mountains and the Urals (Table 1). In the Altai, bones and teeth of this porcupine were found at the Strashnaya, Razboinichya, and Ust-Kan caves. The Strashnaya Cave (51°10′ N, 83°01′ E) contains the largest quantity of porcupine remains in North Asia: 15 teeth and two tooth fragments (Fig. 2); two fragments of maxilla (one with two teeth); two fragments of mandible (one with a tooth); three fragments of canine tooth; the axis; the scapula; an ulna; a fragment of lower epiphysis of a femur; a patella; an astragalus; a calcaneus; and two metapodia. Remains of other mammals are also identified from the Strashnaya Cave (Vasiliev and Zenin, 2009; Vasiliev et al., 2016; Serdyuk and Zenin, 2016; see Table 1). In the Razboinichya Cave (51°18′ N, 84°28′ E) (e.g. Ovodov et al., 2010, 2011), porcupine finds include a small skull fragment containing one molar tooth (Ovodov, 2000) (Fig. 3), as well as other fossils (see Table 1). In the Ust-Kan [also known as Ust'-Kansk and Ust'-Kanskaya] Cave (50°54′ N, 84°48′ E), a single porcupine tooth was found in the cave's deposits together with other animal bones (Agadjianian and Serdyuk, 2005; Derevianko et al., 2002; Turner et al., 2013; see Table 1).

In the Ural Mountains, five cave localities have yielded porcupine fossils: Makhnevskaya Ledyanaya [Ice] Cave (59°26′ N, 57°41′ E), Viasher Cave [also known as Kizelovsksya Cave] (59°06′ N, 57°39′ E), Barsuchii Dol Cave (55°11′ N, 57°25′ E), Pallas Cave (55°11′ N, 58°38′ E), and Idrisovskaya Cave (55°03′ N, 58°10′ E) (Fig. 1). In Makhnevskaya Ice Cave, an almost complete cranium, fragments of maxilla and mandible, incisors, and other teeth and bones from several individuals were found (Baryshnikov, 2003; Fadeeva et al., 2011). In Viasher Cave, one tooth was identified (Fadeeva et al., 2010; see Fig. 4). In Barsuchii Dol Cave, incisors and postcranial bones of several individuals were found. In Pallas Cave, a complete mandible was discovered. In Idrisovskaya Cave, a first phalanx was found.

Species identification was conducted using comparative material, crania and skeletons of modern species of *Hystrix*, from collections of the Zoological Institute (St. Petersburg), the Institute of Ecology of Plants and Animals, the Institute of Ecology and Systematics (Novosibirsk), as well as published sources on modern and

Table 1
Faunal remains (selected taxa) from the localities in the Altai Mountains and the Urals under consideration.

Species	Altai Mountains			The Urals				
	Strashnaya Cave	Razboinichya Cave	Ust-Kan Cave	Makhnevskaya Ice Cave	Pallas Cave	Viasher Cave	Barsuchii Dol Cave	Idrisovskaya Cave
Hedgehog (*Erinaceus* sp.)	X		X	X			X	
Common mole (*Talpa* cf. *europaea)*				X			X	
Altai mole (*Talpa altaica*)	X	X	X					
Russian desman (*Desmana moschata*)							X	
White-toothed shrew (*Crocidura* cf. *leucodon*)				X				
Eurasian shrew (*Sorex araneus*)		X		X				
Even-toothed shrew (*S. isodon*)				X				
Laxmann's shrew (*S. caecutiens*)				X				
Lesser shrew (*S. minutus*)				X				
Northern bat (*Eptesicus nilssonii*)				X				
Long-eared bat (*Plecotus auritus)*				X				
Siberian flying squirrel (*Pteromys volans*)	X		X					
Red squirrel (*Sciurus vulgaris*)			X					
Siberian chipmunk (*Tamias sibiricus*)			X					
Marmot (*Marmota* sp.)	X	X	X	X	X	X	X	X
Forest dormouse (*Dryomys nitedula*)							X	
Beaver (*Castor fiber*)	X		X			X		X
Altai zokor (*Myospalax myospalax*)	X	X	X					
True lemmings (Lemmini gen.)			X	X			X	X
Gray red-backed vole (*Clethrionomys rufocanus*)	X						X	X
Ruddy vole (*Clethrionomys rutilus*)	X			X			X	X
Eurasian water vole (*Arvicola amphibius*)		X	X	X			X	X
Yellow-necked mouse (*Sylvaemus flavicollis*)				X				X
Porcupine (*Hystrix brachyura vinogradovi*)	X	X	X	X	X	X	X	X
Dhole (*Cuon alpinus*)	X		X					
Cave bear (*Ursus spelaea*)					X	X	X	X
Small cave bear (*U. savini*)	X					X	X	X
Asian black bear (*U. thibetanus*)				X				
Asian badger (*Meles leucurus*)	X	X	X					
European badger (*M. meles*)				X		X	X	
European mink (*Mustela lutreola*)						X	X	
Lynx (*Lynx lynx*)	X						X	
Cave hyena (*Crocuta spelaea*)	X	X	X		X			X
Siberian roe deer (*Capreolus pygargus*)			X					
Ovodov's horse (*E.* (*Sussemionus*) *ovodovi*)	X		X					
Merck's rhinoceros (*Stephanorhinus kirchbergensis*)							X	X
Baikal yak (*Poëphagus mutus baicalensis*)	X							
Spiral-horned antelope (*Spirocerus kiakhtensis*)	X							

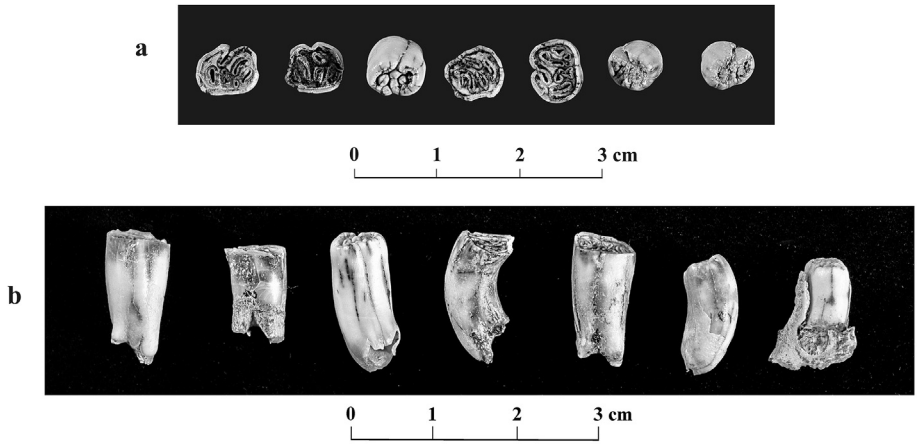

Fig. 2. Molars of *H. brachyura vinogradovi* from the Strashnaya Cave: a – view from above; b – view from the side. Teeth are from several individuals found in different strata.

fossil porcupines (Argyropulo, 1941; Baryshnikov, 2003; Baryshnikov and Baranova, 1982; Gromov, 1952; Weers, 1979, 1990, 1994). All finds from the Urals described here are in the collection of the Institute of Ecology of Plants and Animals (Yekaterinburg), and specimens from the Altai are at the Institute of Archaeology and Ethnography (Novosibirsk).

Fig. 3. Molar (M1 dex) of *H. brachyura vinogradovi* from the Razboinichya Cave (after Ovodov, 2000; modified).

Fig. 4. Premolar (p4 dex) of *H. brachyura vinogradovi* from the Viasher Cave (photo by P. Socha).

AMS ^{14}C dating was performed at the Arizona AMS Laboratory using routine procedures for bone sample preparation (e.g., Ovodov et al., 2011:3). Bone was demineralized, and collagen extracted using a continuous flow acid-base-acid treatment, followed by gelatinization, 7 μm filtration and lyophylization. The collagen was combusted and the extracted carbon dioxide reduced to graphite. The carbon isotope ratios were measured at the 3 MV NEC Pelletron Accelerator Mass Spectrometer. At the Arizona AMS Lab, bone blank is 0.01 ± 0.003 Fm (fraction of modern carbon). The limit of detection for a sample with this kind of blank is < 0.006 Fm, giving the ^{14}C value of >41,000 BP. We also measured the collagen yield and carbon yield on combustion as quality control indicators for the extracted collagen (Table 2). A ^{14}C date from a bone sample with collagen yield of less than 1% wt., should be considered as less reliable (e.g., Brock et al., 2010). Similarly, a carbon yield on combustion is another indicator of collagen purity and preservation. Values between 30 and 40% indicate good preservation.

3. Results and discussion

According to the results of palaeontological studies, the fossil remains of porcupine from caves in the Altai and the Urals (Ovodov, 2000; Baryshnikov, 2003), as well as from other localities in Europe and the Caucasus, have a smaller stature than modern porcupines. We conducted the comparison of size for maxilla, mandible, and teeth of modern representatives of genus *Hystrix* and fossil *H. brachyura vinogradovi* (Argyropulo, 1941; Baryshnikov, 2003; Baryshnikov and Baranova, 1982; Gromov, 1952; Weers, 1979, 1990, 1994, 2003, 2005). It was established that fossil porcupines from Altai and the Urals are most closely associated with *H. brachyura vinogradovi*.

AMS ^{14}C dating was applied to bone and teeth from five localities in the Urals and Siberia (Table 2). In the Altai Mountains, a sample of a porcupine's tooth from the Ust-Kan Cave with relatively good yields of collagen and carbon returned the infinite age: > 39,000 BP (Table 2). The pre-40,000 BP age of the Ust-Kan sediments is supported by the composition of small mammals which implied the existence of mainly forest landscape around the cave, typical for the interglacial or interstadial (Derevianko et al., 2002; Agadjianian and Serdyuk, 2005; Serdyuk and Zenin, 2016; see Table 1). Therefore, we assume that here porcupines are associated with the last interglacial, Marine Isotope Stage (MIS) 5e; or with the Moershoofd interstadial (ca. 43,000–50,000 BP), MIS 3, immediately after the cold MIS 4.

Other ^{14}C dates allow us to place the occurrence of porcupine in the Altai Mountains in later times (Table 2). At the Strashnaya Cave, a tooth with good collagen and carbon yields gave the finite age of 37,500 ± 2800 BP. The calendar range of this ^{14}C date is relatively wide due to large measurement error, centered at ca. 41,000 cal BP. According to ecological analysis of mammal remains, steppe-like landscapes dominated around the cave; forest formations were also present in the river valleys and gorges (Agadjianian and Serdyuk, 2005).

The ^{14}C value from the Razboinichya Cave specimen is even younger than from the Strashnaya Cave: 27,600 ± 525 BP (corresponds to ca. 30,800–32,900 cal BP) (Table 2). Good collagen parameters and presence of other animal fossils with similar age in this cave (see Ovodov et al., 2011) suggest this ^{14}C date is reasonable. Palaeoecological reconstruction based on fossil mammal assemblage suggests a moderately cool climate.

Cave deposits from the Urals containing porcupine remains were initially dated by using the species composition of associated mammalian assemblages (Table 1), and the results of geochemical and mineralogical analyses. In all Uralian localities under consideration, species typical for the Late Pleistocene *Mammuthus–Coelodonta* complex (see Kahlke, 1999) were identified, including Pleistocene horse and bison, woolly mammoth and rhinoceros, and other species (see details: Kosintsev, 2007; Kosintsev and Bachura, 2013). In the Makhnevskaya Ice Cave, bones of the hedgehog, common mole, the Asian black bear, and the badger were found. In the Barsuchii Dol Cave, bones of the hedgehog, common mole, Russian desman, forest dormouse, forest moles, European badger and mink, and Merck's rhinoceros were identified. The occurrence of these assemblages indicates that they existed in warm climatic conditions probably corresponding to an interglacial (Kolfschoten, 2000; Kahlke, 2002; Kühl and Litt, 2003). A study of the Arvicola molars from these caves shows that it belongs to the modern species, *Arvicola amphibius*, which appeared at the end of the Middle Pleistocene (Kalthoff et al., 2007; Maul and Markova, 2007), and is therefore not older than Eemian interglacial (MIS 5e).

Based upon this evidence, the deposits of Makhnevskaya Ice and Barsuchii Dol caves have been dated to the Eemian interglacial, and the remains of porcupine can be associated with this time period. In the Viasher Cave, the tooth of a porcupine was found in deposits which are also dated to MIS 5e, based on mineralogical and geochemical analyses (Kadebskaya et al., 2010). In the Pallas and

Table 2
AMS ^{14}C dates of porcupine (*Hystrix brachyura vinogradovi*) from Altai Mountains and the Urals.

Site, region	AA- No.	^{14}C date, BP	Material	Calendar age, cal BP[a]	δ^{13}C, ‰	Collagen yield, %	C yield, %
Razboinichya Cave, Altai	83718	27,600 ± 525	bone	30,780–32,870	−20.4	5.0	30.0
Strashnaya Cave, layer 5(1), Altai	90662	37,500 ± 2800	tooth	35,640–46,370	−19.4	2.7	30.0
Ust-Kan Cave, Altai	90663	>39,000	tooth	–	−19.9	2.8	32.0
Makhnevskaya Ice Cave, Urals	90664	>27,500	tooth	–	−20.0	0.4	18.0

[a] IntCal13 dataset was used (http://calib.qub.ac.uk/calib/), with ±2 sigma.

Idrisovskaya caves, porcupine bones can be dated by association with other mammals as not older than the Late Pleistocene (MIS 5e – 2). All these data indicate that porcupine remains from three Uralian localities, Makhnevskaya Ice, Barsuchii Dol, and Viasher caves, date to MIS 5e, ca. 115,000–130,000 years ago (e.g., Otvos, 2015). In Pallas and Idrisovskaya caves the deposits suggest porcupine remains are not older than MIS 5e.

The ^{14}C dating results from porcupine bones from one of the two Uralian localities weakly support this conclusion. The porcupine incisor from the Pallas Cave did not yield collagen, but an infinite (i.e., greater than) ^{14}C date of >27,500 BP was obtained for the porcupine incisor recovered from the Makhnevskaya Ice Cave (Table 2). It should be noted that collagen yield is quite low, only 0.4%, and the carbon (C) content is also relatively low (18.0%). Finally, the measured graphite was small, resulting in a large measurement error, suggesting this is not a reliable ^{14}C value. Nevertheless, we argue that its age is likely beyond the limit of ^{14}C dating, based upon the geological age of the stratum where the porcupine remains were found.

The modern Malayan porcupine (*Hystrix brachyura* L., 1758) inhabits various types of forest habitats as well as open areas near forests in East and Southeast Asia. The finds of its fossil close relative in the Urals show that sometime during the Eemian interglacial this region was covered by forests with large open spaces, and climatic conditions were moderately warm. This corresponds well to palaeogeographic reconstruction for MIS 5e based on palynological data (Grichuk, 2002). At that time, the forest zone connected mountains of southern Siberia (Altai and the Sayans) and Central Asia (Tian-Shan system) with the Urals. Following the regions on the boundary between forests and forest steppes, the porcupines were able to expand into the Urals. After that, periglacial treeless landscapes were formed in the Urals and Siberia, and porcupine in the Urals went extinct. Only in the Altai Mountains during the first part of the Late Pleistocene (MIS 5 a-d – MIS 3) forests and open spaces coexisted (e.g. Derevianko et al., 2002), and this created suitable habitat for porcupine. It seems that in the Altai porcupine went extinct in the cold conditions of the Last Glacial Maximum (MIS 2).

4. Conclusions

The existence of small Late Pleistocene refugia for porcupine (*Hystrix brachyura vinogradovi*) in the Altai Mountains of Siberia at the late MIS 3 is now securely established by palaeontological and radiometric data. This is the northernmost occurrence of this relatively temperate species known to date.

While small porcupine populations were able to persist in the Urals and Altai Mountains in warmer MIS 5e environment, its existence in the Altai under colder conditions at the MIS 3, ca. 32,000–41,000 cal BP, is noteworthy. Probably, local landscapes were still favourable for this species in late MIS 3.

This study also shows that unexpected refugia could have existed outside of the main habitats for some Pleistocene species in northern Eurasia, and scholars should be open-minded to these finds.

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References

Agadjianian, A.K., Serdyuk, N.V., 2005. The history of mammalian communities and paleogeography of the Altai Mountains in the Paleolithic. Paleontol. J. 39 (Suppl. 6), S645–S821.
Argyropulo, A.J., 1941. Rodents and insectivore of the Quaternary fauna of Binagady. Priroda 3, 88–91 (in Russian).
Baryshnikov, G.F., 2001. The Pleistocene black bear (*Ursus thibetanus*) from the Urals (Russia). Lynx 32, 33–44.
Baryshnikov, G.F., 2003. Pleistocene small porcupine from the Ural Mountains, Russia, with note on taxonomy of *Hystrix vinogradovi* (Rodentia, Hystricidae). Russ. J. Theriol. 2, 43–47.
Baryshnikov, G.F., Baranova, G.I., 1982. On the finding of the Vinogradov's porcupine in the Caucasian Paleolithic. Proc. Zool. Inst. Russ. Acad. Sci. 115, 46–53 (in Russian).
Brock, F., Higham, T., Bronk Ramsey, C., 2010. Pre-screening techniques for identification of samples suitable for radiocarbon dating of poorly preserved bones. J. Archaeol. Sci. 37, 855–865.
Derevianko, A.P., Agadjanyan, A.K., Martynovich, N.V., Ovodov, N.D., Postnov, A.V., Serdyuk, N.V., Chevalkov, L.M., 2002. Palaeoecological reconstruction of the late Pleistocene of Kanskaya Depression based on materials of multi-year studies of the Ust-Kan Cave (mountainous Altai). In: Krivoshapkin, A.I. (Ed.), Problems of the Stone Age of Central and Northern Asia. Institute of Archaeology & Ethnography Press, Novosibirsk, pp. 37–48 (in Russian).
Fadeeva, T.V., Kosintsev, P.A., Ridush, B.T., 2010. Late Pleistocene site in the Kizelovskaya (Viasherskaya) Cave: palaeontological aspects. Peshchery 33, 96–110 (in Russian).
Fadeeva, T.V., Kosintsev, P.A., Kadebskaya, O.I., Maksimova, E.G., 2011. Results of research of the zoogene deposits at the Makhnevskaya Ice Cave (Perm Region). Peshchery 34, 71–99 (in Russian).
Grichuk, V.P., 2002. Vegetation of the late Pleistocene. In: Velichko, A.A. (Ed.), Dynamics of Terrestrial Landscape Components and Inner Marine Basins of Northern Eurasia during the Last 130,000 Years. GEOS Publishers, Moscow, pp. 64–88 (in Russian).
Gromov, I.M., 1952. Fauna of the Pleistocene rodents (Rodentia) of Binagady and its nature. Proc. Nat. Hist. Mus. Named after Zardabi 5, 203–349 (in Russian).
Gromov, I.M., Erbaeva, M.A., 1995. Mammals of Fauna in Russia and Neighbouring Territories. Lagomorphs and Rodents. Zoological Institute of the Russian Academy of Sciences, St. Petersburg (in Russian).
Kadebskaya, O.I., Ridush, B.T., Tchaikovskiy, I.I., 2010. Late Pleistocene site in the Kizelovskaya (Viasherskaya) Cave: geological aspects. Peshchery 33, 87–95 (in Russian).
Kahlke, R.-D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene *Mammuthus–Coelodonta* Faunal Complex in Eurasia (Large Mammals). Fenske Publishers, Rapid City.
Kahlke, R.-D., 2002. The Quaternary large mammal faunas of Thuringia (Central Germany). In: Meyrick, R.A., Schreve, D.C. (Eds.), The Quaternary of Central Germany (Thuringia & Surroundings): Field Guide. Quaternary Research Association, London, pp. 59–78.
Kalthoff, D.C., Mors, T., Tesakov, A., 2007. Late Pleistocene small mammals from the

Wannenkopfe volcanoes (Neuwied Basin, western Germany) with remarks on the stratigraphic range of *Arvicola terrestris*. Geobios 40, 609–623.
Kolfschoten, T. van, 2000. The Eemian mammalian fauna of central Europe. Nether. J. Geosci. 79, 269–281.
Kosintsev, P., 2007. Late Pleistocene large mammal faunas from the Urals. Quat. Int. 160, 112–120.
Kosintsev, P.A., Bachura, O.P., 2013. Late Pleistocene and Holocene mammal fauna of the southern Urals. Quat. Int. 284, 161–170.
Kuzmin, Y.V., 2010. The extinction of woolly mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) in Eurasia: review of chronological and environmental issues. Boreas 39, 247–261.
Kühl, N., Litt, T., 2003. Quantitative time series reconstruction of Eemian temperature at three European sites using pollen data. Veget. Hist. Archaeobot. 12, 205–214.
MacDonald, G.M., Beilman, D.W., Kuzmin, Y.V., Orlova, L.A., Kremenetski, K.V., Shapiro, B., Wayne, R.K., Van Valkenburgh, B., 2012. Pattern of extinction of the woolly mammoth in Beringia. Nat. Comm. 3 (893), 1–8. http://dx.doi.org/10.1038/ncomms1881.
Maul, L.C., Markova, A.K., 2007. Similarity and regional differences in Quaternary arvicolid evolution in central and eastern Europe. Quat. Int. 160, 81–99.
Orlova, L.A., Kuzmin, Y.V., Dementiev, V.N., 2004. A review of the evidence for extinction chronologies for five species of Upper Pleistocene megafauna in Siberia. Radiocarbon 46, 301–314.
Otvos, E.G., 2015. The Last Interglacial stage: definitions and marine highstand, North America and Eurasia. Quat. Int. 383, 158–173.
Ovodov, N.D., 2000. The fossil porcupine (Hystrix sp.) on the Altai Mountains. In: Drozdov, N.I. (Ed.), Correlation of Natural Events and Archaeological Cultures of the Palaeolithic in Northern Asia and Adjacent Territories. Institute of Archaeology and Ethnography, Krasnoyarsk, pp. 100–102 (in Russian).
Ovodov, N.D., Crockford, S.J., Kuzmin, Y.V., Higham, T.F.G., Hodgins, G.W.L., van der Plicht, J., 2011. A 33,000-year-old incipient dog from the Altai Mountains of Siberia: evidence of the earliest domestication disrupted by the Last Glacial Maximum. PLoS One 6, e22821.
Ovodov, N.D., Kuzmin, Y.V., Cruz, R.J., 2010. AMS ^{14}C dating of “exotic” mammals from south Siberian caves. Curr. Res. Pleistocene 27, 181–183.
Serdyuk, N., Zenin, A., 2016. Small mammals from the Strashnaya Cave (Northwest Altai, West Siberia, Russia). Quat. Int. 406, 162–168.
Stuart, A.J., Kosintsev, P.A., Higham, T.F.G., Lister, A.M., 2004. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. Nature 431, 684–689.
Stuart, A.J., Lister, A.M., 2012. Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of Late Quaternary megafaunal extinctions in Northern Eurasia. Quat. Sci. Rev. 51, 1–17.
Stuart, A.J., Lister, A.M., 2014. New radiocarbon evidence on the extirpation of the spotted hyaena (*Crocuta crocuta* (Erxl.)) in northern Eurasia. Quat. Sci. Rev. 96, 108–116.
Stuart, A.J., Sulerzhitsky, L.D., Orlova, L.A., Kuzmin, Y.V., Lister, A.M., 2002. The latest woolly mammoths (*Mammuthus primigenius* Blumenbach) in Europe and Asia: a review of the current evidence. Quat. Sci. Rev. 21, 1559–1569.
Turner II, C.G., Ovodov, N.D., Pavlova, O.V., 2013. Animal Teeth and Human Tools: a Taphonomic Odyssey in Ice Age Siberia. Cambridge University Press, Cambridge.
Turvey, S.T., Tong, H., Stuart, A.J., Lister, A.M., 2013. Holocene survival of Late Pleistocene megafauna in China: a critical review of the evidence. Quat. Sci. Rev. 76, 156–166.
Tong, H., 2008. Quaternary *Hystrix* (Rodentia, Mammalia) from north China: taxonomy, stratigraphy and zoogeography, with discussions on the distribution of *Hystrix* in Palearctic Eurasia. Quat. Int. 179, 126–134.
Vasiliev, S.K., Krivoshapkin, A.I., Zenin, V.N., Shalagina, A.V., 2016. The preliminary results of megafauna remains study from Strashnaya Cave (northwestern Altai). In: Derevianko, A.P., Molodin, V.I. (Eds.), Problems of Archaeology, Ethnography, Anthropology of Siberia and Adjacent Territories, vol. XXII. Institute of Archaeology and Ethnography Press, Novosibirsk, pp. 56–62 (in Russian).
Vasiliev, S.K., Zenin, A.N., 2009. Faunal remains from the Strashnaya Cave (northwestern Altai) based on materials of the 1988–2008 excavations. In: Derevianko, A.P., Molodin, V.I. (Eds.), Problems of Archaeology, Ethnography, Anthropology of Siberia and Adjacent Territories, vol. XV. Institute of Archaeology and Ethnography Press, Novosibirsk, pp. 56–62 (in Russian).
Weers, D.J. van, 1979. Notes on Southeast Asian porcupines (Hystricidae, Rodentia). IV. On the taxonomy of the subgenus Acanthion F. Cuvier, 1823 with notes on other taxa of the family. Beaufortia 29, 215–272.
Weers, D.J. van, 1990. Dimensions and occlusal patterns in molars of *Hystrix brachyura* Linnaeus, 1758 (Mammalia, Rodentia) in a system of wear categories. Bijdr. tot Dierkd. 60, 121–134.
Weers, D.J. van, 1994. The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus *Hystrix*. Scr. Geol. 106, 35–52.
Weers, D.J. van, 2003. The porcupine *Hystrix (Acanthion) brachyura punungensis* subsp. nov. from Late Pleistocene fissure deposits near Punung. Java. Scr. Geol. 126, 217–225.
Weers, D.J. van, 2005. A taxonomic revision of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia with notes on the evolution of the family. Contrib. Zool. 74, 301–312.