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Woolly rhino discovery in the lower Kolyma River

Gennady G. Boeskorov [a,*], Peter A. Lazarev [b], Andrei V. Sher [c], Sergei P. Davydov [d], Nadezhda T. Bakulina [e], Marina V. Shchelchkova [f], Jonas Binladen [g], Eske Willerslev [g], Bernard Buigues [h], Alexey N. Tikhonov [i]

[a] Diamond and Precious Metals Geology Institute, Siberian Branch of Russian Academy of Sciences (SB RAS), 39 Prospect Lenina, 677980 Yakutsk, Russia
[b] Institute of Applied Ecology of the North, 5 Kulakovskogo St., 677891 Yakutsk, Russia
[c] Severtsov Institute of Problems of the Evolution and Ecology, RAS, 33 Leninskiy Prospect, 119071 Moscow, Russia
[d] North-East Science Station, Pacific Institute of Geography, Far East Branch of Russian Academy of Sciences (FEB RAS), 2 Malinovy Yar St., 678830 Chersky, Russia
[e] State Mine-Geological Company "Yakutskgeologia", 13 Kirova St., 677000 Yakutsk, Russia
[f] Ammosov Yakutsk State University, 58 Belinskogo St., 677007 Yakutsk, Russia
[g] Center for Ancient Genetics, Institute of Biology, University of Copenhagen, 30 Juliane Maries vej, DK-2100 Copenhagen, Denmark
[h] "Mammuthus", 2 avenue de la Pelouse, 94160 St. Mande, France
[i] Zoological Institute of Russian Academy of Sciences (RAS), 1 Universitetskaya naberezhnaya, 199034 St. Petersburg, Russia

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ABSTRACT

A nearly complete frozen mummy of a woolly rhinoceros (*Coelodonta antiquitatis* Blum., 1799) was discovered in a gold mine on the lower reaches of the Kolyma River, north–eastern Siberia. This is the first find of the whole body of woolly rhino in permafrost. A large part of the mummified body was preserved, including the left part of the body, covered by skin, including skin of the head and ear, fore and hind legs. The skull with 2 horns and the lower jaw were also preserved. Most of the internal organs were lost, except the intestines, stomach, and their contents. A rib fragment from this individual was dated by AMS-radiocarbon method to 39,140 ± 390 years BP (OxA-18755). Spore and pollen analyses of the stomach contents indicate that grasses and sagebrushes formed the main part of the diet of *C. antiquitatis* in this region of Arctic Siberia.

1. Introduction

The woolly rhinoceros (*Coelodonta antiquitatis* Blum., 1799) was one of the most widespread and prominent members of the Pleistocene megafauna of Eurasia. The remains of this species have been discovered from the British Isles in the west to the Chukchi Peninsula, Kamchatka and Primorsky Krai in the east of Russia (Garutt et al., 1970; Borsuk-Byalynicka, 1973; Vereshchagin, 1979; Lazarev and Tomskaya, 1987; Lazarev, 1998; Boeskorov, 2001; Garutt and Boeskorov, 2001).

Nevertheless, this species was not uniformly distributed across Eurasia. Notably it was absent from the Taimyr Peninsula of northern Russia, and it never penetrated North America during the Pleistocene. *C. antiquitatis* is thus an important biostratigraphic indicator from the late Middle Pleistocene (MIS 12) up to the final of Late Pleistocene (MIS 2) of Northern Eurasia. The Pleistocene distribution of this species has been fairly well studied for the European part of its range, in the Urals, and in the south–western parts of Western Siberia. There have also been numerous discoveries of woolly rhino remains in Eastern Siberia. Nevertheless, until now there have only been a few woolly rhino discoveries in north–eastern Siberia, i.e. in the Kolyma River Basin, on the Chukotka peninsula, and in adjoining regions (Kahlke, 1999; Boeskorov, 2001; Garutt and Boeskorov, 2001).

Because woolly rhino remains occur less frequently than the remains of other megafaunal mammals, they are of high scientific value. Mummified remains that include soft tissues are even more rare and valuable. Until now, only four woolly rhino mummies have been found. In Yakutia, mummified remains of a woolly rhino were found in the vicinity of Verkhnevilyuisk village (1771) and on the Khalbui River (tributary of the Bytantai River, Yana River basin, 1877), however only two legs (anterior and posterior) and a head were recovered from the first mummy, and the head and one leg, from the second one (Brandt, 1849; Chersky, 1879; Schrenck, 1880; Garutt et al., 1970). Two mummified woolly rhinos were found in 1907 and 1929 in bitumen-ozocerite deposits in the vicinity of Starunia village (Carpathian region, Western Ukraine) (Niezabitowski et al., 1914; Nowak et al., 1930; Kubiak, 1969). A whole corpse of a female without horns, found in 1929, has been deposited in the Natural History Museum of the Polish Academy of Sciences in Krakow. The second discovery (the anterior part of the body with head and horns) was placed in the Lvov Natural History Museum (Ukraine). Complete skeletons of woolly rhino with

* Corresponding author. Tel.: +7 41122 49 71 26; fax: +7 41122 33 58 01.
E-mail address: gboeskorov@mail.ru (G.G. Boeskorov).

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preserved soft tissues are also extremely rare. The best known of these was found in 1972 in the vicinity of Churapcha settlement, 200 km east of Yakutsk. This specimen was a nearly complete skeleton of a woolly rhino female. The skin and woolly pelt of the right leg were partially preserved, and the stomach contents were also found (Lazarev, 1998).

2. History of the discovery

In June 2007 a well-preserved, frozen mummy of woolly rhino (*C. antiquitatis* Blum., 1799) (Fig. 1) was discovered by gold miners as they removed the overburden of Pleistocene sediments at a gold mine of the Kolyma Co Ltd., at 8 km east of Chersky settlement, the administrative centre of the Nizhnekolymsk Region of Sakha Republic (Yakutia), Russia.

Our examination of the rhino remains showed that a large part of the mummified corpse of the animal was preserved: the left part of the body with skin cover, including skin of the head and ear, fore and hind legs (Fig. 2), the skull (Fig. 3a) and the lower jaw. A large part of the right half of the body is absent; the right legs and skull were torn off. Most of the internal organs were lost, but the intestines and stomach, and their contents were preserved. Other parts of the woolly rhino were found separately at the site, including two horns (Fig. 3b and c), the bones of the fore right leg (torn from the body) (Fig. 3d and e), the right femur (Fig. 3f), and the lower part of the hind right leg with soft tissues (Fig. 3g). A short preliminary report on this discovery has been published (Boeskorov et al., 2009).

3. Description of the study area

A large part of the Kolyma Lowland, as well as the foothills on its right bank, is draped in ice-rich loess-like loams of classified in Russia as Yedoma (Ice Complex). These are Late Pleistocene in age, and contain thick polygonal ice wedges. Yedoma sediments of the Kolyma Lowland and the megafauna buried in them are well studied, but mainly from the lower elevations (Sher, 1971; Sher et al., 1979; Lazarev and Tomskaya, 1987; Vasilchuk, 2003; Mikhalev et al., 2006). The foothills region, particularly the frozen sediments of small stream valleys, is poorly known. The development of placer gold mining in the foothills zone has led to numerous discoveries of megafaunal mammal remains (Davydov, 2007; Davydov et al., 2009), particularly numerous among them are the remains of woolly rhino, including the unique discovery of a mummified corpse. Our studies of placer deposits on the Finish, Drevnyi and Malaya Filippova rivers in

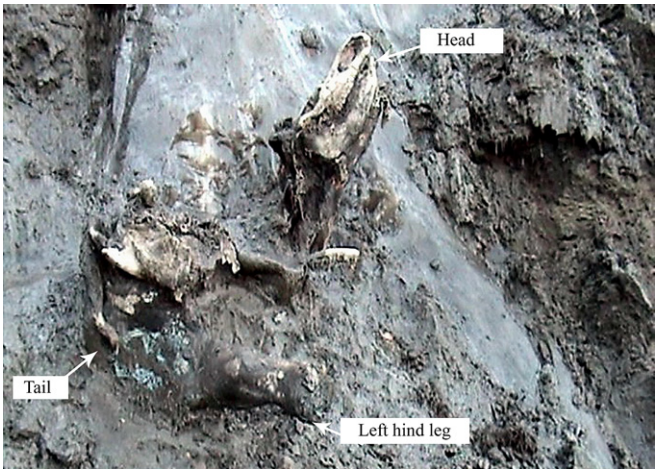

Fig. 1. Melting corpse of the Kolyma woolly rhino.

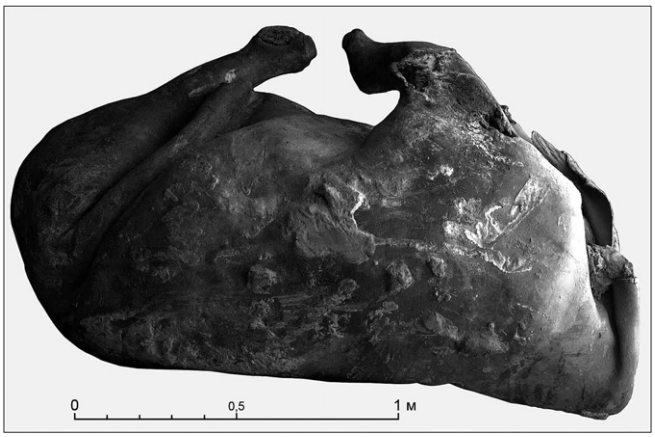

Fig. 2. Left half of the Kolyma woolly rhino mummy.

2006–2009 show that sedimentation rates were relatively uniform throughout the study area, as the sediments were deposited under similar tectonic, geomorphologic and climatic conditions, from bedrock formations of similar genesis and lithology.

The studied region is situated in the forest-tundra zone, a region with sparse tree growth in the Kolyma Lowland of the Verkhoyansk-Kolyma Landscape Region (Mikhailov, 1964; Parmuzin, 1964) (Fig. 4). The vegetation in the site vicinity and surrounding territory is mostly sparse larch woodland (*Larix cajanderi*) with continuous moss-lichen cover, with a thick undergrowth of shrubs, including birch and alder, 5–6 species of willows and diverse dwarf shrubs. The herbaceous cover is sparse. Flood plain and thermokarst depression vegetation cover consists of shrubs, tussock sedge cotton–grass swamps and scattered larches. Miscellaneous herb and grassland communities have been reported on terraces of thermokarst lakes, bank vaults and the banks of streams.

The region is characterized by low-mountain relief of the spurs of the Anyui mountains. Local topography ranges from 200 to 630 m in elevation. Regional soils fall on the boundary between the Tundra-forest Plain Province and Alazeya-Yukagirsk Plateau-tundra-taiga Province of the Forest-tundra subzone (Agricultural Atlas of Yakutian ASSR, 1989). The modern soils of the study site are typical peaty gleyzem, gleyic cryozem soils of varying degrees of peat content and gleization. The Kolyma Lowland and mountain ranges surrounding it fall within the continuous permafrost zone. Permafrost is believed to have been established here during the Pliocene (Sher et al., 1979). Mean annual temperatures of the permafrost of the study region are −3 ° to −6 °C for the Yedoma uplands, and −5 ° to −8 °C on floodplains. In the foothills the permafrost temperature patterns are more variable, depending on slope, aspect, and elevation. The regional thickness of the active layer in summer varies from 0.15 m to 1.80 m, but in most localities it does not exceed 1 m.

4. Location of the rhino corpse

We carried out a study of the locality of the Kolyma rhino mummy, beginning in October 2007 and then during field seasons of 2008 and 2009. The burial site is situated in the upper reaches of a small river (stream) Malaya Filippova, a right tributary of the lower Kolyma River in the left eastern edge of the valley, situated at an altitude of 130 m above sea level (68° 46′ 15″ N, 161° 38′ 08″ E) (Fig. 4). The stream drains the northern slopes of Rodinka Mountain (elevation 351 m above sea level). The valley has a width of 50–100 m; its edges are gently sloping and its orientation is approximately north–south (submeridianal).

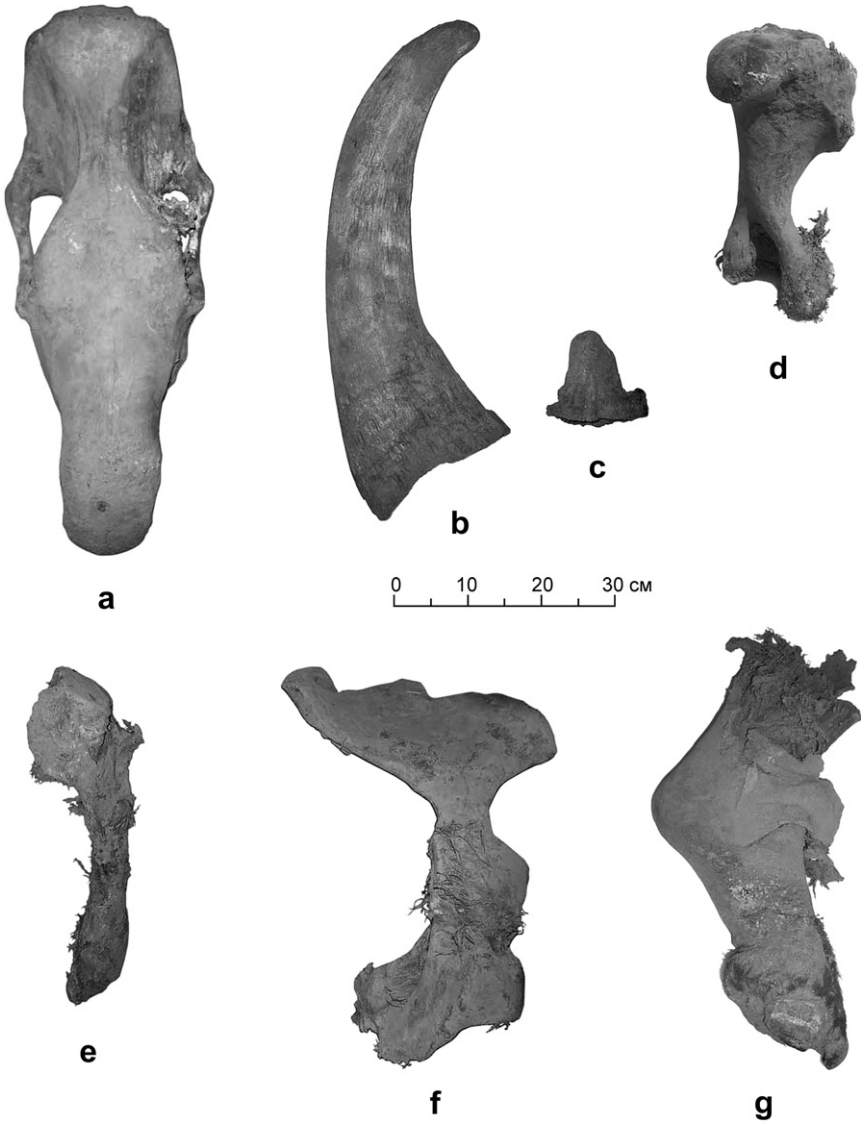

Fig. 3. Separate remains of the Kolyma rhino: a – skull, b – anterior horn, c – posterior horn, d – humerus, e – ulna, f – pelvis, g – lower part of hind right leg.

The woolly rhino mummy in the upper Malaya Filippova River, as well as other fossil remains, occurred in a layer of loess-like loams with polygonal ice wedges (Figs. 1 and 5). The thickness of Yedoma here is 15–17 m. The rhino mummy was found 5–9 m from the excavation surface.

The post mortem position of the corpse (Fig. 1) suggests that the animal died when it got trapped in a depression or, more probably, in a narrow cut of a small stream in the left edge of the Malaya Filippova River valley where it went through a zone of polygonal-wedge ice. It can be stated with a high degree of probability that at the moment of

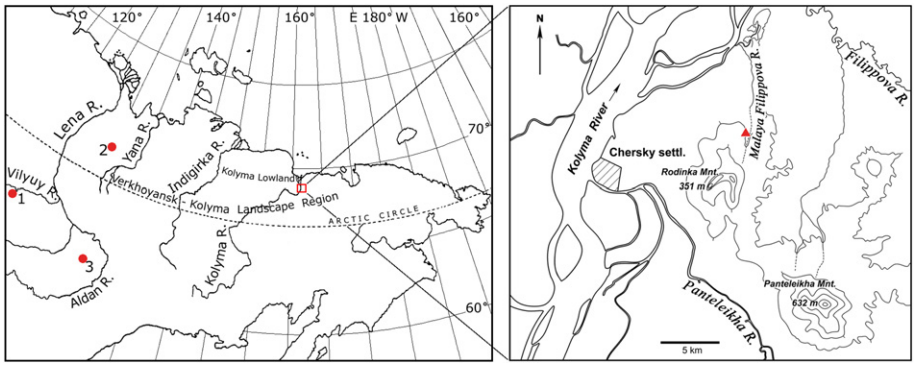

Fig. 4. Map of the study region in north–east Siberia. Location of the Kolyma rhino shown by triangle. Previous important finds of the woolly rhino remains in Eastern Siberia: 1 - mummified corpse, vicinity of Verkhnevilyuisk village (1771); 2 - mummified corpse, Khalbui River (1877); 3 – complete skeleton, vicinity of Churapcha settlement (1972).

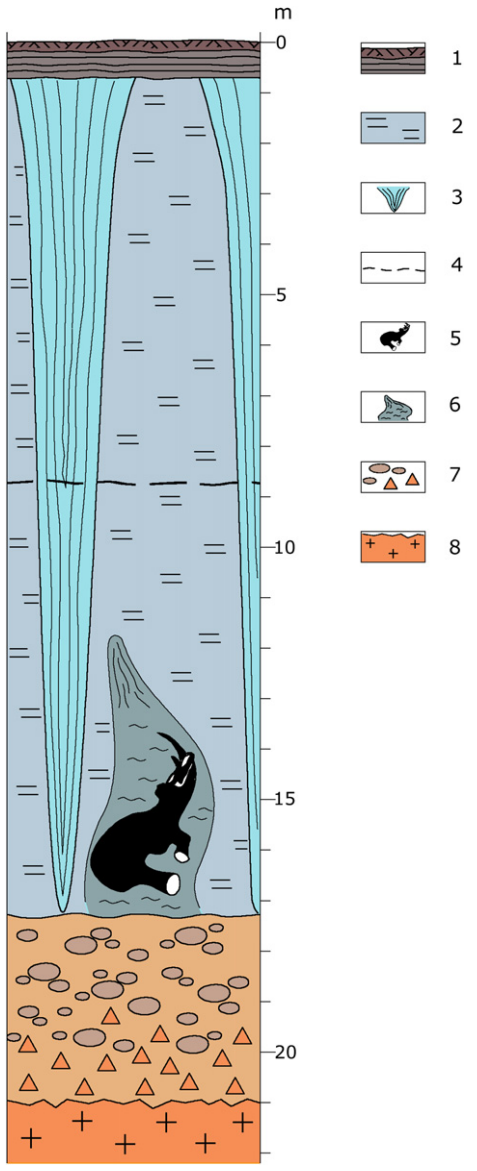

Fig. 5. A section of Quaternary deposits on the place of Kolyma woolly rhino mummy. 1 – modern soil (cryozem); 2 – Yedoma sediments; 3 – polygonal ice wedges; 4 – line of the excavation surface; 5 - mummy of the woolly rhino; 6 – congelation (buried) ice; 7 – gravel and pebble deposits; 8 – weathering crust of intrusive rocks, Paleogene–Neogene.

death the trap was filled with superfluous, moist and thixotropic sediments that later formed ground-ice, and that the transverse profile of the stream channel was less than the rhino body length (Fig. 5), which also was the major cause of its immobilization.

The depth of the trap has been reconstructed on the basis of the position of the animal's head (stretched upwards) coinciding in its level with the layers enriched by organic remains (grass roots and shrubs) on both edges of the stream channel. These layers probably represent the surface in which the stream was formed. Frozen loamy soils formed its edges and bottom. The bottom, particularly its right edge, was formed by ice. The site is situated in the lowest part of the layer of Yedoma sediments, immediately above the underlying horizon of pebble-gravel material (Fig. 5).

The stratigraphic position of the woolly rhino indirectly indicates its age: the initial phase of accumulation of the Ice Complex. The large amount of plant organic matter in the deposits enclosing the paleochannel of the stream testifies to stabilization of the surface. From this evidence we infer the animal died during the Early Karginian interval (MIS-3). After the rhino died the stream persisted until it was buried under sediments, causing it to shift course to the right (Figs. 1 and 5). This is indicated by the pillar like lump, approximately 1–1.5 m tall, formed on the right above the rhino mummy, and enclosed into cryoturbated, loamy soils enriched with organic material (interbedded peaty lenses), composed of plant remains (roots and branches of shrubs). It should be noted that ground-ice, included the specimen is not a polygonal-wedge ice but congelation (buried) ice. This is suggested by the large number of relatively large inclusions and the state of preservation of the mummy, which was undisturbed by frost processes.

Near the rhino mummy site in the Malaya Filippova River valley we also found skeletal remains of other Pleistocene megafaunal mammals, including woolly mammoth (*Mammuthus primigenius*), Lena horse (*Equus lenensis*), reindeer (*Rangifer tarandus*), Pleistocene bison (*Bison priscus*) and cave lion (*Panthera spelaea*). The mummified remains of at least two other specimens of woolly rhinoceros were also found in the mine.

5. Palynological research of the Kolyma rhinoceros

We analyzed the fossil pollen and spores from a sample of sediment that had stuck to the rhino mummy. The sample is characterized by high content of pollen grains (574 per preparation within "eyeshot" (24 mm × 24 mm), method by G. Levkovskaya (1965)) in various states of preservation. Grass and prostrate shrub pollen dominates the assemblage (61.0%), especially grass pollen (23.9%). Sagebrush pollen was also important (15.3%), followed by Caryophyllaceae (7.3%), Cyperaceae (4.9%), and Asteraceae (1.4%). The taxonomic diversity inferred from the pollen of various herbs suggests the existence of various plant communities, including steppe and meadow-steppe (Asteraceae, Saxifragaceae, Chenopodiaceae, Fabaceae, Plantaginaceae, etc.), and meadows (Ranunculaceae, Polygonaceae, Valerianaceae, Umbelliferae, *Thalictrum* sp., *Sanguisorba officinalis*).

Woody-shrubs (23.7%) are represented mostly by the pollen of small leaved angiosperms (18.0%), predominant among which is pollen of *Betula middendorffii* (9.7%), alder (3.8%), willow (few) and high birches (3.4%). Conifer pollen included single grains of larch, and both haploid and diploid pines. On the whole, the pollen spectrum obtained from soils enclosing the rhino mummy indicates plant communities living in the dry, sharply continental climate associated with the cold phases of the Karginian interglacial (Boeskorov et al., 2009). Similar pollen spectra have been identified from samples taken from exposures of the Ice Complex on the Coastal Lowlands of Yakutia (Giterman, 1963; Sher et al., 1979; Vasilchuk, 2003), for example in the upper part of the stratotype of the Ice Complex (Yedoma Suite), in the section of Duvanny Yar situated on the right bank of the Kolyma River (130–140 km upstream of Chersky settlement).

6. Analysis of stomach contents

The stomach content sample is characterized by a very high concentration of pollen and spores (more than 1700 grains in one preparation). The state of preservation of the majority of pollen grains is very good. The pollen spectra are dominated by herbaceous plants (98.88%) (Table 1). The pollen of trees and shrubs comprises 0.62%, and of spores, 0.51%. Herbaceous pollen is dominated by Poaceae (46.07%) and Compositae (41.46%) of which sagebrush pollen is dominant (41.01%). Sagebrush pollen likewise showed great diversity, apparently comprising *Artemisia* cf. *arctica*, *Artemisia* cf. *scoparia*, *Artemisia* cf. *tilesii*, *Artemisia* cf. *macrantha*, *Artemisia borealis*, and others. There is a rich variety of

miscellaneous herb pollen in the assemblage, dominated by the pollen of steppe and meadow-steppe plants, with a relatively high content of pollen of Caryophyllaceae (3.31%), including *Selene repens*, *Stellaria* sp., *Lychnis sibirica*, and other taxa. Plantaginaceae pollen (to 2.25%) included *Plantago* cf. *lanceolata*, *P.* cf. *media*, and *Plantago* sp. Rose family pollen (to 3.09%) included *Sanguisorba officinalis*, *Potentilla*. cf. *nivea*, *Potentilla* sp., and unidentified taxa of Rosaceae. Small amounts of pollen from the poppy family (Papaveraceae) were found, including *Papaver aceae*. Pollen from the Ranunculaceae family included *Ranunculus* cf. *borealis*, *Ranunculus* cf. *repens*, *Thalictrum* sp., and others. Pollen from the Polygonaceae family included *Rumex* cf. *sibirica*. Legume pollen (Leguminosae) included cf. *Lathyrus humilis*, cf. *Astragalus* sp., *Vicia cracca*, and *Oxytropis adamsiana*. Pollen from the Polemoniaceae family included *Polemonium* cf. *boreale*, *P.* cf. *acutiflorum*, and *Phlox sibirica*.

Table 1
Specific definition, number and quantity of spores and pollen in the sample from the stomach content of Kolyma woolly rhino.

##	Specific definition of the spores and pollen	Number of grains	Percentage
Trees and shrubs			
1	*Picea* sp.	1	0.06
2	*Picea* sect. Omorica	1	0.06
3	*Pinus* s\g Haploxylon (mineralized)	1	0.06
4	*Pinus* s\g Haploxylon	3	0.17
5	*P. pumila* (Pall.) Rgl.	3	0.17
6	*Pinus* s\g Diploxylon	1	0.06
7	*Salix* spp.	1	0.06
	Trees and shrubs, total	*11*	*0.62*
Miscellaneous herbs			
8	Papaveraceae gen. sp.	1	0.06
9	Ranunculaceae gen. sp. (*Ranunculus* sp., *R.* cf. *repens* L., *R.* cf. *borealis* Trautv., *Thalictrum* sp.	11	0.62
10	Chenopodiaceae gen. sp.	2	0.11
11	Caryophyllaceae gen. sp.(*Stellaria* sp., Selena cf. repens Patr, *Cerastium* sp., *Lychnis* cf. *sibirica* L.	59	3.31
12	Polygonaceae gen. sp. (*Rumex* cf. *sibiricus* Hult.)	4	0.22
13	Cruciferae gen. sp.	1	0.06
14	Rosaceae gen. sp. (*Sanguisorba officinalis* L., *Potentilla* sp., *P. nivea* L., *Rubus chamaemorus* L.	55	3.09
15	Leguminosae gen. sp. (*Lathyrus* cf. *humilis* Fisch ex DC, *Astragalus* sp., *Vicia* cf. *cracca* L., *Oxytropis adamsiana* (Torutv) Vass.	11	0.62
16	Polemoniaceae gen. sp. (*Polemonium boreale* Adams, *P. acutiforum* Willd., *Phlox sibirica* L.)	6	0.34
17	Umbelliferae gen. sp.	5	0.28
18	*Plantago* cf. *lanceolata* L., *P.* cf. *media* L.	40	2.25
19	Cichoriaceae gen. sp.	5	0.28
20	Asteraceae gen. sp.	3	0.17
21	Valerianaceae gen. sp. (*Valeriana officinalis* L., *V. capitata* Pall.)	4	0.22
22	*Artemisia* sp., *A.* cf. *macrantha* Ledeb., *A.* cf. *arctica* Less., *A.* cf. *scoparia* Waldst., *A.* cf. *tilesii* Ledeb.	730	41.01
23	Cyperaceae gen. sp.	3	0.17
	Total herbs	*940*	*52.8*
Grasses			
24	Poaceae gen. sp.	820	46.07
	Total herbs and grasses	1760	98.88
Spores			
25	Hepaticae	1	0.06
26	*Riccia* sp. (mineralized)	2	0.11
27	*Lycopodium pungens* La Pyl.	1	0.06
28	*Selaginella sibirica* (Milde) Hieron.	4	0.22
29	*Equisetum* sp.	1	0.06
	Total spores	*9*	*0.51*
	Total grains	*1780*	*100*

Pollen from the valerian family (Valerianaceae) included *Valeriana capitata* and *Valeriana officinalis.* We also identified pollen from the following families: Cruciferae, Chenopodiaceae, Lactuceae (Cichorieae), Asteraceae, and Cyperaceae.

Conifer pollen numbers were extremely low in the assemblage. We found only single grains of spruce (*Picea* sect. *Omorica*, *Picea* sp.), and single grains of Pinus s/g Haploxylon and s/g Diploxylon, Japanese stone pine and willow. The conifer pollen was in a very poor state of preservation, from which we infer that it predates the woolly rhinoceros, and was accidentally ingested.

Few spores were preserved in the sample. These include single spores of Hepaticae, Equisetaceae, *Selaginella sibirica* (*Selaginella rupestris*), and an arctic species of clubmoss (*Lycopodium pungens*). Apart from pollen and spores, the remains of colonies of green algae of the genus *Pediastrum* were identified, as well as various small fungi.

The pollen spectrum reflects a taxonomic diversity of herbaceous plants associated with different plant communities. It is evident that the vegetation cover of the study area was highly mosaic in nature. Based on the pollen data, the diet of the woolly rhino was dominated by various species of grasses and a rich mixture of other herbs. The large amount of sagebrush pollen suggests that this also formed part of the animal's diet. For example, modern reindeer *R. tarandus* and Yakutian domestic horse *Equus caballus* in the territory of Yakutia eat *A. tilesii* Ledeb. and *Artemisia kruhsiana* Bess. (Tomskaya, 2000).

The vegetation cover inferred from the gut-content pollen spectrum correlates well with the pollen spectrum from the dark-gray loamy soils with ice strata enclosing the remains of the woolly rhino, and with the spectrum from the sediment sample taken from the rhino corpse. All the pollen spectra are characterized by abundant pollen of herbaceous plants with predominant grasses and sagebrushes and rich composition of miscellaneous herbs.

The dominance of herbaceous plants over woody-shrubby vegetation had been noted previously in the analysis of food remains from the teeth of the woolly rhino from the Khalbui River (grasses consisted 68.2%, sagebrushes 17.1%) (Garutt et al., 1970) and from the plant remains recovered from the alimentary canal of the Churapcha rhino (grasses consisted 89%, sagebrushes 2.5%) (Lazarev and Tirskaya, 1975).

7. Age of the Kolyma rhino

A fragment of a rib of this individual was dated in the Oxford radiocarbon laboratory by the AMS-radiocarbon method (Sher et al., 2009). This yielded an age of 39,140 ± 390 yr BP (OxA-18755). Hence, this rhinoceros existed at the beginning of the Karginian Interstadial (correlated with the Middle Valdai Interstadial of the East European Plain and the Middle Weichselian (Würm-II) of Western Europe or Middle Wisconsin in Northern America – MIS-3).

From another stream (Finish Stream) located in a few kilometers from the Malaya Filippova stream close radiocarbon date of Coelodonta antiquitatis bone is obtained - 39,165 ± 415 yr BP (SOAN-7582). Other radiocarbon data indicates that woolly rhinos were inhabited Kolyma Lowland territory during Karginian Interstadial up to the Sartanian glaciation 43,700 ± 1000, 37,700 ± 1100, 33,100 ± 400, 27,300 ± 300, 26,900 ± 400, 15,130 ± 90, 15,130 ± 50 yr BP (Sulerzhitsky and Romanenko, 1997).

8. Anatomical-morphological description of the Kolyma rhino

8.1. Condition of the body

The rhino body was deformed after death, the fore and hind legs were pressed to the trunk. Between the hind leg and the abdomen

there is a large fold of skin that is also characteristic of modern rhinos. Before it was removed from the sediments, the rhino carcass had a slightly different position: and the skull was connected to the trunk. The position of the legs was also different. Unfortunately the skull became detached from the body when the mummy was removed. The trunk is practically intact on the left side (Fig. 2). A large part of the skin is missing from the right side and the right legs are torn off, so that the skin covers only a part of the spine and the abdominal cavity.

8.2. Skull

The skull and lower jaws were preserved virtually intact. The remains of tendons are present in some places. In the bottom of the mouth cavity, the mummified remains of a greyish–brown tongue were preserved. The tongue is round in cross-section, and consists of a root, body and part of tip of the tongue (the anterior edge was missing). The tongue papillae were not preserved. The length of the tongue from the root to the anterior edge of the preserved part of the tongue tip is 310 mm. The width across the tongue in the middle is 68 mm; its height in the same area is 82 mm. Even though four mummified heads of wooly rhino have previously been found, this is the only example in which the tongue has been preserved. The right os hyoideum is 208 mm in length and is well preserved. The width of the processus muscularis is 74 mm; the width of the stylohyoid is 25 mm. In shape the tongue is most similar to a horse tongue.

The teeth bear notable traces of wear, M3 are in a process of abrasion. Cranial sutures of the Group II according to M. Borsuk-Byalynicka's classification of the woolly rhino individual age (Borsuk-Byalynicka, 1973) (frontonasal, nasomaxillary, sagittal sutures) on the skull are fused, and the nasal septum ossified. Nasal bones are extended and their lateral margins are of convex shape. These characteristics suggest that the Kolyma rhino was an adult individual. According to M. Borsuk-Byalynicka's classification it could be placed in the age group "old adult".

The dimensions of the skull are noticeably large and the skull is characterized by considerable length (Table 2). The majority of measurements of the dimensions of various parts of the skull exceed those of the Churapcha woolly rhino, thought to represent an elderly female (Table 2). On the other hand, the width of the skull of the Kolyma specimen is generally smaller than that of the Churapcha specimen. This suggests that the Kolyma rhino was a much younger individual whose skull had not yet reached its maximum size. On the other hand, such a difference in proportions of the skull could represent the existence of two ecomorphs of the woolly rhinoceros (Garutt and Boeskorov, 2001). The lower jaw of the Kolyma specimen exceeds the Churapcha specimen in length, but ranks below the latter in height and thickness (Table 3).

8.3. Horns

The anterior (nasal) horn (Fig. 3b) is scimitar-shaped and flattened on its sides. The anterior part of the horn is considerably worn. Horn length along the external curvature is 845 mm, on the internal curvature it is 627 mm long. The anterior–posterior length of the base is 229 mm; the transverse width in the middle part is 123 mm; the thickness of the horn at the middle is 26 mm. The length of the worn area on the external rib of the horn is 510 mm. Such medium sizes of anterior horns are characteristic of young rhinos at the age of approximately 14–20 years. We noted 17–19 transverse-annual bands on the horn of the Kolyma rhino. As it was proven that these bands correspond with individual age of woolly rhino (Fortelius, 1983; Garutt, 1998), we therefore estimate the age of the animal at approximately 20 years More mature specimens of

Table 2
The measurements of the skulls of Kolyma and Churapcha woolly rhinoceroses from Yakutia.

Measurements, mm	Kolyma rhino	Churapcha rhino (Lazarev, 1998)
Total length	653	617
Parietal length	763	706
Premolar basal length	536	499
Length from position until the rear edge of the palatum	292	–
Length from rear edge of the palate to basion	365	–
Premolar length (position – front edge of P2)	130	126
Length of dentition	217	201
Width in ossis incisivi	115	158
Maximum width of nasal bones	133	162
Minimum width of nasal bones	102	107
Width across orbits	237	236
Zygomatic width	332	344
Temporal width	123	117
Temporal sutures width	69.5	68
Width in the region of auditory meatus	233	252
Maximum width of jaw near the external edges of alveolus	224	197
Width of palate in the region of nasal septum	69	60
Minimum width of choanae	49	64
Maximum width in pterygoid processes of sphenoid bone	89	103
Width between the external edges of occipital condyles	162	158
Height of the diastem	178	175
Temporal height	149	151
Maximum occipital height	217	241
Minimum occipital height	192	168
Angle of temporal bone	32°	36°

Table 3
The measurements of the mandibles of Kolyma and Churapcha woolly rhinoceroses.

Measurements, mm	Kolyma rhino	Churapcha rhino (Lazarev, 1998)
Length from the anterior point of symphysis to the rear edge of the ascending ramus	More than 525	507
Length from the anterior point of symphysis to the rear edge of the articular processes	More than 550	552
Premolar length (from the front edge of alveolus to the rear edge of the ascending ramus)	429.2	393
Length from the rear edge of the articular processes	–	266
Length of symphysis by sagittal line	–	122
Length of diastema (premolar)	94.8	109
Length of dentition	216	196
Minimum width of the jaw	–	93
Minimum width between M1 (near alveolus)	–	152
Minimum width between outside edges of articular processes	–	332
Minimum width of articular processes	100	101
Minimum width of the ascending ramus in the angle region	–	155
Height of the ascending ramus to the top of coronoid process (perpendicular to the base of jaw)	270	–
Height of the ascending ramus to the top of articular processes	–	229
Height in front of P2 (near alveolus)	–	85
Height behind M3 (near alveolus)	103	108
Thickness of bone under M1	62	67

C. antiquitatis, from 25 to 35 years (based on the number of transverse bands) are usually characterized by larger horns, with the length along the external curvature ranging from 1000 to 1350 mm (Boeskorov and Issakova, 1999; Tchernova et al., 1998; Garutt, 1998; Lazarev, 1998).

The length of the second (frontal) horn is 150 mm; the length of its base is 146 mm; the width of the base at the middle is approximately 80 mm; the width of the horn in the middle part is 78 mm, with a thickness in that area of 48 mm. The terminal part of the second horn is missing (Fig. 3c). We estimate that the intact horn would have been 170 mm in length. We found not fewer than 10–11 transverse bands on this horn. Only a few frontal horns of the woolly rhino have previously been found. The largest of the described horns were 395–405 mm (Lazarev, 1998; Garutt, 1998). The largest second horn measured by one of us (BG) from the Omyakon Plateau had a length of 475 mm. The dimensions of the frontal horn of the Kolyma rhino are characteristic for adult specimens, but not animals of great age (see Fortelius, 1983; Garutt, 1998; Lazarev, 1998; Tchernova et al., 1998).

8.4. Skin and fur

The skin on the left side of the body and on the left feet is well preserved, practically without damage (Fig. 2). In the region of the left foreleg there are two large cuts. These appear to be the result of excavations carried out by the workers of the mine. The skin is mummified and hardened, and so stiff that it can scarcely be moved. For the most part, the skin has retained its natural dark brown color; in some areas it is covered by blue vivianite crystals.

The thickness of skin of the Kolyma rhino mummy varies in different parts of the body, from 5 to 15 mm. The thinnest skin is noted on the lateral side of the head (on average 5.5 mm), and thickest skin was found in the glutaeal region (average of 11.2 mm), in the thoracic area (average of 10.5 mm), and in the dorsal area (average of 10.4 mm). In the rhino female found in 1929 from Starunia, Ukraine, the maximum thickness of skin (28 mm) was noted on the lower lip (Nowak et al., 1930). For comparison, in the adult woolly mammoth, skin thickness varied in different parts of the body from 9 to 30 mm (Garutt, 1964; our data). In modern cattle skin thickness varies from 3 to 13 mm, with the maximum thickness found on the forehead and crupper, and minimum thickness on the neck (Yudichev et al., 2003).

Hair was only preserved on the lower parts of the legs, above the hooves. It was formed in the shape of clumps, and had a reddish–brown color, that could be a diagenetic alteration of the color. Mummified remains of Pleistocene animals buried in permafrost are generally devoid of fur. During the first few years after death, the skin of the animal is exposed to the action of seasonal cryogenic processes (freeze-thaw cycles), as long as it remains in the active layer. As sediments accumulate on top of these carcasses, they gradually move down into the permanently frozen region of the permafrost, where the physical abrasion of freeze-thaw activity ceases.

A ear, the orbit and part of the anterior edge of the muzzle were preserved on the large preserved piece of skin on the left side of the head. The ear has lost its natural shape, and become elongated and flattened on the sides. In modern rhinos the upper part of the ear is extended. The length of the ear from its base is 215 mm, and from the lower edge, 185 mm. The anterior–posterior length of the left orbit is 36 mm. In the Starunia rhino specimen found in 1907, the length of the orbit is 40 mm (Niezabitowski et al., 1914). Inside the facial skin, a mummified eyeball with muscles and fascia were found. The posterior–anterior diameter of the eyeball is 51 mm; the transverse diameter is 31 mm. The distance from the posterior edge of the orbit to the anterior edge of the ear is 315 mm.

8.5. Abdominal cavity

In the abdominal cavity we found the remains of the muscular wall of the stomach, as well as the stomach contents, which formed a hardened mass of semidigested plant remains. The total length of the stomach remains is approximately 70 cm. They were situated in the thorax between the 7th or 8th to 16th ribs. There were also some small remains of mummified intestines.

8.6. Legs

The fully preserved left legs and the lower part of the right hind leg have the columnar shape characteristic of rhinos. Only the bones of the right foreleg have been preserved, including the humerus and ulna, metacarpus and carpus, and two hoof phalanges. There are three hoof phalanges on each of the other legs that have been fully preserved. Above the hooves, areas of short coarse light brown wool have been preserved. The legs are large, typical of the size of legs found on other adult woolly rhino skeletons (Table 4). The hooves are well-preserved. On the right rear foot the hooves have the following sizes: the width of the middle hoof is 96 mm, the height at the middle is 54.5 mm. On the right hoof the sizes are 74 mm and 57.5 mm respectively: on the left, 71 mm and 53 mm.

The tail has been completely preserved, but without the fur. The length of the tail is 47 cm. The base of the tail is thickened, gradually tapering towards the tip. The circumference of the base of the tail is 30 cm; the circumference in the middle is 23 cm, and the dorsal width at the base of the tail is 13 cm. In the Starunia rhino found in 1929, the tail is two cm longer, the circumference at the base of the tail is 29 cm, and the circumference of the middle part of the tail is approximately 20 cm, while the dorsal width at the base of the tail is 15.5 cm (Nowak et al., 1930).

The anus and *labia pudendi* of the Kolyma mummy have also been preserved. In the inguinal area of the mummy, there are two nipples, which is characteristic of odd-toed ungulates in general and rhinos in particular. The nipples are not large. The length of the right nipple is 20 mm, the greatest width is 17 mm. The length and width of the left nipple are 8 mm and 16 mm, respectively. The inner edges of the base of the nipples are 31 mm apart. Nipples were previously found preserved on the female woolly rhino specimen from Starunia (Nowak et al., 1930).

8.7. General dimensions of the Kolyma woolly rhino

The Kolyma woolly rhino is a large animal (Table 4). The total weight of the mummified corpse, including the skull, horns, remains of two right legs and other bones found separately, is approximately 1000 kg. Considering the fact that most of the viscera, and parts of the musculature and skin have been lost, and that the soft tissues have been desiccated through cryogenic sublimation, we estimate that the live weight of this animal was at least 1.5 tons. In our opinion, the body mass of adult males apparently reached 2000 kg at maturity. With a relatively low stature, the Kolyma rhino had a long, massive body on short legs, a suitable adaptation for foraging on landscapes with little snow cover in winter.

9. Other woolly rhino specimens found in the “Kolyma” mine

In the mine near the location of the Kolyma rhino mummy, the mummified remains of two other female woolly rhinos have been found. The first is a juvenile specimen, consisting of a piece of skin from the hind part of the trunk with tail and perinaeum area, the lower parts of two hind legs (Fig. 6), fragments of five thoracic vertebrae, and tufts of dark red fur. The second consists of two fragments of skin of an adult specimen (Fig. 7).

Table 4
Body measurements of the woolly rhinoceroses.

Measurements, cm	Yakutia					Western Ukraine	
	Lower reaches of Kolyma, Malaya Filippova River				Lena-Aldan interfluve, village of Churapcha	Corpses of rhinos from Starunia (Niezabitowski et al., 1914; Nowak et al., 1930)	
	Corpse of adult female		Corpse fragments of young female		Skeleton of adult female*	Young female (1907)	Adult female (1929)
Length of head and body	about 350		–		323	355	358
Height at withers	145		–		155–165	153	158**
Girth	280		–		260	–	–
Length of ear	18		–		–	22	28
Length of tail	47		47,5		–	–	49
Circumference of tail in the midpoint	23		18		–	–	about 20
Length of manus from top of carpus to anterior edge of middle hoof, perpendicular	34		–		–	–	35
Anteroposterior diameter of anterior foot	18.5		–		–	–	20
Transverse diameter of anterior foot	18		–		–	–	19.5
Metacarpus circumference in the middle	42		–		–	–	37
Length of hind foot from top of tarsals to anterior edge of middle hoof, perpendicular	right 39	left 41	right 36	left 35	39	–	36**
Anteroposterior diameter of hind sole	16.5	17,4	13	13	15.2	–	16
Transverse diameter of hind foot	15.7	15,9	13.5	13	about 16	–	14
Metatarsus circumference in the middle	39.5	37	35.5	35	39	–	32

*Lower part of right hind leg with soft tissues was preserved in the Churapcha rhino.
**Measurements were made by Prof. Henric Kubiak.

9.1. Remains of the young female

The fragments of hind limbs are the lower extremities of the left and right legs, torn off slightly above the tarsal joints; they are not large (Table 4). Tufts of red and light brown hair have preserved on these leg fragments. On the right leg, the middle hoof is 84 mm wide and 41 mm high; the right hoof is 71 mm wide and 46 mm high; the left hoof is 62 mm wide and 39 mm high (the latter is partly destroyed). The thickness of skin in the area adjoining the tail is thin, 7–9 mm. The anal opening and a part of the vaginal area have preserved. All characteristics indicate that this individual was an immature female.

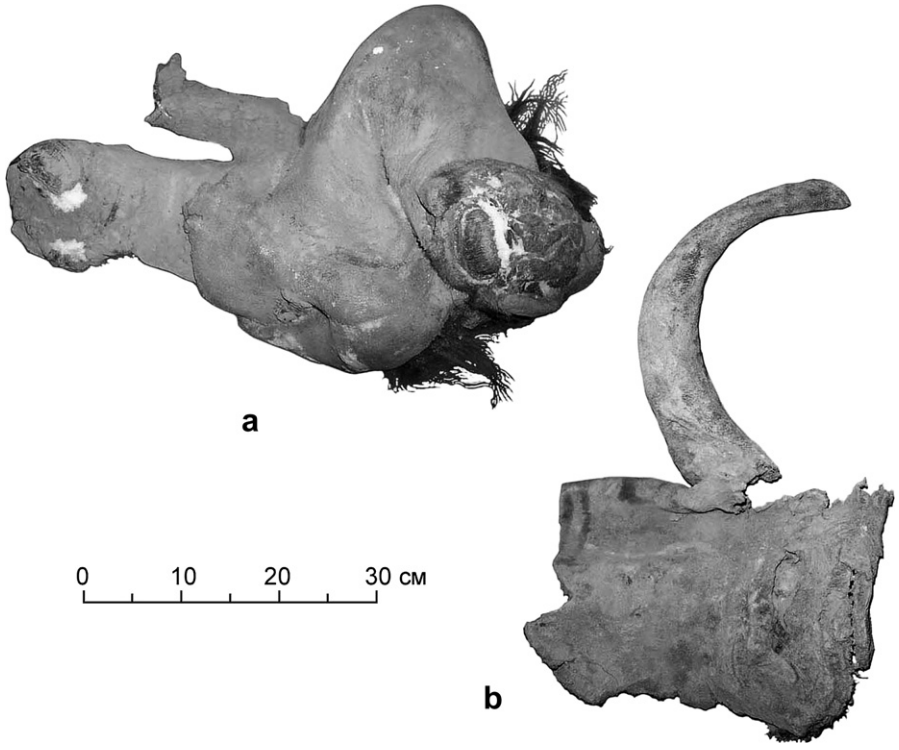

Fig. 6. Remains of the young specimen of woolly rhino: a – lower parts of hind legs; b – piece of skin with tail.

9.2. Ancient DNA analysis

The tail is long but thin (Table 4). No hair has been preserved on the tail, or on the adjoining piece of skin. This tail is somewhat different in size and shape from the tail of the Kolyma mummy (Table 4), its identity was therefore doubtful, because it could have belonged to a different species of large mammal. However, analysis of 18 mitochondrial DNA carried out at the Center for Ancient Genetics, Institute of Biology, University of Copenhagen (Copenhagen, Denmark) showed that the tail did belong to a woolly rhinoceros. Furthermore, 97 base pairs of sequences of mitochondrial D-loop isolated from the tail are identical to the sequences obtained from the legs of the young specimen. Thus these two specimens can be considered with a high degree of probability to belong to the same individual. Molecular genetic studies of mitochondrial DNA isolated from legs and tail have revealed no daughter relationship with the Kolyma rhino.

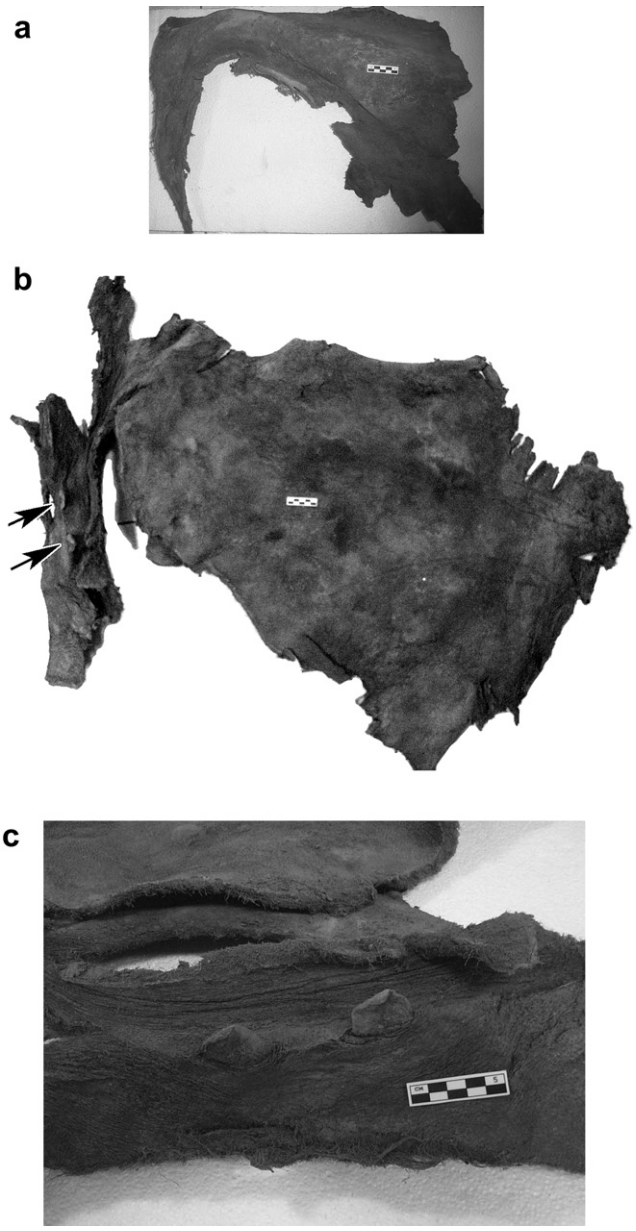

Fig. 7. Fragments of skin of the second adult specimen of woolly rhino from the Malaya Filippova River: a – from the area of the back and from the lateral side; b – from the lower part of the body; c – expanded area of skin with udder.

9.3. Remains of the adult specimen

Two pieces of skin have been preserved, one with an udder. The color of the specimens is brown. The first piece of skin is of irregular shape (Fig. 7a). Its maximum length is 70 cm, and width 51 cm. To judge by the configuration of folds, it is a fragment of skin from the area of the back and lateral side of the animal. The skin thickness varies from 5 to 12 mm. Inside the skin folds we found short, light brown hairs. The second piece of skin is larger (Fig. 7b): its maximum length is 101 cm; its width is 82 cm. The shape is irregular and there are numerous ruptures and cuts. We consider this to be a fragment of skin from the lower part of the body from the area of the lower part of thorax, belly and groin. In the groin part of the skin, there are nipples (Fig. 7c). The dimensions of the nipples are similar to those of the aforementioned Kolyma rhino mummy. The length of each nipple is approximately 20 mm, but they are wider than those of the Kolyma mummy. The maximum width of the right nipple is 35 mm; the maximum width of the left nipple is 33 mm. The inside edges of the nipples are 44 mm apart from each other. We consider that these remains with the large nipples could be from a lactating female. The skin thickness of this specimen varies from 6 to 12 mm.

10. Discussion

The discoveries of the Kolyma rhino mummy and remains of carcasses of other woolly rhinos on the Malaya Filippova River, in combination with previous studies, have allowed us to refine a number of morphological and ecological characteristics of the woolly rhinoceros, and to reveal new ones. We have established that woolly rhinoceros females had two nipples, hence they probably produced one, seldom two calves, as do females of modern rhinos (Walker et al., 1968). We have expanded our knowledge of the body size of *C. antiquitatis*. It was a very large animal, second in size only to the woolly mammoth among the Pleistocene megafauna of Northern Eurasia. In general body dimensions (body length 320–360 cm, height at withers, 145–160 cm, body mass, 1500–2000 kg), the woolly rhinoceros compares to the larger species of modern rhinos. The largest of the modern rhinos are the white rhinoceros, *Ceratotherium simum* (body length up to 284 cm, height at withers to 188 cm, body mass up to 2400 kg), and the greater one-horned rhinoceros, *Rhinoceros unicornis* (body length up to 380 cm, height at withers up to 186 cm, body mass up to 2132 kg). The black rhinoceros, *Diceros bicornis*, has a long body (to 300–375 cm), but it is lower (up to 158 cm at the withers) and lighter (up to 1316 kg). The Javan rhinoceros, *Rhinoceros sondaicus*, has a long body (up to 320 cm in length), is relatively tall (up to 166 cm), and is relatively massive (to 1500 kg). The smallest among the modern rhinos is the Sumatran rhinoceros, *Dicerorhinus sumatrensis*. This species has a body length up to 317 cm, a height at the withers up to 145 cm, and a body mass up to 950 kg (Zukowsky, 1965; Walker et al., 1968; Groves and Kurt, 1972; Groves, 1982; Laurie et al., 1984). In its size and body proportions, the woolly rhinoceros is evidently very similar to the Javan rhinoceros. The woolly rhinoceros had short ears. Based on available data, their length was 18.5–24 cm (Table 3). In a mummy of a young individual of this species found on the Khalbui River in 1877, the ear length was 14.1 cm. Modern rhinos usually have larger ears, for instance the white rhino, females have ear lengths 25–30 cm (Heller, 1913; our unpublished data). The tail of the woolly rhino was also relatively short (Table 4), about 50 cm. In recent rhinos, including the white, black and greater one-horned rhinos, tails are 70–75 cm

long (Walker et al., 1968). The shortening of the protruding parts of the body (ears and tail) in the woolly rhino, as compared to modern tropical and subtropical rhinos, evidently reflects Allen's rule. Shortened appendages are commonly found in arctic mammals, past and present. An analogous shortening of tail length and decrease of ear sizes has been noted in woolly mammoth *M. primigenius*, as compared to recent elephants (Garutt, 1964; Vereshchagin and Tikhonov 1990; Boeskorov et al., 2007).

11. Conclusion

The woolly rhinoceros was well adapted to the cold and dry climates of the Late Pleistocene, having long, thick hair and very thick skin. At the same time it had a large body mass with relatively short legs, making it difficult for this species to traverse deep and ice-encrusted snow. Moreover, natural traps formed by thermokarst processes such as the margins of melted ice wedge polygons, deep thermoerosion scours, and boggy margins of thermokarst lakes and streams, would have posed a serious danger for such short-legged, massive animals (Boeskorov et al., 2009). Its long, flattened anterior horns would have served as a good weapon for self-defense. During the rutting season these were likely used by males as a sparring weapon. During winter they were certainly used to sweep away snow to gain access to dried grasses and other herbs.

Palynological analysis of the stomach contents of the Kolyma rhino supported the findings of previous researchers (Garutt et al., 1970; Lazarev and Tirskaya, 1975) indicating that grasses and sagebrushes played dominant role in the diet of *C. antiquitatis* in the Arctic zone, where this species was mostly a grazer. Such specialization is indicated by the elongated head of this rhino, its low carriage, the loss of incisors and canines, and also the high-crowned teeth. The rich pastures in river valleys and parts of watersheds, where little snow accumulated in winter and where there was hard ground in summer, provided favorable conditions for the Pleistocene megafauna of Western Beringia (Sher, 1971). In North–East Asia, most woolly rhino remains have been found on plateaus and in mountain river valleys (Sher, 1976; Boeskorov, 2001). While these landscapes provided good grazing, they also posed a threat. The dissected relief contained many thermokarst features that were hazardous for this short-legged, massive animal. In such places rhinos could get mired in natural traps, such as thermokarst lakes, interstice and deep scours from melting ice wedges, and narrow river channels of small watercourses filled with thixotropic sediments. Apparently, on a bank of the Malaya Filippova River the woolly rhino lost its footing and drowned in a mud trap. This reconstruction of events is suggested by the position of the corpse. It was found in ice-rich Yedoma sediments on its left side, with its head stretched upwards. Probably the left half of the animal's body was trapped by thixotropic liquid and the swampy thawed Yedoma deposits and it suffocated, although it tried to raise its head above the mud trap. Other carcasses of Pleistocene megafaunal animals have been found in a similar position, including the Selerikan horse (Vereshchagin, 1977) and the Yukagir mammoth (Boeskorov et al., 2007). Parts of the body (the right side of the head and the right half of the torso) apparently remained above the mud trap. These were probably gnawed by small predators and scavengers (large predators would have most probably carried away the head and legs).

In recent years, the extraction of gold from gravel deposits in the vicinity of the Rodinka Mountain has yielded incomparable numbers of woolly rhino remains. This region is the richest yet found, in terms of woolly rhino fossils. Hundreds of bones have been excavated during gold mining works in three deposits in a region of just 20 square km on the slopes of the Rodinka Mountain (351 m) (Malaya Filippova River and Finish Stream) and near Panteleikha Mountain (632 m) (Drevnyi Stream). At present, most of these specimens are housed in the Ice Age Museum in Moscow, which holds approximately 50 woolly rhino horns (whole or partial), more than the total amount of these rare fossils held in all the other museums of the world.

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