

Frozen Mummy of a Subadult Woolly Rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) from the Late Pleistocene of Yakutia

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Abstract—In this study we describe a newly found frozen mummy of a young woolly rhinoceros (4–4.5 years old), dated to the Karginian Interstadial of the Late Neopleistocene ($32\,440 \pm 140$ years ago). The dimensional characteristics of this specimen are compared to those of 1- to 1.5-year-old juvenile, as well as adults, of *Coelodonta antiquitatis* found previously. Studies of the new find allowed to fill some of the information gaps concerning the features of the ontogenesis of the woolly rhinoceros, illustrate age-related changes in the color of its fur, and reveal a new anatomical peculiarity of *C. antiquitatis*—the presence of a fatty hump. Numerous remains of microscopic crustaceans were found in the wool, including representatives of the genus *Moina* (Cladocera: Moinidae), currently absent in the region. The latter were relatively common in Pleistocene temporary water bodies of Yakutia. The carcass of the rhinoceros was buried in a shallow (apparently temporary), fishless reservoir.

Keywords: woolly rhinoceros, *Coelodonta antiquitatis*, morphology, coat, crustaceans, Pleistocene, Yakutia, paleoecology

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INTRODUCTION

The woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) is one of the most widespread and well-represented species of mammoth fauna of Northern Eurasia in the fossil record: its remains have been found on the territory from the British Isles in the west to Chukotka and Kamchatka in the east [1]. Despite more than 300 years of studies on the woolly rhinoceros, many anatomical, morphological, and ecological features of this extinct species remain unexplored. A significant amount of information concerning the characteristics of this fossil animal and its habitat was obtained in course of the study of the carcasses of adult *C. antiquitatis* found on the territory of

Yakutia: in the vicinity of the village of Verkhneilyuisk in 1771, on the Khalbui River (Yana River basin) in 1877 [1], in the village of Churapcha (skeleton with partially preserved skin and fur and remains of the stomach) in 1972 [2], and in the lower reaches of the Kolyma River in the vicinity of the settlement of Chersky in 2007 [3]; as well as from the territory of Western Ukraine: two mummified carcasses were found in 1907 and 1929 in deposits of ozokerite bitumen near the city of Starunia [1].

Despite these findings, researchers knew rather little about the growth and ontogenesis of this animal until a frozen mummy of a baby *C. antiquitatis* was found in 2014 on the Semyuelyakh River (Indigirka River basin, Abyisky district of Yakutia), called “Sasha rhinoceros.” The dental system of the found calf consisted of functioning deciduous teeth and corresponded to that of a 1- to 1.5-year-old calf of white rhinoceros (*Ceratotherium simum* Burchell, 1817), which allowed the researchers to estimate its age as comparable [4]. The duration of lactation in modern rhinoceroses is approximately one to two years [5]; thus, the Sasha rhinoceros could have fed on his mother’s milk until death. Radiocarbon dating of calf bones (GrA6329) showed an age of 42000 years ago, while a

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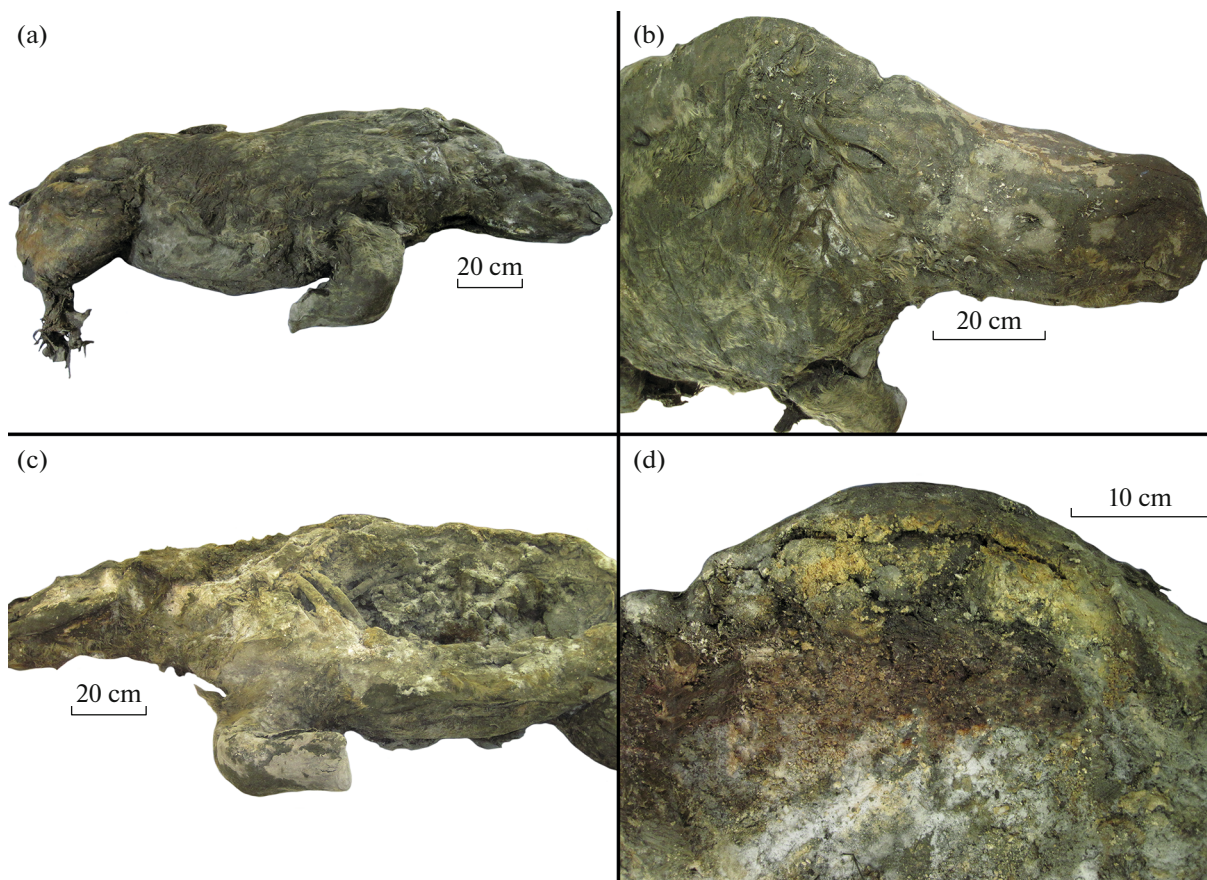


Fig. 1. Frozen carcass of the Abyisky woolly rhinoceros: (a) lateroventral view from the right side, (b) view of the rhino's hump from the right side of the body, (c) lateroventral view from the left side, (d) view of the rhino's hump from the left side of the body.

skin sample (GrA63289) indicated an age of 34700 years ago [4].

A study of the Semyuelyakh juvenile coat and its comparison with the adult *C. antiquitatis* specimens showed that it has both similarities and differences. Thus, the hair color of the calf is much lighter than that of adults. The juvenile hair was uniformly short over the entire surface of the body, while the length of the fur of adult rhinoceroses varied significantly in different parts of the body and was noticeably longer on average. Unlike adult individuals, the juvenile's coat was poorly differentiated, devoid of overhair, coarse hair, and a multitiered layer of guard and downy hairs [6]. The body size characteristics of the Semyuelyakh calf have not been published yet. Here we report on finding of a new young specimen carcass.

MATERIALS AND METHODS

In August 2020, on the banks of the Tirekhtyakh River (right tributary of the Indigirka River, Abyisky district of Yakutia; geographic coordinates of the find: 68°35'18.19" N, 147°7'13.21" E) a relatively well-pre-

served frozen carcass of a *C. antiquitatis* was found with soft tissues, skin, and wool (Fig. 1), called the "Abyisky rhinoceros." The history of the discovery of this rhinoceros is described by V.V. Plotnikov [7]. Currently, the rhinoceros's carcass is stored frozen in the Department for the Study of Mammoth Fauna of the Academy of Sciences of the Republic of Sakha (Yakutia) and has the temporary collection number DMFS-2020-01.

To conduct anatomical and morphological studies, the mummy was temporarily defrosted, the surface of the carcass was cleared of the deposits, and the following samples were taken for research: skin and fur from different parts of the body and soft tissue from the withers (hump) area.

To identify tissue (presumably adipose) from the withers area, standard qualitative chemical reactions were carried out on the components of fat—fatty acids and glycerol [8]. To do this, hydrolysis of the tissue under study was carried out in an alcoholic solution of potassium hydroxide. The hair structure and arthropod remains were studied under a scanning electron microscope (SEM).

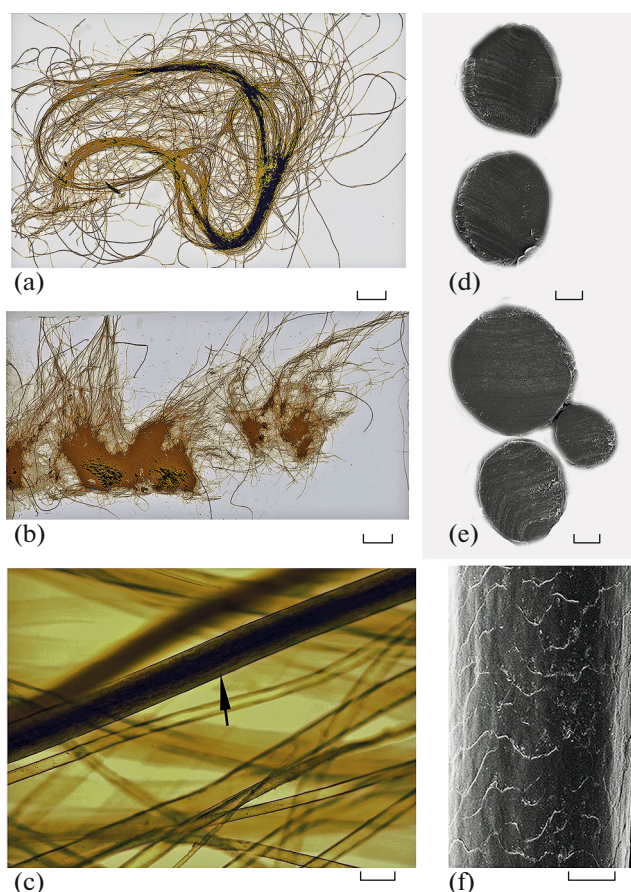


Fig. 2. Appearance and microstructure of hair of the Abyisky rhinoceros: (a) back hair in the shoulder blade area, (b) belly hair, (c) polymorphism of the hair at the nape (overhair is indicated by an arrow), (d) cross section of the guard hair of the back, (e) cross section of the guard hairs of the belly, (f) dorsal hair cuticle ornament. (a), (b) Scanned images, (c) photomicrograph, (d)–(f) SEM data. Scale: (a), (b) 10 mm; (c) 100 μ m; (d)–(f) 10 μ m.

RESULTS

The age of the discovery was estimated by radiocarbon dating of the rhinoceros fur, carried out at the Center for Applied Isotope Studies at the University of Georgia (United States), which showed a value 32440 ± 140 years ago (UGAMS 65491). This dating corresponds to the Karginian Interstadial of the Late Pleistocene (roughly corresponding to the marine isotopic stage MIS3), to which most of the frozen mummies of mammoth fauna on the territory of Yakutia belong.

Anatomy of the mummy. On the upper part of the calf's head, the skin was damaged, which allow us to establish a number of juvenile features of the skull of this individual: a narrow end of the rostrum, without extensions; nonfused nasal, frontonasal, frontal, parietal, and other sutures of the skull. The nasal septum is not completely ossified; ossification occurred only in its anterior part. The complete ossification of the nasal septum in the woolly rhinoceros coincided with the onset of M3 functioning, after the age of five years [9].

Development of the dental system. The presence of P2 with traces of abrasion and unworn P3, as well as the last upper molars that have not erupted from the alveoli (M2 and M3), allow us to attribute the rhinoceros to juvenile group C-IV according to the age gradations of *C. antiquitatis* developed by N.V. Garutt [9], which corresponds to more than four years of age. The height at the withers of this individual is close to that of a four-year-old woolly rhinoceros calf [10]. A similar age is indicated by the development of the nasal horn of the Abyisky rhinoceros (length on the outer side 240 mm), as well as the number of dark transverse patches on the horn, 3–4. This number approximately corresponds to the number of years lived by the animal [11, 12]. Thus, based on the combination of characteristics, we estimate the individual age of the Abyisky rhinoceros to be 4–4.5 years; this individual had not yet reached sexual maturity, which occurs in modern rhinoceroses at the age of about five years [5].

The right side of the mummy is well preserved, represented by soft tissues, skin, and fur (Figs. 1a, 1b). The left side of the carcass is worse preserved: from the upper part of the thigh to the level of the shoulder blade, it is severely destroyed; the internal cavity of the body is exposed, and most of the intestines are missing. It is obvious that the left side of the mummy was eaten by predators (Fig. 1c).

Abyisky rhinoceros has a well-preserved area of the withers, on which a hump of up to 13 cm is clearly visible (Figs. 1b, 1d), filled with fat mass. As a result of hydrolysis of tissue from the hump, soluble potassium soap, insoluble lead soap (fatty acid salts), fatty acids (in the reaction of soap decomposition with mineral acids), and glycerin (in reaction with sodium hydroxide and copper sulfate) were detected in the hydrolysate, which confirms lipid nature of the tissue studied.

The morphometric features of the body, skull, and nasal horns of the Sasha and the Abyisky rhinoceroses and their comparison with similar parameters of adult individuals of *C. antiquitatis* are presented in Table 1. The height at the withers of the 1- to 1.5-year-old Sasha rhinoceros is 55.2% of the average height of an adult; by this age, white rhinoceros calves reach approximately 67 to 80% of the adult height [13]. By 4–4.5 years, the height of subadult woolly rhinoceros approached the height of adults; thus, in the Abyisky rhinoceros it is 85.1% of the adult height. Other dimensional characteristics of the Abyisky rhinoceros (body length, skull length, anteroposterior diameter of the forefoot) are notably inferior to the average values for adult woolly rhinoceroses (accounting for 68.3, 69.3, and 72.3% of the indicated lengths, respectively). This disproportion in body size is explained by the peculiarities of rhinoceros growth that are also noted in extant species. Young rhinoceroses grow in height quite quickly and reach a height comparable to an adult female at the age of about three years for black (*Diceros bicornis* L., 1758) [14] and 4.5–5 years for

Table 1. Body sizes of fossil woolly rhinoceroses of different ages found in Yakutia

Measurements, cm	Sasha rhinoceros, 1–1.5 years	Abyisky rhinoceros, 4–4.5 years	Adult sexually mature individuals	
			range (M)	<i>n</i>
Body length	172	236.5	323–355 (346.5)	4
Height at withers	85	131	145–160 (154.0)	4
Chest circumference behind forelimbs	130 (restored)	214 (restored)	260; 280	2
Hindfoot length	About 30		39; 45	2
Ear length	13	15.9	18.5–24 (21.5)	3
Tail length	About 20	Over 17	47–49 (47.8)	3
Antero-posterior diameter of the forefoot	12.7	13.8	18.2–20 (19.1)	2
Transverse diameter of the forefoot	12	13	18–19.5 (18.75)	2
Manus circumference in the middle	28	37	37–42 (39.5)	2
Skin thickness	0.3–0.6 (head) 0.3–0.7 (back)	0.3–1.0 (back, sides)	0.5–1.2 (back, sides); 0.6–1.2 (chest, belly); Up to 1.5 (thigh)	
Parietal length of skull	45.5	52.8	70.6–83.2 (76.18)	18
Zygomatic width	About 16	25.7	32–36.1 (34.55)	15
Lower jaw length	–	38.7	49–52.8 (50.76)	11
Nasal horn				
External curvature length	10.4	About 24*	37–128.9 (94.0)***	20
Horn base (sole) length	11	17.6**	13.6–25 (21.0)***	20
Number of dark transverse patches	2	3–4	9–35 (20.7)***	17

* Measured from photo; ** measured by V.V. Plotnikov; *** according to [Garutt, 1998].

white and Indian (*Rhinoceros unicornis* L., 1758) rhinoceroses [15]. However, full development of the body and attainment of the size and weight of adults in the Indian rhinoceros occurs after 6.5–10 years and even later in African rhinoceroses [15]. Most likely, the rapid growth in height in young individuals is an adaptive property, which may indicate the evolutionary conservation of this trait in rhinoceroses. The horns of *C. antiquitatis*, on the contrary, grew throughout life; so, even in sexually mature 14-year-old individuals [10], the horns were significantly shorter than in old males [12].

Features of rhinoceros fur. The fur of the Abyisky rhinoceros has a uniform light brown color (Figs. 2a, 2b) due to the combination of white, beige, and brown hair of different shades, as well as different hair densities. The upper tier (pile) is always darker than the lower one (underfur) due to dark brown, sometimes almost black, overhair and beige guard hairs (Figs. 2a, 2c). The underfur has a lighter shade because it contains numerous beige and white downy hairs. The coat is darker on the ears and feet and lighter on the back, belly, and hind legs. Morphometry

allows us to distinguish overhair (113–158 μm thick), guard hairs, and downy hairs of three size orders (56–79, 33–45, and 11–23 μm , respectively; Fig. 2c). The thickest hair covers the lower jaw and shin, and the thinnest hair grows on the auricle. The guard hair are of a regular cylindrical shape (Figs. 2d, 2e), and the down is slightly convoluted (Figs. 2a, 2b). Of the layers of hair, only two are developed: a thin tiled cuticle and a powerful dense cortex, while the medulla is absent. The cuticle has a similar pattern in hair from different parts of the body. Its large scales wrap the shaft halfway or entirely and have a strongly indented apical edge and triangular projections (Fig. 2e), sometimes oriented at an angle of 20°–25° to the transverse axis of the shaft. The height of the scales varies slightly (26–29 μm) but is slightly greater in the hairs of the thigh and belly (31–33 μm). A comparison with previously studied individuals (Sasha rhinoceros, young and old females [16–18]) shows that (1) juvenile rhinoceroses had uniform, light (up to blond), and relatively thin hair without dark and coarse hairs; (2) at 4–4.5 years, rhinoceroses acquired a darker color with long (especially on the lower back) polymorphic layered hair;

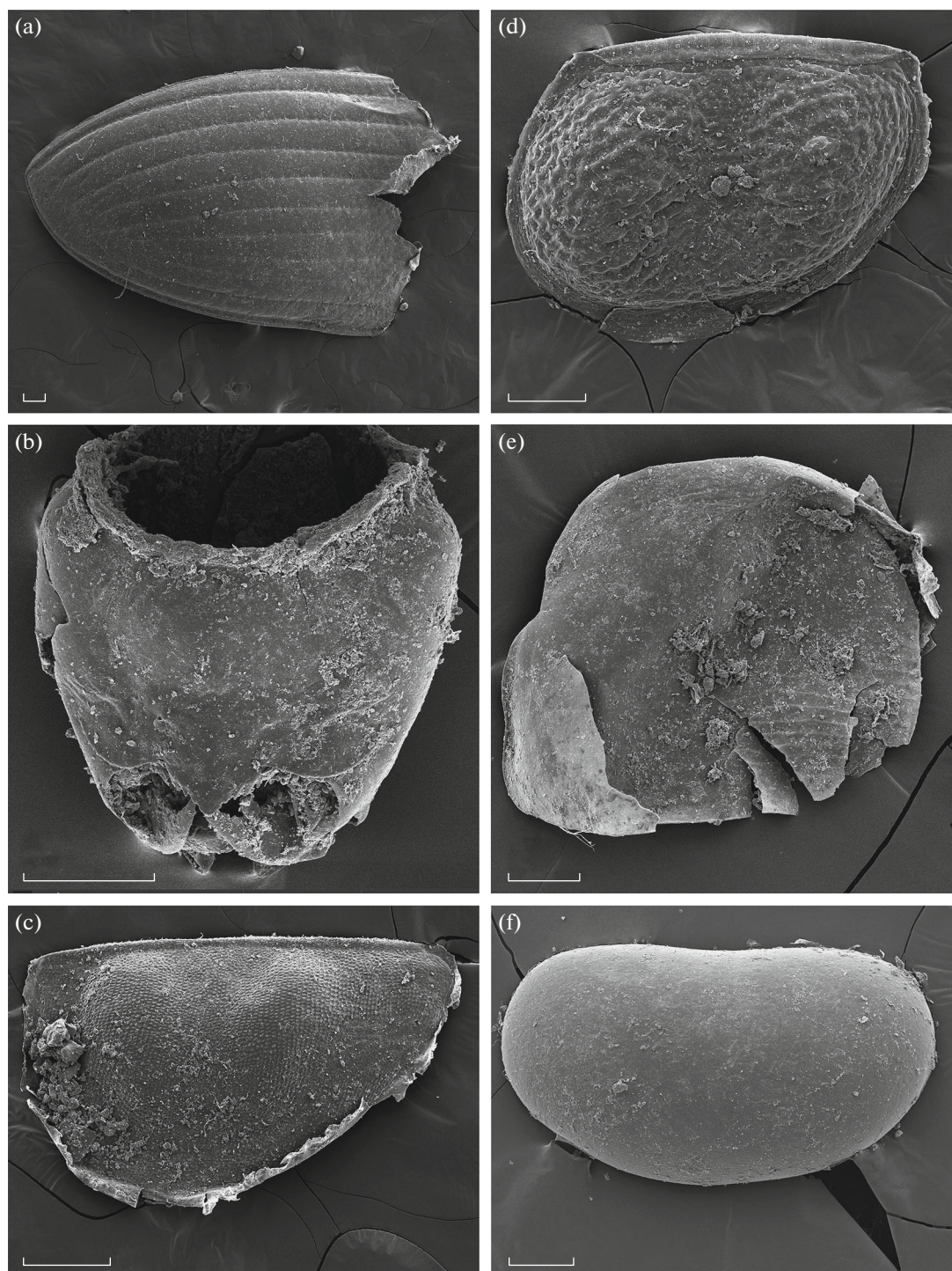


Fig. 3. Remains of arthropods extracted from wool under a scanning electron microscope: (a) Coleoptera elytra, (b) Chironomidae (Diptera) head capsule, (c) *Daphnia* (*Daphnia*) sp. (Daphniidae) ephippium, (d) *Moina* sp. (Moinidae) ephippium, (e) *Acroperus* sp. (Chydoridae) valve, (f) Ostracoda valve. Scale: (a)–(f) 0.1 mm.

they grew long, thick, and dark hair; (3) adults were covered with dense and coarse dark brown fur with black pile and white, light beige, or reddish local spots, which had excellent heat-protective and mechanical properties that effectively protected these animals

from external influences. Of the main microstructures of hair, the cortex and cuticle are developed. In adults, the medulla is sometimes still present in the hair and has a cellular structure, which allows to distinguish the hair of a woolly rhinoceros from the hair of a

woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799), which has no medulla.

Arthropod Remains in Rhinoceros Fur

The wool of mammoths and woolly rhinoceroses found in permafrost contains numerous biogenic remains, and, in addition to its value for understanding the anatomy, morphology, and ontogenesis of the animals, is of interest for reconstructing their habitat [19]. In the fur of the Abyisky rhinoceros, numerous chitinous remains of various arthropods were found, including freshwater cladoceran crustaceans (Cladocera) of the genera *Daphnia*, *Ceriodaphnia*, *Simocephalus*, *Moina*, *Bosmina*, and *Eurycercus*, as well as unidentified representatives of the family Chydoridae, class Anostraca, and class Ostracoda (Fig. 3). A similar set of taxa characterizes a small, well-warmed, fishless freshwater body of water. Such reservoirs apparently existed in the region throughout the Pleistocene and are also found today. However, ephippia (modified exuvium of a gamogenetic female containing resting eggs) of representatives of the genus *Moina*, which currently live much southwest of the point where the rhinoceros was found, were also detected in the wool. Representatives of the genus *Moina* were found in the Yana basin during the periods MIS3–MIS4 [20]. Most likely, it should be assumed that they got into the wool at the time of burial of the rhinoceros carcass. It is known that the reservoirs of the Beringian zone at that time were often inhabited by communities of microscopic crustaceans that had no modern analogues [21]; apparently, they included the reservoir in which the Abyisky rhinoceros was buried.

CONCLUSIONS

Studies of a newly discovered mummy of a 4–4.5 years old woolly rhinoceros has allowed to fill the gaps in information concerning the features of the ontogenesis of this fossil animal, illustrate the process of changing color of its fur, and also identify a new anatomical peculiarity of *C. antiquitatis*—the presence of a fatty hump, as well as obtain information about the reservoir in which the carcass had been buried.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work involved the study of only fossil organisms.

CONFLICT OF INTEREST

The authors of this article declare that they have no conflicts of interest.

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