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Some Specific Morphological and Ecological Features of the Fossil Woolly Rhinoceros (*Coelodonta antiquitatis* Blumenbach 1799)

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Abstract—The results of anatomical and morphological studies of new corpse remains of the fossil woolly rhinoceros found in 2007 in the lower reaches of the Kolyma River are described. These new data provide additional details of the specific features of the structures and sizes of individual body parts of the fossil rhinoceros and allow for several inferences on the specific adaptations of this species to the cold climate of the Ice Age. Palynological data for the stomach contents of the woolly rhinoceroses that lived during the Karginian interglacial period of the Late Pleistocene are given. It is been shown that herbs (cereals and forbs) account for the major part of the woolly rhinoceros diet.

Keywords: woolly rhinoceros, Late Pleistocene, anatomy, morphology, ecology

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Currently, there are five rhinoceros species living in the tropical zones of Africa (two species) and Southeast Asia (three species). The extant rhinoceros are just remains of an odd-toed ungulate group once rich in species. Over the long-term history of its existence, the rhinoceros family has given rise to several specific forms, including those living far beyond the optimal zones of the contemporary species. In particular, rhinoceros during the Quaternary inhabited not only temperate latitudes of Eurasia (the giant unicorn *Elasmotherium sibiricum* Fischer 1809 and two rhinoceros species of the genus *Dicerorhinus* Gloger 1841), but also high latitudes with an extremely cold climate (woolly rhinoceros).

The woolly rhinoceros was one of the most abundant species and an indicator of the Eurasian mammoth fauna: its fossils have been found on the area spanning from the British Isles in the west to Chukotka and Kamchatka in the east (Garutt et al., 1970; Vereshchagin, 1979; Lazarev et al., 1998; Garutt and Boeskorov, 2001; Boeskorov, 2001). The first researchers who studied the *C. antiquitatis* Blum. 1799 in Siberia could not imagine the possibility that the rhinoceros lived under cold climatic conditions. For example, Pallas (1769, 1772; according to Garutt, 2001) initially assumed that the remains of the rhinoceros and elephants (mammoths) in Siberia suggested a warmer climate there during their lives; later Pallas explained such findings by the fact that the carcasses were moved by "the Flood" from more southern regions.

Later information about several specific morphological features of the woolly rhinoceros was obtained when examining the bone remains and, especially, whole carcasses belonging to this species. Only four findings of their whole carcasses are known. In Yakutia, one carcass was found near the village of Verkhnevilyuisk (1771; Fig. 1a) and the other, near the Khalabui River (a tributary of the Bytantai River, in the basin of the Yana River, 1877; Fig. 1b); however, only two legs and the head were taken from the first carcass and the head and one leg were taken from the second one (Chersky, 1879; Brandt, 1849; Schrenck, 1880). Two mummified carcasses were found, one in 1907 (Fig. 1c) and the other in 1929 (Fig. 1d) in ozokerite deposits near the town of Starunia, Western Ukraine (Niezabitowski et al., 1914; Nowak et al., 1930; Kubiak, 1969). The former finding as the forepart of the carcass with the head and horns is at the Natural History Museum of Lvov (Ukraine) and the latter (a whole female carcass without horns), at the Natural History Museum of the Polish Academy of Sciences in Krakow (Poland). Whole skeletons of the woolly rhinoceros with retained soft tissues are also extremely rare. The best known one was found in 1972 in the village of Churapcha, 200 km east of Yakutsk. The skin and fur coat partially remained on the right leg, and stomach remains were preserved (Lazarev et al., 1998).

Examination of these findings has allowed for clarification of specific morphological and ecological features of *C. antiquitatis*, including the presence of a thick coat of wool and thick skin, flattened front horn, full bony nasal septum (additional support for the nasal bones carrying the front horn), predominant

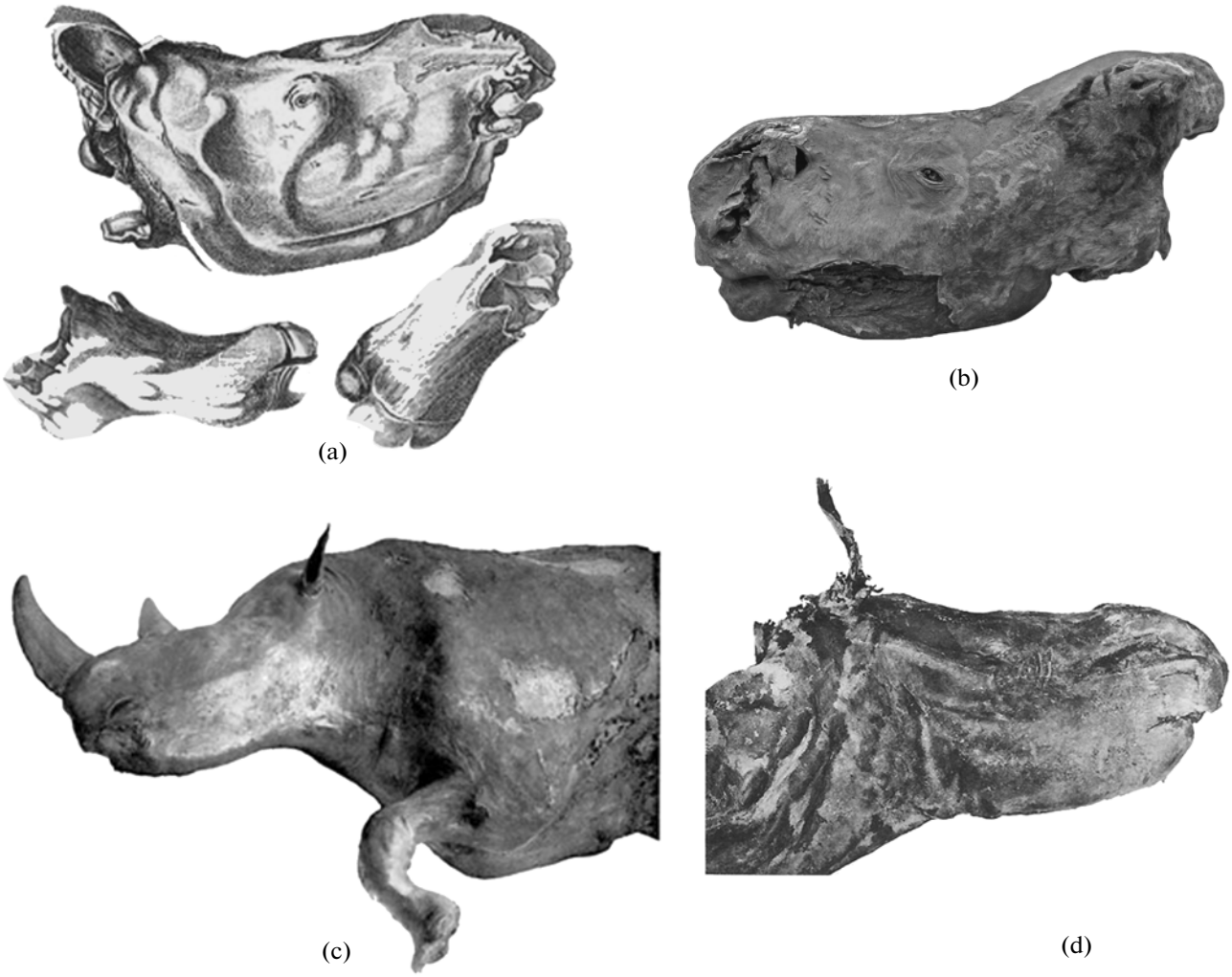

Fig. 1. Mummified remains of woolly rhinoceros carcasses: (a) the head, carpus, and foot of the Verkhnevilyuisk rhinoceros, 1771 (according to Garutt, 2001); (b) the head of the Khalabui rhinoceros, 1877 (according to Garutt, 2001); (c) part of the young female carcass found in 1907 in Starunia (according to Niezabitowski et al., 1914); and (d) the head of the adult female carcass found in 1929 in Starunia (according to Nowak et al., 1930).

herbaceous diet, and specific body type (elongated trunk and relatively short legs).

On the other hand, the insufficient number of woolly rhinoceros carcasses (or their parts) and whole skeletons prevented reliable statements about many specific morphological and ecological features of this extinct animal.

MATERIALS AND METHODS: BRIEF DATA ON THE EXAMINED FRAGMENTS OF THE RHINOCEROS CARCASSES

We have studied several specific metric and nonmetric features of the woolly rhinoceros carcass remains found in 2007 in the Kolyma gold mine located in the upper reaches of the Malaya Filippova River (8 km east of the village of Cherskii, Nizhnekolymskii district, Republic Sakha (Yakutia)), now stored frozen in Yakutia at the Museum of Mammoths with the Institute of Applied Ecology of the North.

(1) Part of the mummified carcass and skeleton remains: left part of the trunk with skin, including the head skin with ear, front and hind legs, collection no. MM 7938 (Fig. 2); skull, no. MM 7938/1 (Fig. 3a) with the mandible; two horns, nos. MM 7938/2 and MM 7938/3 (Figs. 3b, 3c); bone remains of the right front leg, nos. MM 7938/4 and MM 7938/5 (Figs. 3d, 3e); right part of the hip bone, no. MM 7938/6 (Fig. 3f); and the distal part of the right hind leg with soft tissues, no. MM 7938/7 (Fig. 3g). The major part of the internal organs has been lost; however, the stomach remains with the contents are available. This finding, similar to all the large specimens (carcasses and skeletons) of Pleistocene animals, obtained its own name,

Fig. 2. Left part of the Kolyma woolly rhinoceros (no. MM 7938).

the Kolyma rhinoceros. Preliminary information about this finding was published earlier (Boeskorov et al., 2009).

(2) The remains of a young animal carcass comprising the distal parts of hind legs, nos. MM 7940/1–2; a piece of skin from the hind trunk part with the tail and inguinal region, no. MM 7941 (Fig. 4); fragments of five thoracic vertebrae, nos. MM 7940/3–7; and tufts of brown wool.

(3) Two skin fragments of an adult individual, nos. MM 7939/1–2 (Fig. 5).

The woolly rhinoceros carcasses from the upper reaches of the Malaya Filippova River were found in the Upper Pleistocene icy pulverous loamy clay layer with polygonal veined ice (Fig. 6) with a thickness amounting to 15–17 m in the upper reaches of this river. These deposits belong to the yedoma suite of the second half of the late Pleistocene (Zyryanka–Sartan glaciation, about 70–11 TYA; Sher, 1971). The Kolyma rhinoceros carcass was buried at a depth of 5–9 m from the surface of a mine opening. The postmortem carcass position (Fig. 6) suggests that the animal fell into a washout.

The absolute age of the Kolyma rhinoceros is dated to 39140 ± 390 years, OxA-18755 (Davydov et al., 2009). Thus, this individual lived at the beginning of the Karginian interstadial (an analog of the Middle Valdai interglaciation in the Russian Plain and Würm II of Western Europe).

Some size parameters were measured in the Churapcha woolly rhinoceros, deposited at the Geological Museum with the Institute of Diamond and Precious Metal Geology, Siberian Branch, Russian Academy of Sciences (collection no. IGABM 2114). At our request, Prof. H. Kubiak (Poland) made several measurements of the Starunia rhinoceros at the Natural History Museum of the Polish Academy of Sciences (Krakow).

N.T. Bakulina and L.M. Fartunatova (Palynological Laboratory with the Central Geological Laboratory, state enterprise of the Republic of Sakha (Yakutia) Yakutskgeologiya) conducted palynological analysis of the specimens of host deposits and stomach contents of the Kolyma rhinoceros.

The available literature data on the specific morphometric features of the extant rhinoceros were used for comparison; we have studied a number of these specific features using the stuffed woolly rhinoceroses from the Zoological Museum (St. Petersburg, Russia), the Zoological Museum of Moscow State University (Moscow, Russia), and the Natural History Museum in Beijing (China).

Fig. 3. Individual remains of the Kolyma rhinoceros: (a) skull, no. MM 7938/1; (b) front horn, no. MM 7938/2; (c) back horn, no. MM 7938/3; (d) humerus, no. MM 7938/4; (e) elbow bone, no. MM 7938/5; (f) hip bone, no. MM 7938/6; and (g) lower part of the right hind leg, no. MM 7938/7.

Fig. 4. Remains of a young woolly rhinoceros individual: (a) lower parts of hind legs, nos. MM 7940/1–2, and (b) a patch of skin with tail, no. MM 7941.

RESULTS AND DISCUSSION

Palynological Analysis of the Deposits Housing the Kolyma Rhinoceros Remains

To clarify the paleofloristic environment that accompanied the life of this individual, we performed a palynological analysis of the host deposits where the rhinoceros carcass was buried (Boeskorov et al., 2009). In the examined specimen, the herb and undershrub pollen is predominant (accounting for 61.0%), cereal pollen being the most abundant (23.9%). Wormwood (15.3%) and caryophyllaceous (7.3%) pollen is rather abundant; sedge (4.9%) and aster (1.4%) are less abundant. The species diversity of the forb pollen suggests the plant communities belong to different habitats, namely, steppe and steppe–meadow cenoses (aster, saxifrage, goosefoot, legume, plantain, etc.) and meadow cenoses (ranunculaceous, buckwheat, valerian, umbellate, meadow rue, burnet, etc.). The trees and bushes (23.7%) are mainly represented by the pollen of small-leaved angiosperms (18.0%) with predominance of dwarf birches (9.7%), alders (3.8%), willow (solitary cases), and birch trees (3.4%). Of the coniferous pollen, solitary pollen grains of the larch *Larix* sp. and pine *Pinus* sp. were observed. In general, the range of data obtained examining the host deposits for the rhinoceros carcass suggests vegetation types characteristic of sharply continental and dry climate characteristic of the cold phases in the Karginian interglaciation, namely, open steppificated landscapes with alternation of scrubs and thin forest stands. The current plant composition at the site of the rhinoceros carcass find (right bank of the lower reaches of the Kolyma River) is considerably different. This area belongs to the subzone of northern thin larch forests (Karavaev and Skryabin, 1971). This is a complex of

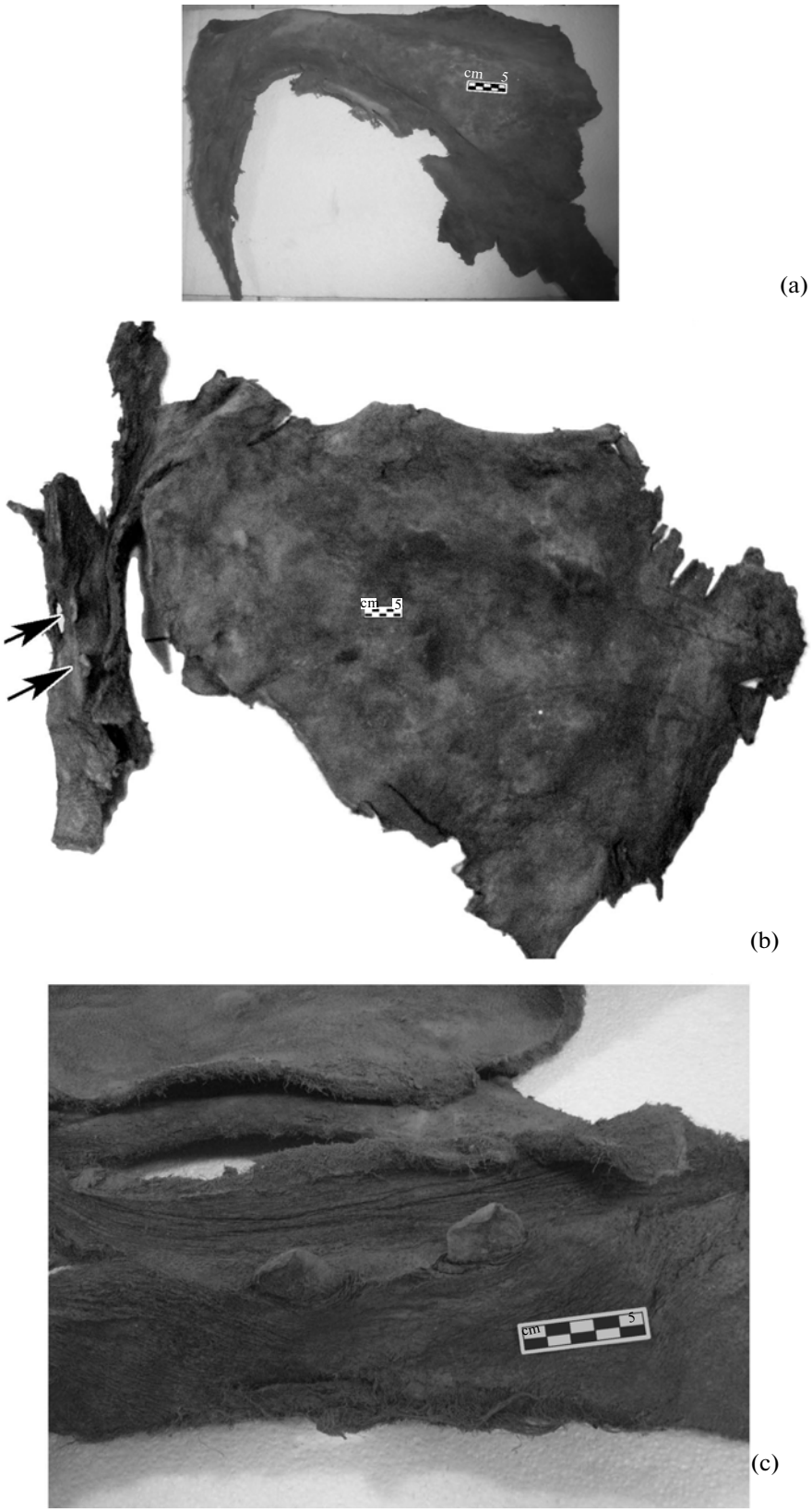

Fig. 5. Skin fragments of the second adult woolly rhinoceros individual from the Malaya Filippova River, no. MM 7939: (a) from the back and trunk side, no. MM 7939/1; (b) from the lower body part, no. MM 7939/2 (arrows denote nipples of the udder); and (c) enlarged skin fragment with the udder, no. MM 7939/2.

Fig. 6. The Kolyma rhinoceros carcass melting out at the site of its finding.

thin larch forest stands with scrubs, marshes, and near-lake herb communities.

Analysis of the stomach contents. Herb pollen is predominant (98.5%) in the specimen of feed remains (Boeskorov et al., 2011). The pollen of trees and bushes accounts for 0.9%, and spores, for 0.6%. The most abundant among the herb pollen is the pollen of cereals (45.9%) and composite family (40.6%), where wormwood pollen is the most abundant (40.1%). Forb pollen is rather richly represented, mainly the steppe and meadow–steppe plants with a rather high content of the caryophyllaceous (to 3.4%), plantain (to 2.3%), and rosales (to 3.2%) families. The pollen of papaveraceous, ranunculaceous, buckwheat, cruciferous, goosefoot, leguminous, polemonium, valerian, chicory, aster, and sedge species is observed in small amounts.

The content of the pollen of trees and shrubs is extremely low, being represented by solitary pollen grains of the spruce (*Picea* sp. and *P.* sect. *omorica*), haploid and diploid pines, dwarf pine, and willow. The spruce and pine pollen grains are poorly preserved; their appearance suggests their more ancient age, and it is likely that they got there accidentally.

The group of spores is also small. Solitary spores of liverworts, horsetail, Siberian spike moss, and Arctic fir moss have been observed.

Thus, the detected pollen and spore range suggests that various cereal species and forbs formed the main part of the woolly rhinoceros diet. The predominance of herb plants over trees and shrubs was observed earlier when examining the feed remains from the teeth of the woolly rhinoceros from the Khalabui River in Verkhoyan'e (Garutt et al., 1970) and the remains from the gastrointestinal contents of the Churapcha rhinoceros (Lazarev and Tirskaya, 1975).

ANATOMICAL AND MORPHOLOGICAL DESCRIPTION OF THE KOLYMA RHINOCEROS CARCASS

Preservation and Sizes of Individual Body Parts and Organs

The skull and mandible are completely preserved. Tendon remains are occasionally present. A mummified grayish brown tongue oval in cross section is preserved at the bottom of the mouth cavity. The tongue retains the root, body, and part of the tip (the ventral part is destroyed). The papillae are not preserved. The tongue length from its root to the ventral part of the retained tongue tip is 310 mm. The tongue cross-sectional width is 68 mm, and the height at the same place is 82 mm. The right lingual bone (*os hyoideum*) with a length of 208 mm is well preserved. The width of the muscular process (*processus muscularis*) is 74 mm, and that of the stylohyoid is 25 mm. In its shape, the rhinoceros tongue is closest to the horse tongue.

The teeth including M3 (the anterior part, including parastyle and protoloph) display signs of considerable abrasion. The frontonasal, nasomaxillary, and sagittal sutures are obliterated; the nasal septum is completely ossified. Nasal bones are elongated, and their lateral edges are convex (Fig. 3a). These specific features suggest that the rhinoceros was a sexually mature individual that had completed its growth (see Borsuk-Byalynicka, 1973). The skull sizes are rather large: the total length is 653 mm; zygomatic breadth, 332 mm; and maximum height in the frontal horn region, 178 mm. For comparison, note that Borsuk-Byalynicka (1973) gave the following parameters (variation range and the mean) for the corresponding measurements of the *C. antiquitatis* skull: 580–685 mm (M = 634.06 mm), 300–386 mm (M = 335.08 mm), and 155–190 mm (M = 169.9 mm).

Horns. The front (nasal) horn (Fig. 3b) displays a characteristic saber-shaped bend and is flattened from its sides. The horn anterior surface is considerably abraded; the length of the abraded region is 510 mm. The horn length according to its external curvature is 845 mm, and internal curvature is 627 mm; the anteroposterior length of its base is 229 mm, and the transverse breadth in the middle part is 123 mm; its thickness in the middle part is 26 mm. Such rather small sizes of the front horns are characteristic of a young adult rhinoceros with an age of about 14 to 20 years old. The Kolyma rhinoceros horn has 17–19 transverse bands of annual growth; correspondingly, the individual age of the animal was about 20 years old (see Lazarev et al., 1998; Fortelius, 1983; Garutt, 1998). Typically, larger horns are characteristic of more mature *C. antiquitatis* individuals at an age of 25 to 35 years old with an external curvature length of 100 to 1350 mm (Lazarev et al., 1998; Chernova et al., 1998; Boeskorov and Isakova, 1999; Garutt, 1998).

The length of the second (back) horn reaches 150 mm; the length of its base is 146 mm, and its width in the middle part is about 80 mm; the horn breadth in the middle part is 78 mm, and the thickness at this site is 48 mm. The tip of this horn is abraded (Fig. 3c); the intact horn reached 170 mm in length. This horn displays at least 10–11 detectable transverse bands. Only a few back horns of the woolly rhinoceros have been found. The largest of the described horns reaches 395–405 mm (Lazarev et al., 1998; Garutt, 1998). The largest back horn from the Oimyakon Upland that we examined has a length of 475 mm. The sizes of the Kolyma rhinoceros back horn are characteristic of sexually mature yet not old individuals (Lazarev et al., 1998; Garutt, 1998).

The skin integuments on the left side of the trunk and left legs are well preserved (Fig. 2). The skin is mummified and hardened; in its greater part, it is dark brown, being here and there covered with blue crystals of vivianite. The skin thickness of the Kolyma rhinoceros mummy varies from 5 to 15 mm. The thinnest skin is on the lateral side of its head (on average, 5.5 mm), and the thickest (in descending order) is observed in the rump (on average, 11.2 mm), thorax (on average, 10.5 mm), and back (on average, 10.4 mm). The thickest skin of the Starunia female rhinoceros found in 1929 is on the lower lip, amounting to 28 mm (Nowak et al., 1930). For comparison, the skin thickness in an adult mammoth varies in different body areas from 9 to 30 mm (Garutt, 1964; own data). As for the extant cattle, the skin thickness in different body areas varies from 3 to 13 mm, the thickest skin being observed in the frontal area and rump and the thinnest, on the neck (Yudichev et al., 2003). Hair is preserved only on the lower parts of the legs, over the nail plates of the hoof phalanges, as tawny brushes. Usually, the carcasses of fossil animals buried in the upper layers of permafrost are deprived of the hair coat due to the impact of annual freezing–thawing.

The preserved large patch of skin has an ear on its left side, eye pit, and part of the anterior snout edge. The ear (Fig. 7) has lost its natural shape, is flattened from the sides, has a lancet shape (the ear of the extant rhinoceros has a widened upper part), and is mummified. Its length from its base is 215 mm, and that from the edge of the auricular notch is 185 mm. The anteroposterior length of the left eye pit is 36 mm. The eye pit length of the Starunia rhinoceros found in 1907 (Niezabitowski et al., 1914) is 40 mm. The eyeball with eye muscles and fasciae in a mummified state is preserved on the inner part of the eye pit skin. The anteroposterior eyeball diameter is 51 mm, and the transverse diameter is 31 mm. The distance from the posterior eye pit edge to the anterior ear edge is 315 mm.

The rhinoceros body is deformed; the front and hind legs are pressed against the trunk. A large skin fold is present between the hind leg and abdomen (Fig. 2), which is characteristic of the extant rhinoceros. *The trunk* is almost complete from the left side (Fig. 2), while a considerable part of the skin is absent from the right side and the legs are torn off; the skin covers only

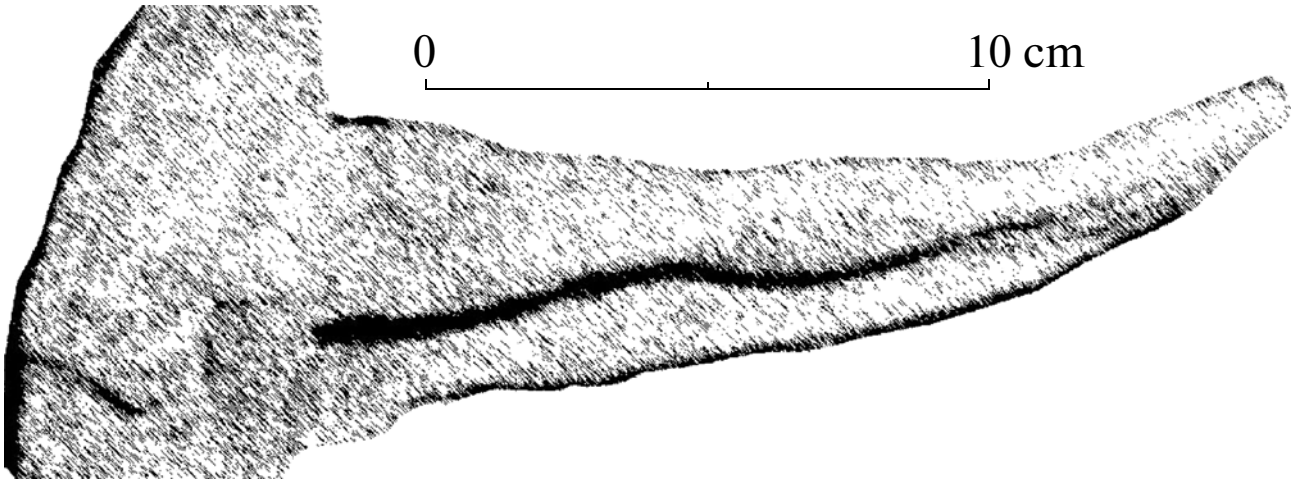

Fig. 7. Ear of the Kolyma rhinoceros.

the dorsal part of the back and part of the abdomen. The abdominal cavity contains the remains of mummified stomach bags with contents, namely, a hardened grout of half-digested plant remains. The total length of the stomach remains is about 70 cm. Small remains of mummified intestines are also present.

Legs. The left legs are completely retained (Fig. 2). The right hind leg is represented by only its distal part (with a fragment of the gaskin above the hock to the sole; Fig. 3g). The legs are pillar-like, as is characteristic of the rhinoceros. The front right leg retained only bone remains, including the humerus (Fig. 3d), cubitus (Fig. 3e), pastern and carpus bones, and two hoof phalanges. Each of the three preserved legs has three "claw horns" (nail plates of hoof phalanges). As in the Churapcha rhinoceros, the level of the elbow joint in this individual is slightly above the ventral abdominal surface. On the other hand, these body parts in the Starunia rhinoceros found in 1929 are approximately at the same level. Presumably, the woolly rhinoceros according to this characteristic almost did not differ from the extant rhinoceros, whose ventral abdominal surface is either approximately at the same level with the elbow joint or slightly above the latter (see Groves, 1982; Laurie et al., 1984; Walker et al., 1964; Zukowsky, 1965).

The leg dimensions are large (table). We have calculated the bearing surface area of the left legs for this rhinoceros, which amounts to 230 cm^2 for the front leg and 185 cm^2 for the hind one. Correspondingly, the total bearing surface area of the legs for this individual is about 830 cm^2.

The hoofs are well preserved. On the right foot, they have the following sizes: the width of the middle hoof is 96 mm, and its height in the middle part is 54.5 mm. The corresponding measurements for the right hoof are 74 and 57.5 mm, and those for the left one are 71 and 53 mm, respectively.

The tail is completely preserved but has no hair. Its length is 47 cm. The tail base is thickened; and the tail gradually tapers to the tip. The circumference of the tail base is 30 cm; in the mid-tail, it is 23 cm; and the dorsal breadth of the tail base is 13 cm. The tail of the Starunia rhinoceros found in 1929 is 2 cm longer; the circumference of the tail base is 29 cm; in its mid-part, it is about 20 cm; and the dorsal breadth of the tail base is 15.5 cm (Nowak et al., 1930). Presumably, the tail of the Kolyma rhinoceros was completely covered with hair, since the orifices of hair follicles remained over the entire tail skin surface; note that the orifices of larger diameter are present at the tail tip (Fig. 8f). The extant rhinoceros have a long and free dock with tufts of long and thick hair at the end from both the outer and inner sides (Fig. 8). Such a tail is efficiently used for whisking away biting insects from their hips and groin. The Kolyma rhinoceros is also likely to have a switch of bristly hair at the tip of its tail (Fig. 8h).

The inguinal region of the mummy abdomen has two nipples (Fig. 9); this number of nipples is characteristic of the odd-toed ungulates in general and the rhinoceros in particular. The nipples are small: the right nipple is 20 mm long with the largest breadth of 17 mm; the dimensions of the left one are 18 and 16 mm, respectively. The inner sides of the nipple bases are located at a distance of 31 mm from one another. The *C. antiquitatis* nipples were described for the Starunia female found in 1929 (Nowak et al., 1930).

Overall Dimensions of the Kolyma Rhinoceros Body

The Kolyma rhinoceros body has large dimensions (table). The total weight of the mummified carcass is 875 kg; together with the skull, horns, remains of two right legs, and other bones found separately, this weight is about 950 kg. Taking into account that a considerable part of the viscera and part of the muscle tissue and skin have been lost, as well as that the soft tis-

Measurements of the woolly rhinoceros specimens

Measurement, cm	Yakutia					Western Ukraine	
	Lower reaches of the Kolyma River, Malaya Filippova River				Lena–Aldan interfluve, village of Churapcha, Churapcha rhinoceros skeleton, adult female, no. IGABM 2114*	Starunia (Niezabitowski et al., 1914; Nowak et al., 1930)	
	Kolyma rhinoceros corpse, adult female, no. MM 7938		Fragments of young female carcass, nos. MM 7940–7941			1907, young female carcass	1929, adult female carcass
Body length	350		–		323	355	358
Shoulder height	145		–		160	153	158**
Thoracic circumference backward of front legs	280		–		260	–	–
Ear length	18.5		–		–	22	24
Tail length	47		47.5		–	–	49
Tail circumference in the middle part	23		18		–	–	About 20
Carpal length directly from the underside of the carpal joint to the front edge of the middle hoof	34		–		30	–	35
Anteroposterior diameter of front foot	18.5		–		–	–	20
Transverse diameter of front foot	18		–		–	–	19.5
Circumference of mid-pastern	42		–		–	–	37
Foot length directly from the hock to the front edge of the middle hoof	Left 41 Right 39		Left 35 Right 36		39	–	36**
Anteroposterior diameter of the hind foot	16.5	17.4	13	13	15.2	–	16
Transverse diameter of the hind foot	15.7	15.9	13.5	13	About 16	–	14
Circumference of hind mid-pastern	39.5	37	35.5	35	39	–	32

Notes: * The lower part of right hind leg of the Churapcha rhinoceros retained soft tissues.
** Measurements by H. Kubiak.

sues have been subject to cryogenic sublimation, it is likely that the intravital weight of this individual was no less than 1.5 tons. The body weight of adult males was even larger, reaching 2 tons. With its relatively low height, the rhinoceros had a long ponderous trunk on short legs. With a body weight of 1.5 tons and bearing surface area of 830 cm^2, this rhinoceros had a tremendous load per cm^2 of the foot bearing surface, amounting to approximately 1807 g. For comparison, note that the load for the bearing surface area of the extant moose is 420–560 g/cm^2 and that of bison is 1000–1300 g/cm^2 (Formozov, 1946; Kuz'mina, 1977).

ANATOMIC AND MORPHOLOGICAL DESCRIPTION OF BODY PARTS OF THE RHINOCEROS INDIVIDUALS FOUND AT THE KOLYMA GOLD MINE

Remains of a juvenile individual. The fragments of hind legs are represented by distal leg parts torn off above the hocks (Fig. 4a); their sizes are rather small (Table). They retain locks of tawny or light brown hair. The skin is grayish brown. The hoofs are well preserved. The middle hoof of the right leg is 84 mm in width and 41 mm in height; the right hoof has measurements of 71 and 46 mm, and the left one, 62 and 39, respectively (the last is partially destroyed). The tail is long but thin (Fig. 4b, table). The hair on the tail and the adjacent skin patch was lost; however, the hair follicle orifices are present over the entire tail; note that, similar to the Kolyma rhinoceros, the tail end contains orifices with a larger diameter (Fig. 8b). The skin thickness near the tail is small, amounting to 7–9 mm. The anal orifice is preserved; the vulva with *rima pudendi* and elongated *labia pudendi* is present ventrally of the anus (Fig. 4b). All these dimensions and specific features suggest that this was a juvenile female individual that had not completed its growth.

The remains of an adult individual are represented by two patches of skin. The skin is brown. The first

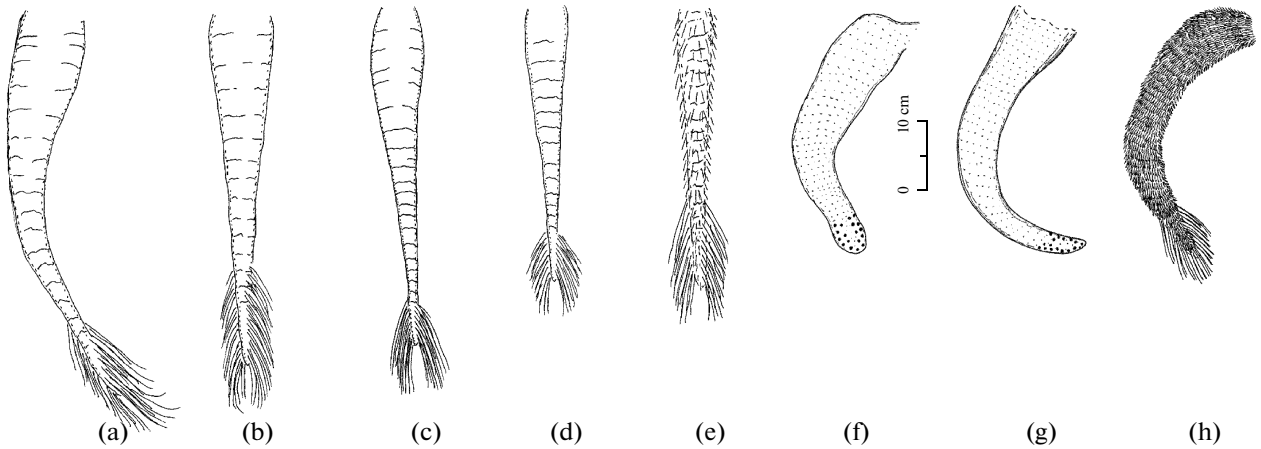

Fig. 8. Tails of the following rhinoceroses: (a) white (*Ceratotherium simum* Burchell 1817); (b) black (*Diceros bicornis* L. 1758); (c) Indian (*Rhinoceros unicornis* L. 1758); (d) Javan (*R. sondaicus* Desmarest 1822); (e) Sumatran (*Dicerorhinus sumatrensis* Fischer 1814); and (f)–(h) wooly (*Coelodonta antiquitatis* Blum. 1799), including (f) adult individual (no. MM 7938), (g) young individual (no. MM 7941), and (h) reconstruction.

patch is of an irregular shape (Fig. 5a) with a maximal length of 70 cm and a width of 51 cm. According to the fold shapes, this is part of the skin from the back and side surface of the trunk. The skin thickness varies from 5 to 12 mm. Short light brown hairs are preserved in skin folds.

The second piece of skin is larger (Fig. 5b): its maximal length is 101 cm and its width is 82 cm. This piece has an irregular shape and numerous breaks and incisions. This is a skin fragment from the ventral trunk part, covering the lower part of the thorax, abdomen, and groin. Two nipples are present on the udder in the inguinal part (Fig. 5c), which are similar to those of the Kolyma rhinoceros (about 20 mm) but wider: the maximal width of the right nipple is 35 mm, and that of the left one is 33 mm. The inner sides of the nipple bases are located at a distance of 44 mm from one another. Presumably, these remains belonged to an adult lactating female. The skin thickness of this skin fragment varies from 6 to 12 mm.

CONCLUSIONS

The find of the Kolyma rhinoceros and carcass remains of other rhinoceroses near the Malaya Filippova River together with the data of previous researchers has allowed for clarification of additional specific morphological and ecological features of the woolly rhinoceros, as well as for detection of new ones.

It has been demonstrated that the udder of the woolly rhinoceros had two nipples; correspondingly, it is likely that they bore one or, rarely, two calves. Note that by analogy with the extant rhinoceros (Walker et al., 1964), this could take place once every 2–3 years. This suggests that the woolly rhinoceros had a slow rate of reproduction.

So far, the remains of carcasses (or their large parts) of only female woolly rhinoceros have been found. Correspondingly, we have succeeded only in determining more precisely the body dimensions of only the female *C. antiquitatis*. It was a very large animal, the second in size after the mammoth among the North Eurasian mammoth fauna. In the general body parameters (body length, 320–360 cm; shoulder height, 145–160 cm; and body weight, approximately 1500 kg), the woolly rhinoceros is comparable to the female of the extant rhinoceros species. The largest of them are the African white rhinoceros (*Ceratotherium simum* Burchell 1817), with a body length of up to 270 cm, shoulder height of 185 cm, and body weight of 1700 kg, and the Indian rhinoceros (*Rhinoceros unicornis* L. 1758), with a body length of up to 340 cm, shoulder height of 170 cm, and body weight of 1600 kg. The females of the African black rhinoceros (*Diceros bicornis* L. 1758) have a long body (to 300 cm) but are lower in height (shoulder weight, to 150 cm) and weight (to 1000–1200 kg). The Javan rhinoceros (*Rhinoceros sondaicus* Desmarest 1822) with its rather long body (to 300 m) is rather tall (to 170 cm) and heavy (to 1500 kg). The smallest of the extant rhinoceros is the Sumatran rhinoceros (*Dicerorhinus sumatrensis* Fischer 1814), with a body length of up to 317 cm, shoulder height of up to 137 cm, and body weight of up to 1000 kg (Walker et al., 1964; Zukowsky, 1965; Groves, Kurt, 1972; Groves, 1982; Laurie et al., 1984). It was noted earlier, presumably based on the information from popular science literature, that *C. antiquitatis* in its proportions (a long trunk with short legs) almost does not differ from the herbivorous steppe *C. simum* rhinoceros (Garutt et al., 1970). However, according to particular morphometric data (Groves, personal communication), the body length of the white rhinoceros is the smallest of all the extant rhinoceros. It can be preliminary noted that the woolly rhinoceros in the body dimensions and proportions is rather similar to the Javan rhinoceros.

Fig. 9. Nipples of the udder of the Kolyma woolly rhinoceros (one scale, 1 cm).

The drawings of Paleolithic man show the woolly rhinoceros with relatively short narrow lancet-shaped or sharp ears (Fig. 10). The data on preserved mummified *C. antiquitatis* ears confirm this observation. Although the ears of the Khalabui (Fig. 1b), Starunia (Figs. 1c, 1d), and Kolyma (Fig. 7) rhinoceroses are to a certain degree deformed, it is nonetheless evident that they differ from the ears of the extant rhinoceros in the narrower shape (Fig. 11). According to the available data, the ear length of the woolly rhinoceros is 18.5–24 cm (table). The ear length of the woolly rhinoceros mummy found near the Khalabui River in 1877 is 14.1 cm. The ears of the modern black, Indian, Javan, and Sumatran rhinoceroses have, on average, similar lengths of 18–22 cm (Walker et al., 1964; Zukowsky, 1965), and only the white rhinoceros has longer ears, reaching 25–26 cm (Heller, 1913); however, the ears are considerably wider in most species. It is evident that the auricle area on the extant rhinoceros is considerably larger as compared with the woolly rhinoceros (Fig. 11).

The tail of the woolly rhinoceros was rather short, about 50 cm (table). The tail of the modern white, black, and Indian rhinoceroses reaches 75–85 cm (Heller, 1913; Walker et al., 1964; Zukowsky, 1965).

The shortened (or decreased in area) protruding body parts (ears and tail) of the woolly rhinoceros as compared with the extant tropical species is likely to reflect Allen's ecological rule, general for all mammals, and is an adaptation to cold climate of the North Eurasian Ice Age. An analogous shortening in tail length and reduction in ear size as compared with the extant elephants was also noticed in the mammoth *Mammuthus primigenius* Blum. 1799 (Garutt, 1964; Vereshchagin and Tikhonov, 1990; *Yukagirskii mamont* ..., 2007).

Presumably, the woolly rhinoceros used its long (to 1.3 m) and flattened front horns to dig snow during winter pasturing as well as a good weapon for self-defense and contests during rutting season.

Palynological analysis of the Kolyma rhinoceros stomach remains confirmed the data of previous researchers (Garutt et al., 1970; Lazarev and Tirskaya, 1975) that cereals and wormwoods were the major components of the diet of *C. antiquitatis* inhabiting East and Northeast Siberia, that is, that this species was mainly herbivorous. This specialization is also suggested by the elongated head shape of this rhinoceros, the low set of the head, and the short and wide upper lip, which is also characteristic of the white rhinoceros, feeding on grasses.

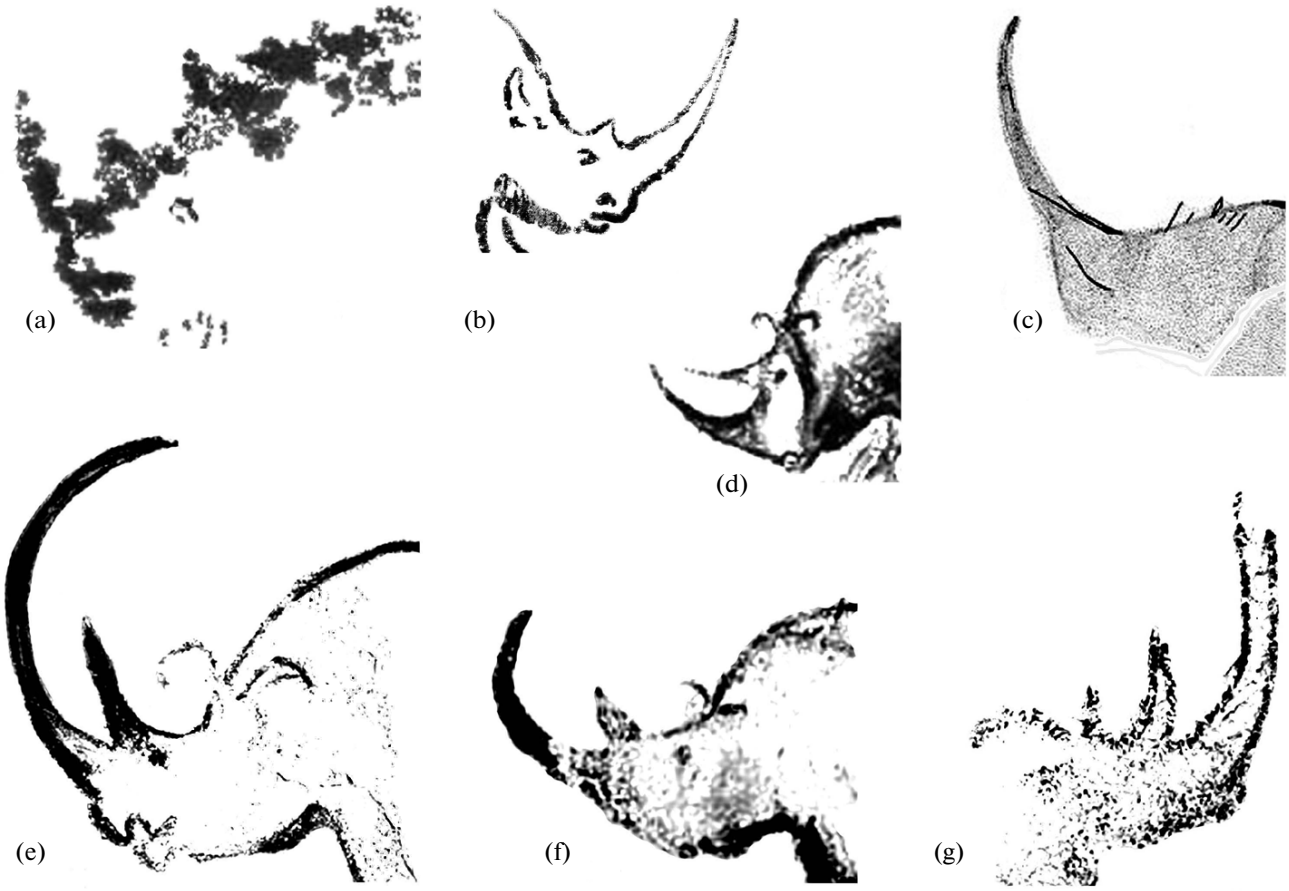

Fig. 10. Paleolithic images of the woolly rhinoceros: (a) Lascaux Cave, Dordogne, Aquitaine, France (Leroi-Gourhan, 1984); (b) Rouffignac Cave, Dordogne, Aquitaine, France (according to photo by the author); (c) Margot Cave, Mayenne, Pays de la Loire, France (Pigeaud et al., 2006); (d)–(f) Chauvet Cave, Ardèche, Rhône-Alps, France (Chauvet et al., 1995); (g) Coliboaia Cave, Judet Bihor, Northwestern Region, Romania (Besesek et al., 2010).

The specific landscape and climate features of the Pleistocene were rather adverse conditions, namely, a sharply continental, mostly arid, climate; winters with little snow; solid soil surface; and predominance of open landscapes with grass and shrub vegetation. The mammoth and other animals of the mammoth fauna, including the woolly rhinoceros, were adapted to such conditions (Velichko, 1973; Vereshchagin, 1979; Sher, 1997; Velichko and Zelikson, 2001). According to indirect data—the wide abundance of the saiga, encountering difficulties when moving in a snow layer thicker than 20 cm, and the musk ox, for which a snow layer deeper than 30 cm is a hindrance in moving and feeding, over East Siberia in the late Pleistocene—it was assumed that the snow height at that time was low, less than 20–30 cm (Sher, 1971; Kuz'mina, 1977).

The woolly rhinoceros was well adapted to the cold and dry climate of the late Pleistocene, since it had a thick and long coat and very thick skin. On the other hand, it had a considerable body weight combined with short legs and a relatively small bearing surface area. The load per bearing surface area for this rhinoceros was three- to fourfold larger as compared with the moose and almost 1.5-fold larger as compared with the bison. As has been demonstrated for the extant ungulate mammals, their movements (and, correspondingly, grazing from under snow) are considerably hindered when the snow layer is higher than the carpal and hock joints; when the snow layer reaches their abdomen and thorax, these animals become almost helpless (Formozov, 1946; Nasimovich, 1955). Therefore, even a relatively thin snow layer (35–40 cm) and the presence of snow crust were doubtless limiting factors for *C. antiquitatis*.

It is quite likely that the nival factor played an important role in extinction of the woolly rhinoceros, as Formozov (1946) stated. In the late Pleistocene–early Holocene, climate warming and moistening led to an increase in the snow height in winter, which is likely the reason that caused the extinction of this species. In addition, the natural traps formed by the thermokarst processes of that time (cavities after melting of ice veins, deep thermal erosion washouts, boggy banks of thermokarst lakes and streams, and so on)

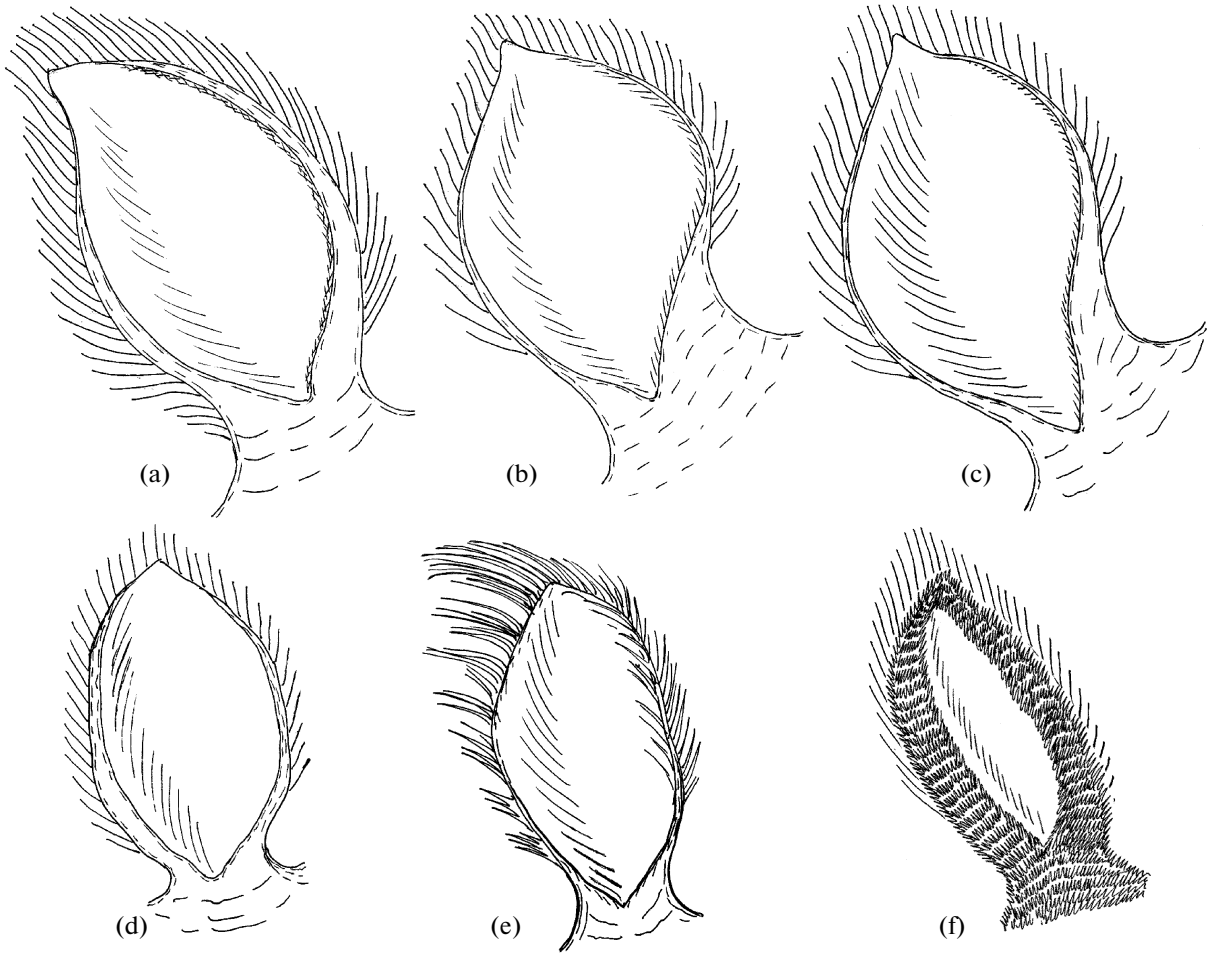

Fig. 11. Ears of the following rhinoceroses: (a) white (*Ceratotherium simum*); (b) black (*Diceros bicornis*); (c) Indian (*Rhinoceros unicornis*); (d) Javan (*R. sondaicus*); (e) Sumatran (*Dicerorhinus sumatrensis*); and (f) woolly (*Coelodonta antiquitatis*), reconstruction.

presented certain danger for such a short-legged and heavy animal (Boeskorov et al., 2009). Presumably, the rhinoceros from the Malaya Filippova River slumped, bogged down, and drowned in such a trap. The carcass position as it was found suggests this situation: it was located in icy yedoma deposits on its left side with its head stretched up (Fig. 6). Presumably, the left side of the animal body was held by thixotropic liquid and viscous soils of melted yedoma deposits and, suffocating, the rhinoceros lifted up its head above the level of its muddy trap. Some carcasses of dead animals of the mammoth fauna displayed similar postures, for example, the Selerikan horse (Vereshchagin, 1977) and Yukagir mammoth (*Yukagirskii mamont ...,* 2007).

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