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Horns of the woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) in the Ice Age Museum collection (Moscow, Russia)

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ABSTRACT

The Ice Age Museum (Moscow, Russia) houses the most representative collection of woolly rhinoceros horns in the world. It consists in about 30 complete and fragmentary specimens from the Late Pleistocene deposits of Northern Yakutia and Chukotka. This collection includes five complete sets of nasal and frontal horns of the same individual (two sets with their own proper skull); series of horns of different individual age: from juvenile to old; horns of specific structure; a series of horns of a different stage of preservation from a relatively good one to a rather poor one, displaying various stages of organic matter decay. The most interesting specimens from this collection are described in brief. The horn collection of Ice Age Museum has important significance for the understanding of the woolly rhinoceros adaptive biology and ecology in the Ice Age period.

1. Introduction

The horns of the woolly rhinoceros *Coelodonta antiquitatis* are very specific paleontological material, and their significance has been underestimated until now. It is even more significant that the subject specimens came from permafrost localities which provide the best preservation of keratin and other soft tissues. Beyond the permafrost area, only an anterior part of a mummified carcass, including the head and both horns, was found in an ozocerite deposit near the village of Starunia, Ukraine (Bayger et al., 1914).

Woolly rhinoceros horns were described for the first time by Pallas (1769), who based his research on Siberian specimens. Pallas also introduced the term 'filament' in order to denote structural units forming a horn. Some further finds of flat woolly rhinoceros horns were described by Schubert (1823) as claws of an enormous extinct bird, *Gryphus antiquitatis*. Schubert's interpretation was disproved by Fischer von Waldheim (1836) who correctly interpreted the "claws" as horn of a wooly rhinoceros.

Later, the results of studying the rhinoceros horn collection from the Zoological Institute (St. Petersburg, Russia) were published by Brandt (1849). The collection consisted of both rounded in cross-section and flattened rhino horn. Brandt concluded that rounded specimens retained the original shape of the woolly rhinoceros horns, and flat horns indicate posthumous changes. Later, Nina Garutt (Chernova et al., 1998; Garutt, 2001) has found the reason for this misunderstanding. Nonetheless, some scientists of the 19th century insisted on a natural flatness of woolly rhinoceros nasal horns (Eichwald, 1835; Schrenk, 1880). The shape of horns of woolly rhinoceroses was discussed in a number of later publications (Fortelius, 1983; Chernova et al., 1998; Garutt, 2001).

Only in the last quarter of the 20th century were new studies of woolly rhinoceros horns performed. Fortelius (1983) carefully examined the morphology of nasal horn from the Museum of Palaeontology at the University of Helsinki (Finland). He reproduced the original figures of Brandt (1849) and discussed the distinctions between the nasal and frontal horns. He drew some conclusions on the significance of the shape and growth of the nasal horn. He supported Eichwald's and Schrenk's opinion on the primary flatness of the nasal horn and on its significance for surviving in ice age conditions as a tool for brushing away snow to uncover the forage. Following Eichwald (1835), Fortelius (1983) interpreted the transverse layers of horns as annual increments and suggested a more clearly defined sexual dimorphism for woolly rhinoceros rather than any recent species. Garutt (1995, 2001) studied the morphology and the size range of horns. She found criteria for a clear distinction between juvenile nasal and frontal horns, and interpreted the distinct expression of transverse periodic banding pattern as a result of seasonal fluctuations in horn growth. She assigned the nasal horn morphology to environmental adaptations.

A research of recent and woolly rhinoceros horns and comparative analysis of architectonics of diverse keratin derivatives of the

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epidermis, such as hair of *C. antiquitatis*, hair and horns of black rhinoceros (*Diceros bicornis*), horny hooves of *Equus caballus*, and baleen filtration plates (whalebone) of gray whale (*Eschrichrius gibbosus*), revealed a striking similarity in structure and size of baleen plates and rhinoceros horn filaments (Ryder, 1962; Lynch et al., 1973; Chernova et al., 1998). The researchers concluded that among all mammals, only whales and rhinoceroses developed massive entirely keratinous organs which are both morphologically convergent and functionally similar.

Until the end of the 20th century, finds of woolly rhinoceros horns were considered to be rare. The largest collection of nine horns was in the Zoological Institute of the Russian Academy of Sciences (St. Petersburg); only a few specimens were held in other countries. At the beginning of this century, the number of horns started to increase in museums due to the development of the paleontology business. By 1998, Russian museums housed about 40 complete and fragmentary horns, mostly nasal ones (Chernova et al., 1998). Now, apart from the Zoological Institute, woolly rhinoceros horns are kept in the Museum of Anthropology and Ethnography (early – Kunstkamera) of the Russian Academy of Sciences (St. Petersburg); the Zoological Institute of the Moscow State University; the Mammoth Museum of the Academy of Sciences of the Sakha (Yakutia) Republic; regional museums of Egvekinot, Ul'yanovsk, Verkhoyansk, Irkutsk, and Yakutsk; the State Natural Reserve "Wrangel Island" (Russia); in Roger Norman's private collection in Reno, Nevada (a pair of horns from Anyuy River, Chukotka, Russia); and in China.

Today, the Ice Age Museum in Moscow possesses the most representative collection of woolly rhinoceros horns in the world. This collection has been formed by Fedor Shidlovskiy since 1995. The first horn was found that year in the Chondon River valley, Laptev Sea basin. Today, the Ice Age Museum collection contains about 30 complete and fragmentary individual specimens including five complete sets of nasal and frontal horns of the same individual (two sets being preserved with their own skull), a juvenile nasal horn, and over 20 horns of varying preservation, size, morphology, and other features.

2. Material and its characteristics

All specimens of woolly rhinoceros horns housed in the Ice Age Museum were collected from Late Pleistocene loose ice deposits (edoma) of two regions of the Russian extreme northeast: northern Yakutia (Terekhtyakh, Malaya Kuropatoch'ya, Alazeya, Kon'kovaya, and Bol'shaya Chukoch'ya river basins) and western Chukotka (Anyuy and Panteleikha rivers) (Fig. 1). A number have been found in situ in the bone horizon of the "Drevniy" gold mine on the Panteleikha River (lower Kolyma River, near Cherskiy settlement), and units in the Terekhtyakh and Alazeya river valleys. The restriction of finds to these localities is mostly due to easy acquisition from localities near settlements rather than to any peculiar pattern of distribution of horns within permafrost caps. Some specimens of extremely good preservation even conserve a smell of 'fresh' organic matter.

The studied specimens include

(1) Five complete sets of nasal and frontal horns belonging to the same individual (Fig. 2, 1–5): F-370 and F-371; F-372 and F-373; F-385 and F-389 from the Terekhtyakh River; F-507 and F-508 from the Malaya Kuropatoch'ya River, F-2528 and F-2529 from the right bank of the Bol'shaya Chukoch'ya River.

The F-370 and F-371 pair is unique in its excellent preservation. The base of the nasal horn retains well-preserved filament caps bearing uneven, longitudinal jet-similar microrelief. This

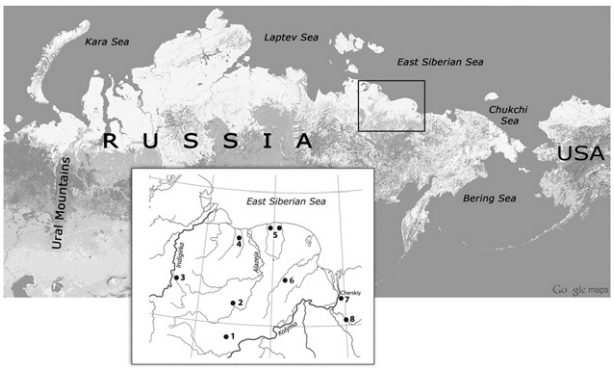

Fig. 1. Principal localities of the woolly rhinoceros horns housed in the Ice Age Museum, 1–6 –Yakutia, 1 – Middle Kolyma river basin, left bank, 2 – Alazeya river basin, 3 – Terekhtyakh river site, 4 – Malaya Kuropatoch'ya river valley, 5 – Malaya and Bol'shaya Kon'kovaya rivers, 6 – Bol'shaya Chukoch'ya river basin, right bank, 7–8 –Western Chukotka, 7 – Panteleikha river valley near Cherskiy Village, "Drevniy" gold mine, 8 – Maliy Anyuy river valley.

microrelief might serve to better interlock the horn with the skull boss at its base.

The F-372 and F-373 pair is not well preserved. The nasal horn remain consists of a medial plate only, but the horn displays a very rare shape resulting from abrasion of its working surface during life. The horn plate is narrower in its middle part compared to the anterior.

The F-385 and F-389 pair shows a moderate state of preservation. The nasal horn of this pair is fairly straight without curvature, and its broader front is abraded for over half of its length.

The F-507 and F-508 pair is part of a set that also includes a skull (F-506) and mandible (F-509) of the same individual. The nasal horn is represented by a medial plate only, and the frontal one is more complete. All of the samples have undergone a strong natural maceration. The nasal horn surface is black which is typical of organic matter "charring" in a burial site. Some specimens in the wholly rhinoceros horn collection of the Ice Age Museum (F-29a, F-1990) have either partially or entirely undergone "charring" similar to F-556.

The F-2528 and F-2529 pair is well-preserved, and the nasal horn is one of the most massive ever found. The horns are affiliated with a skull.

(2) The frontal horn F-1861 from the Alazeya River valley is in an average state of preservation. Its apex is slightly inclined rearward; the horn height is much greater than its base diameter. There is a malformation at the base of the horn (Fig. 3).
(3) The skull F-394 bisected in the midsagittal plane (Fig. 4). This demonstrates a morphological adaptation the woolly rhinoceros developed during evolution to climate change in the direction of cooling and dryness.

3. Interpretation

Complete sets of nasal and frontal horns (associations) belonging to the same individual of a woolly rhinoceros are very rare finds. Until recently, only a few such sets were discovered, among them, finds from the village of Starunia, Ukraine (Bayger et al., 1914), and the village of Churapcha and the Vilyuy River terrace, Yakutia (Belolyubskiy et al., 2008).

The five above named sets are important for an understanding of shape and size ratio of these organs in a woolly rhinoceros

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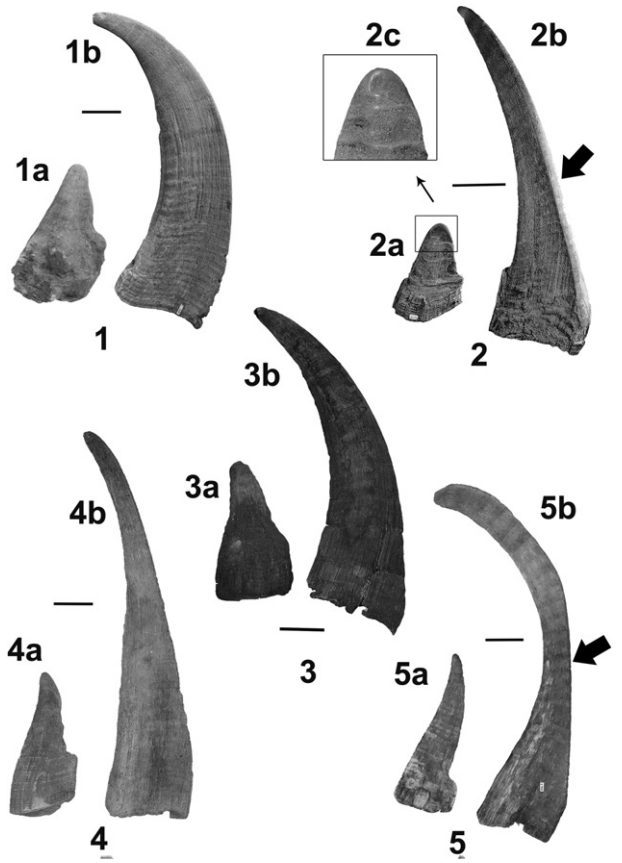

Fig. 2. Horn pairs of the same individuals of woolly rhinoceros, lateral view. Scale – 10 cm, 1 – anterior F-2528 and posterior F-2529 horns from right bank of the Chukochya river. Most massive pair with association of skull, 2 – anterior F-370 (2b) and posterior F-371 (2a) horns from Terekhtekh River. Best-preserved pair, 3 – anterior F-507 and posterior F-508 horns from Malaya Kuropatochya river. Unique association of skull, mandible and both horns. Specific preservation of horns: charred connected with natural posthumous processes, 4 – anterior F-389 and posterior F-385 horns from Terekhtekh River. Very rare straight and elongated shape of the nasal horn, 5 – anterior F-372 and posterior F-373 horns from Terekhtekh River. Unique live wearing of the nasal horn front (working) surface.

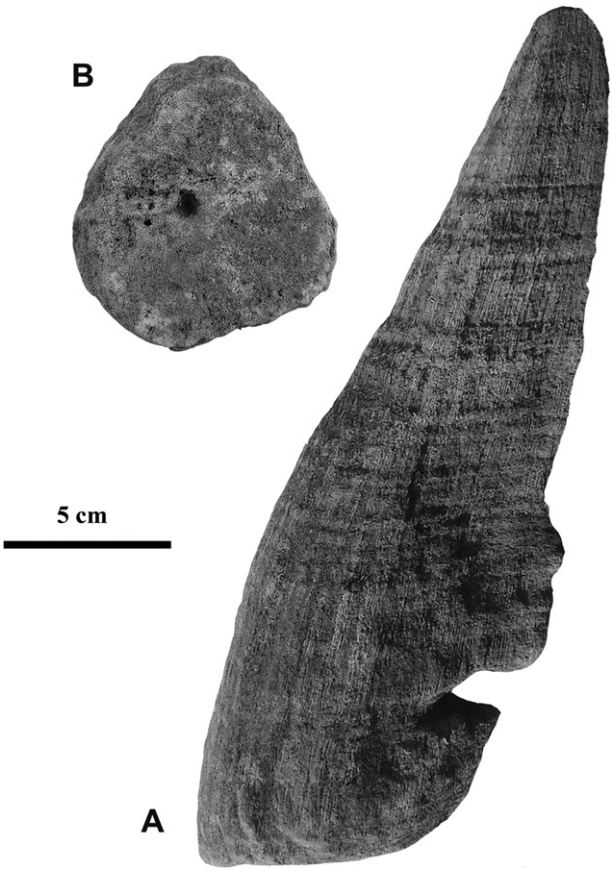

Fig. 3. Live malformation on woolly rhinoceros frontal horn F-1861 from the Alazeya River valley. There is a malformation at the base and on the posterior surface of the horn.

(Table 1). The presence of complete skulls belonging to the same individuals is especially significant (F-507 and F –508, and F-2528 and F –2529, respectively). The maximum anterior and posterior horns lengths ratio (measured by the front surface) is indicated for the pair F-370 and F-371 in Table 1. These horns are the best preserved. The minimum ratio was recorded for a pair of horns in a very poor state of preservation, F-507 and F-508. In the modern black African rhinoceros, *D. bicornis*, nasal and frontal horns may be the same height. However, the white rhino nasal horn is usually much more prominent than the frontal one. The relatives heights for the anterior and posterior horn associations of the woolly rhinoceros are similar to the African white rhinoceros, *Ceratotherium simum*. This is an additional indication of their significant similarities, as manifest in the proportions and sizes of the body, structure of the lips and food preferences.

There is no general agreement on the use of frontal horn by a woolly rhinoceros. One opinion is that the horn may serve as a nominal intraspecific status symbol by increasing the visual size of the body. Here, apices of both nasal (F-370) and frontal (F-371) horns show explicit wear during life (Fig. 2a–c).

The F-370 specimen justifies Eichwald (1835) suggestion of the flatness of the woolly rhinoceros nasal horn. The presence of two facets of erasure on the front surface of the nasal horn (Fig. 2b) confirms its use for grazing. Wear on the apical part of the frontal horns shows lifetime polish (Fig. 2c). This is very likely the result of tournament battles with the enemy. Possible evidence is found in late Paleolithic cave paintings picturing the battle of two woolly rhinoceroses in the Chauvet Cave (France). The figure shows the nasal horn blow of the right rhinoceros blocked by the frontal horn of its rival.

The malformation on the F-1861 frontal horn (Fig. 3) probably resulted from trauma or other damage. It could be the result of an abscess in soft tissues. All these features may be indicative of horn-clashing between individual woolly rhinoceroses. Cases of abnormal horn growth are known in the modern rhino. Their appearance is associated with trauma, illness, and long maintenance in captivity (Nandi and Kumar Deb, 1972; Groves and Fernando, 2010). Thus, the F-371 specimen hints that a frontal horn had a practical significance for blocking an opponent's stabs. If the suggestion on the use of horns for horn-clashing is correct, the nasal horn, being relatively thin and flat, needed to be very strong. Indeed, on the working (front) surface of the nasal horn, a curvature of laminas is noted which is also displayed by specimens F-559, -2451, and –2568. Such a structure of the laminas creates an additional resistance to abrasion of the working surface of a horn and is an adaptive feature.

In the museum collection, the frontal bones of woolly rhinoceros' skulls lack damage incurred while alive, but the skulls F-36, -379, and –2569 apparently reveal nasal bones having such malformations (Fig. 2b, c). Other skulls of woolly rhinoceroses with pathologies of nasal bones are known from the Altay, the low and

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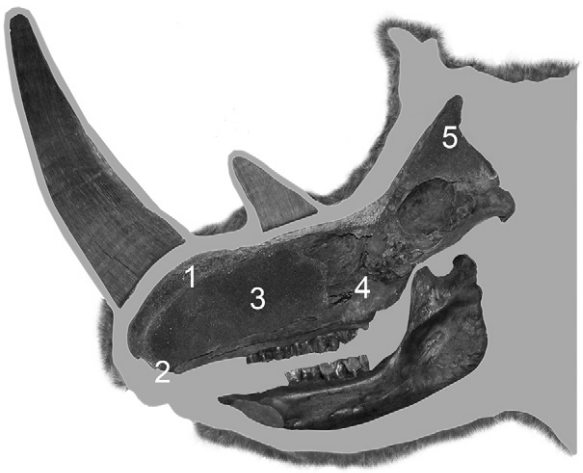

Fig. 4. Sagittal section of skull F-394 from Terekhtekh River in Ice Age Museum exposition. Numbers denote the key anatomical features of woolly rhinoceros skull: (1) nasal bone thickness, (2) nasal and maxillar bone junction, (3) total nasal septum (damaged), (4) extremely long facial part of skull, (5) drawn back the occipital part of skull.

middle Volga River, and the Tomsk Region (Russia). The origins of such pathologies were interpreted as traumatic (Garutt, 1997). Skulls F-36, -379, and −2569, probably, preserve traces of a fistula which developed in each case during an extended period of time. Such a fistula could be caused by horn fracture in a fall or the result of horn-clashing between individuals. It could also be caused by an inflammation from the inculcation of gad-fly larva. However, even the choice of a place for settlement by a gad-fly seemed to be predicted by the weakness of this precise area, either due to common horn-clashing or, more probably, due to the adjacent abundant fleshy tissue (lips, nostrils).

The sagittal section of the skull F-394 clearly shows peculiarities of a structural feature related to the development of horns and their use during grazing (Fig. 2a). The occiput is robust and strongly declined rearwards. A significant height, width, and robustness of the occiput are indicative of strong muscles at the back of the neck connecting the skull and the vertebral column. This muscle system imparted great power to lateral head movements. Such active side-to-side strokes related to grazing are indicated by the F-372 nasal horn which displays a very rare shape resulting from a live abrasion of its working (front) surface. The horn plate is narrowed in its middle part from the anterior. Further use of the horn might cause it to be broken and lost. The nasal horn wear surfaces are always divided into a left and right facet indicating an alternating lateral movement of the head (Fortelius, 1983) especially if low vegetation was covered by snow or ice.

A woolly rhinoceros skull is very long. The enlargement of its frontal part reveals a lengthening of its upper respiratory tract. The mucous membrane warmed and moistened air allowing a better perception of smells in the dry and cold conditions of the ice age. A noticeable feature of the woolly rhinoceros, distinguishing it from other horned rhinoceroses, is manifested in a complete fusion of nasal bones with maxillary ones. A completely ossified nasal septum, at least among males, distinguishes the woolly rhinoceros from other recent and Pleistocene members of the subfamily Dicerorhininae possessing a nasal cartilage (Pallas, 1769; Belyaeva et al., 1962). In addition, both these structures as well as a considerable thickness of nasal bones, the retracted back of the skull bone occiput and provided supplementary mechanical strength for the base of the nasal horn which served as a main weapon during horn-clashing as well as a principal tool during grazing.

These features, clearly observable in the sagittal section, show adaptations to the environment of the Ice Age with its arid and cold climate. The specimen is available in the exhibition of the Ice Age Museum. These observations are in agreement with known anatomical features such as wide lips, body proportions (Brandt, 1849; Nowak et al., 1930) and with Kahlke and Lacombat's (2008) study which revealed a number of morphological evolutionary trends in Eurasian *Coelodonta*, namely, the general elongation and narrowing of the head; its lower and more inclined posture; the shift of orbits towards the rear of skull; changes in the position of the cheek tooth rows and; the thickening of enamel. This is indicative of a progressive adaptation to a very efficient grazing under increasingly cold climatic conditions.

Modern researchers following Eichwald (1835) have considered that the number of dark and light paired bands in woolly rhinoceros horns is either indicative of the individual age of the animal (Fortelius, 1983; Garutt, 1995) or shows its minimal age if the horn was damaged (Chernova et al., 1998). However, such growth increments may not have an annual periodicity, or may be periodic formations which do not display the number of years passed with precision. Moreover, even structures possessing an apparent annual increment, such as teeth dentine and cement, may form two layers during a year (Klevezal, 1988). The unique sets of two horns and skull of the same individuals clarifies the nature of the horn's periodic banding pattern by a comparison of the number of such dark and light paired bands with the number of annual laminas in the pad cement from an upper first molar (Kirillova and Shidlovskiy, 2010). The intensity of the dark color is probably due to differences in the rate of melanin deposition during the process of horn growth, which is shown for extant rhinoceroses (Hieronymus et al., 2006).

4. Results of the investigations and the significance of the ice age woolly rhino horn collection in the Ice Age Museum

The collection of woolly rhinoceros horns housed in the Ice Age Museum has yielded information on one of the most typical representatives of the mammoth fauna. This collection helped to confirm some earlier concepts and scientific hypotheses on the external appearance and biology of the species, and provided new morphological evidence.

Table 1
Measurements of the length of the front surface of the nasal and frontal horns of the woolly rhinoceros in the associations from one individual (characteristic N 2 according to Fortelius, 1983), cm.

Pair 1		Pair 2		Pair 3		Pair 4		Pair 5	
F-370 nasal	F-371 frontal	F-372 nasal	F-373 frontal	F-507 nasal	F-508 frontal	F-389 nasal	F-385 frontal	F-2528 nasal	F-2529 frontal
117.5	28.5	125.0	37.0	99.0	35.0	118.0	44.0	114.0	35.5
4.12		3.38		2.83		2.68		3.21	

Note: The bottom line gives the ratio of the anterior and posterior horns lengths for each pair.

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Thus, the nasal horn is flattened as indicated by a few complete horns from the museum collection. This observation is in agreement with the previous studies of the best preserved horns from mummified Starunia and Churapcha rhinoceroses.

The collection includes a series of specimens showing step by step the natural posthumous processes as well as series illustrating age-related changes and morphological variations. Ontogenetic series illustrating the growth of the nasal horn of a woolly rhino is also represented in the collection.

The new data on the horns and other features of the woolly rhinoceros were established by our intensive study of the Ice Age Museum Collection. Research on the association of the skull and the two horns of one specimen (F-2527, F-2528, F-2529), from the Chukochya River indicated compliance between each pair of transverse bands of annual horn growth, as assumed previously. The rhino horn is a recording structure, as well as the dentine of the tooth (Kirillova and Shidlovskiy, 2010). The first conducted radioisotope analysis of nasal horns (F-10) confirmed the formation of the seasons of light and dark bands of the annual increment, which is due to differences in the availability of food during cold and warm seasons (Tiunov and Kirillova, 2010).

Identified visual heterogeneity of the structure of central and peripheral parts of the nasal horn was confirmed by the study of its microstructure. New data were obtained in the study of macro- and microstructure of the specimen F-23. A specific structure and the connection between filaments and matrix of woolly rhinoceros horns impact strength to horns and their resistance to mechanical wear. The heterogeneous structure of the horns was identified in the horizontal section at different topographical sites. The central part of the horns is more compact and more resistant to fracture compared with the periphery, and its filaments are larger and more strongly united. This complex system ensuring the safety and functionality of the horns is an adaptive feature of the species (Chernova and Kirillova, 2010).

Five specimens, namely, two nasal (F-20 and F-27) and three frontal horns (F-55, F-56, and F-555) are listed in the State Catalogue of the Museum Foundation of the Russian Federation. The Ice Age Museum specimens are important for a more complete reconstitution of the appearance of woolly rhinoceros. Its origin and the adaptation of this rhino species to conditions of the Arctic. Materials in the collection show the general appearance of the sculls of the woolly rhinoceros, the adaptations of the animal for severe horn-clashing, and for grazing in snow-covered environments. An important contribution of the Ice Age Museum's specimens is the possibility to check various suggestions on the significance of dark and light hair bands formed during the horn growth of the woolly rhinoceros. Finally, the horn with *in vivo* obliteration of the front part (the working surface) and sagittal section of skulls exhibited in the Museum allow visitors to better understand the adaptive features of the woolly rhinoceros to the cold and dry conditions of glacial age.

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References

Bayger, J.A., Hoyer, H., Kiernik, E., Kukczyński, W., Łomnicki, M., Mierzejewski, W., Niezabitowski, E., Raciborski, M., Szafer, W., Schille, F., 1914. Wykopaliska staruńskie. Słon mamut (*Elephas primigenius Blum.*). Nosorożec włochaty (*Rhinoceros antiquitatis Blum.* s. tichorhinus Fisch.). Wraz z współczesna flora i fauna. Nakladem Museum imienia Dzieduszyckich, Kraków.

Belolyubskiy, I.N., Boeskorov, G.G., Sergeenko, A.I., Tomshin, M.D., 2008. Catalogue of the Collection of the Quarternary Mammals of the Geological Museum of the Institute of Geology of Diamonds and Precious Metals SO RAN. YSC Publishing House SB RAS, Yakutsk (in Russian).

Belyaeva, E.I., Gromova, V.I., Yanovskaya, N.M., 1962. Order Perissodactyla. Perissodactyls. In: Gromova, V.N. (Ed.), Osnovy paleontologii 13: Mlekopitayuschie. Publishing House of the Academy of Sciences of the USSR, Moscow, pp. 286–336 (in Russian).

Brandt, J.F., 1849. Die *Rhinocerotis antiquitatis*, seu *tichorhini*, seu Pallasii structura externa er osteologica observationes, e reliquiis, quae in museis Petropolitanis servantur erutae. Mémoires de l'Académie Impériale des Sciences de Saint-Péterbourg, Sciences naturalles 5, 161–416 (pl. I–XXV).

Chernova, O.F., Kirillova, I.V., 2010. New data on horn morphology of the woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1799). Proceedings of the Zoological Institute of the Russian Academy of Sciences 314 (3), 333–342 (in Russian).

Chernova, O.F., Sher, A.V., Garutt, N.V., 1998. Morfologiya rogov sherstistogo nosoroga (*Coelodonta antiquitatis*). Zoologicheskiy zhurnal 77 (1), 66–79 (in Russian).

Eichwald von, E., 1835. De pecorum et pachydermorum reliquiis fossilibus, in Lithuania, Volhynia et Podolia repertis. Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher 17 (2), 677–760.

Fischer von Waldheim, G., 1836. Sur le *Gryphus Antiquitatis* des naturalistes allemands. Recherches sur les ossemens de la Russie I. Mosqou, 1–19.

Fortelius, M., 1983. The morphology and paleobiological significance of the horns of *Coelodonta antiquitatis* (Mammalia: Rhinoceratidae). Journal of Vertebrate Paleontology 3 (2), 125–135.

Garutt, N., 1995. Novye dannye o stroenii roga sherstistogo nosoroga Coelodonta.

Garutt, N., 1997. Traumatic skull damages in the woolly rhinoceros, *Coelodonta antiquitatis* Blumenbach, 1799. Cranium 14 (1), 37–46.

Garutt, N.V., 2001. To the study of the woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799). In: Yu Rozanov, A. (Ed.), (Mammoth and it's Environment: 200 Years of Investigations). GEOS, Moscow, pp. 22–33 (in Russian).

Groves, C.P., Fernando, P., Robovský, J., 2010. The sixth rhino: a taxonomic reassessment of the critically endangered northern white rhinoceros. PLoS One 5 (4), 1–15. Article No.: e9703.

Hieronymus, T.L., Witmer, L.M., Ridgely, R.C., 2006. Structure of white rhinoceros (*Ceratotherium simum*) horn investigated by X-ray computed tomography and histology with implications for growth and external form. Journal of Morphology 267 (10), 1172–1176.

Kahlke, R.-D., Lacombat, F., 2008. The earliest immigration of woolly rhinoceros (*Coelodonta tologoijensis*, Rhinocerotidae, Mammalia) into Europe and its adaptive evolution in Palaearctic cold stage mammal faunas. Quaternary Science Reviews 27 (21–22), 1951–1961.

Kirillova, I.V., Shidlovskiy, F.K., 2010. Age estimation of individual age and season of death in woolly rhinoceros, *Coelodonta antiquitatis* (Blumenbach, 1799), from Sakha-Yakutia, Russia. Quaternary Science Reviews 29, 3106–3114.

Klevezal', G.A., 1988. Registriruyushchie struktury mlekopitayushchikh v zoologicheskikh issledovaniyakh. Nauka, Moscow (in Russian).

Lynch, L.J., Robinson, V., Anderson, C.A., 1973. A scanning electron microscope study of the morphology of rhinoceros horn. Australian Journal of Biological Sciences 26, 395–401.

Nandi, S.N., Kumar Deb, S., 1972. Horn cancer in rhinoceroses. Indian Veterinary Journal 49, 881–882.

Nowak, J., Panow, E., Tokarski, J., Szafer, W.ł., Stach, J., 1930. The second woolly rhinoceros (Coelodonta antiquitatis Blum.) from Starunia, Poland (geology, mineralogy, flora and fauna). Bulletin international de l'Académie polonaise des Sciences et des Lettres, Classes des Sciences mathématiques et naturalles 1–47, 10 (pls).

Pallas, P.S., 1769. De ossibus Sibiriae fossilibus craniis praesertium rhinocerontum atquebuffalorum, observationes. Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae 13, 436–477.

Ryder, M.L., 1962. Structure of rhinoceros horn. Nature 193 (4821), 1199–1201.

Schrenk von, L., 1880. Der erste Fund einer Leiche von *Rhinoceros Merckii* Jaeger. Mémoire de l'Académie Impériale des Sciences, Saint-Pétersbourg 27 (7), 1–55.

Schubert, von, G.H., 1823. Die Urwelt und die Fixsterne: eine Zugabe zu den Ansichten von der Nachtseite der Naturwissenschaft. Arnoldischen Buchhandlung, Dresden.

Tiunov, A.V., Kirillova, I.V., 2010. Stable isotope (13C/12C and 15N/14N) composition of the woolly rhinoceros *Coelodonta antiquitatis* horn suggests seasonal changes in the diet. Rapid Communication Mass Spectrometry 24, 3146–3150.

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