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RESEARCH ARTICLE

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A new discovery in the permafrost of Yakutia sheds light on the nasal horn morphology of the woolly rhinoceros

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Abstract

Extinct woolly rhinoceroses were iconic representatives of the Late Pleistocene mammoth fauna of Eurasia. These animals were characterized by two huge keratinous horns. In adults, the length of the nasal horn often exceeded one meter. The nasal horn of *Coelodonta* was characterized by an unusual feature for rhinoceroses—the width of its base was considerably narrower than the width of the rugosity area on the nasal bones of the skull. In this study, a new discovery of woolly rhinoceros' nasal horn in the permafrost of Yakutia is described. This specimen shows that the shape of the base of the woolly rhino's nasal horn corresponds well to the shape (length and width) of the nasal rugosity area. The base of the nasal horn of *Coelodonta* was markedly elongated anteroposteriorly compared to extant rhinoceroses. Its length was about 150% of the width. We therefore suggest that the narrower shape of the nasal horn base in the majority of previously found specimens was associated with secondary damage after burial caused by maceration.

KEYWORDS

Coelodonta antiquitatis, horns, Late Pleistocene, permafrost, Rhinocerotidae, Yakutia

1 | INTRODUCTION

Extant rhinoceroses are well known for their enormous size, prehistoric appearance, and horns. In African species, horns are actively used as the primary weapon during interspecies and intraspecies conflicts (Wilson & Mittermeier, 2011). Outgrowths on the head are not unique feature to ungulates. For example, cervids are characterized by bony antlers, which shed and regrow each year, giraffids by prominent ossicones covered with skin, pronghorn, and bovids by horns covered by keratin surrounding a core of bone (Wilson & Mittermeier, 2011). Contrary to other mammals, the horns of rhinoceroses lack a bony core and appear as an epidermal derivative, consisting of keratinized tubules (filaments) of cells dispersed in a keratin matrix (Hieronymus et al., 2006; Ryder, 1962). Rhinoceros horns do not fuse with skull bones. The horns are attached to the rugosity areas of the nasal and frontal bones with a layer of connective tissue and ligaments covering the horn at the base (Chernova et al., 1998).

The cone-shaped horns are characteristic of all extant rhinoceroses (Supporting Information: Figure S1). The African Black (*Diceros bicornis*) and White rhinoceroses (*Ceratotherium simum*), as well as the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), are characterized by presence of a nasal horn and a frontal horn, while the Greater One-horned (*Rhinoceros unicornis*) and Javan rhinoceroses (*Rhinoceros sondaicus*) have only the nasal horn. Despite the presence of the horn in all modern-day rhinoceroses, its appearance in the evolutionary history of the family Rhinocerotidae dates to the early Oligocene (with *Diceratherium armatum*; Antoine, 2002) or early Miocene (with *Gaindatherium*; Hieronimus, 2009). Due to the unique conditions of the Yakutia permafrost, zoologists were able to study the horn's morphology of another rhinoceros species, the extinct woolly rhinoceros (*Coelodonta antiquitatis*). *Coelodonta* horns are large (Supporting Information: Figure S1), so by the mature age (25–35 years) their nasal horn often exceeds 1 m in length (Boeskorov et al., 2011).

The growth of the rhinoceros keratinous horn occurs at its base. The tubules grow from a generative layer of epidermis covering a dermal papilla, while the amorphous matrix grows from the epidermis between dermal papillae. The smallest structure of horn is presented by a horn lamina (layer ~1–2 mm thick). By the time the process of keratinization is completed, the epithelial cells of the horn are dead, so the living part of the horn corresponds to its growth zone (Hieronymus et al., 2006). Since the horn grows at a fairly constant rate over the entire area of the growth zone, its shape in the base part quite accurately repeats the growth zone in shape and size (Figure 1a,b). However, the distal (formed earlier) part is represented by a more cone-shaped form. This change in form is associated with horn wear and keratin degradation. As it was shown in a study of White rhinoceros' horn (Hieronymus et al., 2006), the core part of the horn is strengthened due to melanization and calcification. As a result, the wear and exposure to UV radiation of the core part of the horn is considerably reduced compared to the periphery.

All the above is in good agreement with the shape of the frontal horn of the woolly rhinoceros. The shape of frontal horn corresponds well to the shape of its growth zone which appears on the skull in the form of rugosity area (Figure 1c). However, the nasal horn of the *C. antiquitatis* is laterally flattened at its base, and its width is significantly less than the width of the rugosity area on the nasal bones (Figure 1c). The flattened shape of the nasal horn was interpreted by Brandt (1849) as secondarily damaged, while other authors considered it consistent with the intravital form (see Fortelius, 1983). In this study, we investigate a new discovery of a woolly rhinoceros' skull with associated frontal and nasal horns from the permafrost of Yakutia that provides new insight on the shape of its nasal horn.

2 | MATERIALS AND METHODS

We describe the features of the nasal horn and the skull of a woolly rhinoceros found in association by Roman Romanov, a local resident of the Srednekolymsky District, Yakutia, in the Upper Pleistocene sediments at the Suruktakh site in the Kolyma River basin in the summer of 2022. The discovery was made under official license from the Ministry of Industry and Geology of the Republic of Sakha (Yakutia), which authorizes the collection of mammoth tusks and other mammoth fauna remains in this certain area. In the late winter of 2022 Romanov officially donated a skull of this rhinoceros to the Mammoth Museum. That was an adult individual, as evidenced by a fully ossified nasal septum (Supporting Information: Figure S2). The dentition is not available on this specimen; however, alveoli of upper permanent premolars are preserved, indicating adult individual age. The nasal horn of this individual was broken intravitally close to the base, and then the spot where it was fractured was worn down (Figure 2 and Supporting Information: Figure S3).

Unlike most of the known nasal horns of *C. antiquitatis*, the horn of this individual had almost no maceration and loss of the peripheral tubules (filaments), and the base of the horn was well preserved

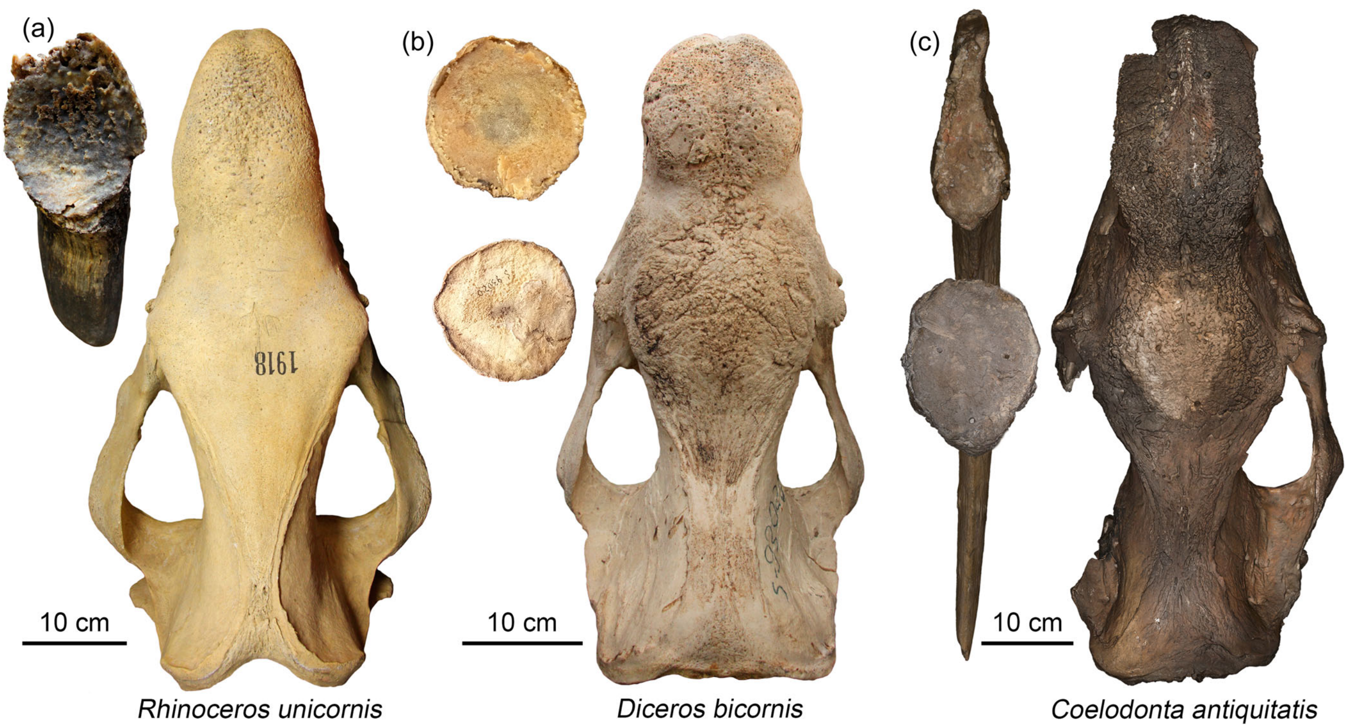

FIGURE 1 Shape of rugosity area and horn base in different rhinoceroses' species: (a) *Rhinoceros unicornis* (ZIN 1918); (b) *Diceros bicornis* (ZMMU S-93020); (c) *Coelodonta antiquitatis* (DPMGI 2114).

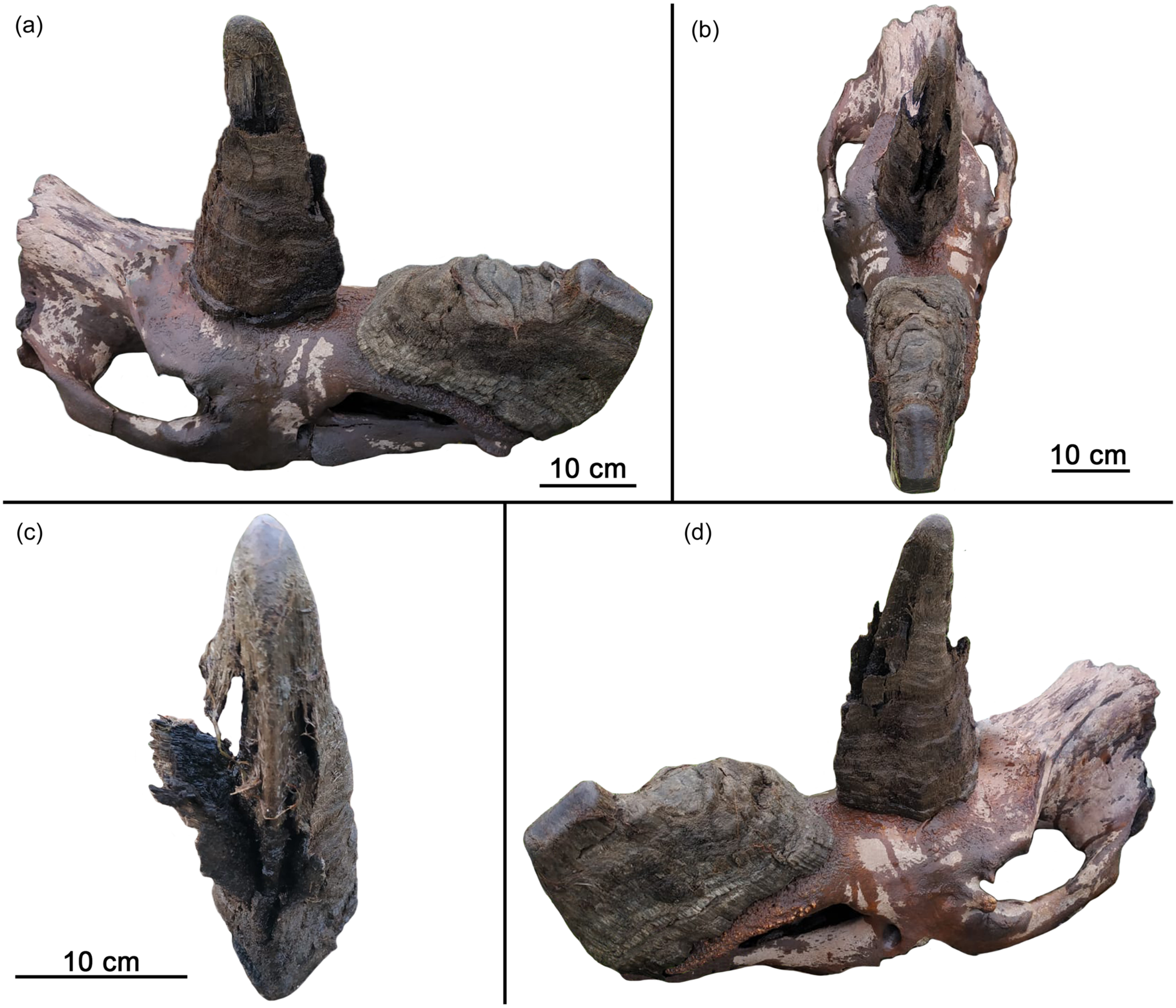

FIGURE 2 The new discovery of the skull with two horns of the Upper Pleistocene woolly rhinoceros (MM 3074) from the Suruktakh site. The skull with two horns is depicted in the right-side (a), dorsal (b), and left-side (d) views; frontal horn in anterior view (c).

(Figure 2a,b,d). The skull of this specimen was handed to the Mammoth Museum and was stored there under the number MM 3074. The horns of this specimen were lost during their transportation. Photographs of the rhinoceros' nasal horn and frontal horn were taken right after their discovery (Figure 2).

As comparative material, we examined the horns and skulls of woolly rhinoceroses belonging to the following individuals: DPMGI 2114 (Figure 1c and Supporting Information: Figure S1C), an adult female, skeleton found in the Churapcha village in 1972, described by Lazarev et al. (1998); MM 7938, an adult female, frozen mummy, found in 2007 in the vicinity of Chersky settlement locality, described by Boeskorov et al. (2011); VMN (no number) found in 1990s in the Sartang River basin.

Abbreviations: DPMGI, Diamond and Precious Metals Geology Institute, Siberian Branch of Russian Academy of Sciences, Yakutsk, Russia; MM, The P. A. Lazarev's Mammoth Museum, Yakutsk, Russia; VMN, Verkhoyansk Museum of Nature, Verkhoyansk, Russia; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; ZMMU, Zoological Museum of the Lomonosov Moscow State University, Moscow, Russia.

3 | RESULTS

In extant rhinoceroses, the shape of the base of the nasal horn varies from roughly circular (in *D. bicornis*, Figure 1b) to oval (in *R. unicornis*, Figure 1a), and quadrangular (in *C. simum*; Figure 3 in Groves, 1972; Figure 2 in Antoine & Rookmaaker, 2013). The shape of the nasal horn base corresponds closely to the shape of the rugosity area on the nasal bones (their length/width ratios differed by <10%; Table 1).

(a)

(b)

FIGURE 3 The longitudinal ridge on the nasal bones of the Upper Pleistocene woolly rhinoceros (DPMGI 993) from the Yana River. The skull is depicted in the rostral (a) and ventral views (b).

The shape of the rugosity area on the skulls of the woolly rhinoceroses is oval; its length exceeds its width by ~1.5 times (142%–180%; Table 1). This ratio is higher than the ratio of the individual of the Greater One-horned rhinoceros we studied. In contrast to extant rhinoceroses, the shape of the nasal horn base in the majority of studied woolly rhinoceroses differed considerably from the shape of the rugosity area (Table 1). The length/width ratio of the nasal horn base exceeds this Ratio of the rugosity area by more than 100% because of its narrower shape. The only exception is the new finding (MM 3074; Figure 2) from the Suruktakh site, in which these two ratios are almost identical (Table 1).

4 | DISCUSSION

The shape of the nasal horn of the woolly rhinoceros has been studied and debated since the XIX century. Thus, Brandt (1849) argued that the laterally flattened shape of the nasal horn of *C. antiquitatis* was the result of secondary damage, while the intravital shape of the horn was roughly circular or oval in cross-section at the base. These conclusions were supported by the images of nasal horns with roughly circular and quadrangular shape of the horn base (Brandt, 1849). However, as it was shown by Garutt (1998), the horns with roughly circular and quadrangular shape of their base were actually represented in Brandt's collection by extant African rhinoceroses (*D. bicornis* and *C. simum*). Other authors considered the laterally flattened shape of the nasal horn to be consistent with the intravital shape and indicate good correspondence between length of rugosity area on the nasal bones of the skull and the length of horn base as well as between the shape of longitudinal ridge on the nasal bone and groove at the horn base (Eichwald, 1835; Fortelius, 1983; Garutt, 1998). Past findings of *C. antiquitatis* horns together with the skulls show that the width of the rugosity area on the nasal bones of the skull is significantly higher than the width of the horn base (Table 1).

The horn (MM 3074) found in the permafrost of Yakutia in 2022 shows that the shape of the base of the woolly rhino's nasal horn corresponds well to the shape of the nasal rugosity area (Table 1). We should note that there is a possibility that this specimen might represent a unique pathology, while the intravital width of the nonpathological nasal horn at its base was indeed significantly narrower than the width of the rugosity area. However, we consider this to be rather unlikely, since it is in contradiction with the pattern of horn growth in rhinoceroses. As was described above, rhinoceros' horn is deposited dorsoventrally in successive sheets (horn laminae) with width ~1–2 mm (Hieronymus et al., 2006). The development of the rugosity area on the nasal and frontal bones in rhinoceroses is associated with irregular mineralization of the extrinsic fibers between the horn-dermis complex and bone surface (Hieronimus & Witmer, 2004). Thus, the shape of the most proximal (youngest) layers corresponds quite accurately to the shape of the growth zone of the horn.

Contrary to the modern-day African rhinoceroses characterized by the roughly circular and quadrangular shape of the horns base, *Coelodonta* nasal horn shape was oval (trapezoidal) and strongly elongated anteroposteriorly (Supporting Information: Figure S3). The elongation of the horn base of the woolly rhinoceros was more pronounced than that of the extant species. The narrower shape of the nasal horn base compared to the shape of the nasal rugosity area on the skull in the majority of previously found woolly rhinoceros is associated with secondary damage after burial caused by physical, chemical, and biological agents. An excellent example of such destruction is the frontal horn of the studied specimen of *C. antiquitatis* (Figure 2c), in which a partially destroyed outer layer of keratin can be observed. The physical basis for

TABLE 1 Linear dimensions of rugosity area and horn base in different rhinoceroses species.

Species	Number	Rugosity area (mm)		Horn base (mm)		Length/width ratio (%)		
		Length	Width	Length	Width	Rug[a]	Horn	Diff
Rhinoceros unicornis	ZIN 1918	175	130	129	101	134.6	127.7	**6.9**
Diceros bicornis	ZMMU S-93020	146	137	137	129	106.6	106.2	**0.4**
Coelodonta antiquitatis	DPMGI 2114	230	162	220	83	141.9	265.1	**−123.2**
	MM 7938	240	133	229	80	180.5	286.3	**−105.9**
	VMN no number	203	136	185	45	150.7	411.1	**−260.4**
	MM 3074	240	155	~230	~150	154.8	153.3	**1.5**

Note: The difference (Diff) between the length/width ratios of rugosity area and horn base is shown in bold.
[a]Rugosity area.

such a pattern of horn destruction are an irregular melanization and calcification of the horn. Thus, in the White rhinoceros, the densest part of the horn is confined to its core part, which provides a characteristic conical horn shape by removing material from the peripheral part of the horn by abrasion and wear (Hieronymus et al., 2006).

The pattern of destruction, abrasion, and wear of the nasal horn of the woolly rhinoceros indicates that its core part (which elongated anteroposteriorly as horn itself) is markedly denser compared to the outer part. This conclusion corresponds well to the horn histology. The central part of the nasal horn of the *C. antiquitatis* consists of markedly larger (two to three times) keratinized tubules than the peripheral part, which clearly divides the horn into two heterogenous areas (Chernova & Kirillova, 2010). The denser core part of the *C. simum* horn corresponds well to the conical outgrowth of the nasal bones (see Figure 1 in Hieronymus et al., 2006). We hypothesize that the longitudinal ridge on the nasal bones of the woolly rhinoceros also morphologically indicates the densest part of the *Coelodonta* nasal horn (Figure 3 and Supporting Information: Figure S3). Unfortunately, the loss of the nasal horn described herein during transportation does not allow us to verify this hypothesis with CT.

To summarize, the intravital shape of the nasal horn of modern-day rhinoceroses is visually well subdivided into two regions along its height. At the base, the horn is wide and rather strictly repeats the shape of the growth zone (Table 1); at about 5.5–8 cm above the base the horn rapidly narrows until the smooth part (Groves & Leslie, 2010; Laurie et al., 1983). The shape of the narrower region corresponds to the strongly melanized and calcified core part of the horn. The same pattern was observed in the woolly rhinoceros. The nasal horn shape at the base was virtually identical to the shape of the nasal rugosity area (Figure 2 and Supporting Information: Figure S3); 5–10 cm above the base the nasal horn exhibited rapid wear and destruction of the peripheral layer of keratin. As a result, above the base the horn became laterally flattened and saber-shaped and should correspond well to the shape of the most of nasal horns known in the fossil record. (e.g., Figure 1 and Supporting Information: Figure S1).

We would like to note that this shape of the nasal horn is unparalleled among extant rhinoceroses. The markedly elongated shape of the rugosity area on the nasal bones is also characteristic of the Sumatran rhinoceros (Groves & Kurt, 1972), which is phylogenetically the closest to the woolly rhinoceros among extant species (Welker et al., 2017). However, after removal of keratin from the peripheral part of the horn above its base in *D. sumatrensis*, it has conical shape typical for other modern-day rhinoceroses (Wilson & Mittermeier, 2011), not a laterally flattened and saber-shaped *Coelodonta* horn. The conical shape of the nasal horn in the Sumatran rhinoceros corresponds well with the conical outgrowth on the nasal bones (as in the White rhinoceros) rather than the longitudinal ridge as in the *C. antiquitatis* (Figure 3). The increase in the anteroposterior length of the core part of the nasal horn in the woolly rhinoceros may have a functional explanation. In lateral view, the anterior surface of the nasal horn of the woolly rhinoceros has a distinct wear facet that intercepts the anterior curvature of the horn (Supporting Information: Figures S1,S3B). In some rare cases, the horn can be worn more than one half of its anteroposterior length (see figure 2 (5b) in Shidlovskiy et al., 2012). This flat surface is divided into left and right facets, which indicates that it was produced by active side-to-side strokes (Fortelius, 1983). It is possible that the size difference of the left and right facets on the surface of the nasal horn of the woolly rhinos may help identify individuals with right- or left-forelimb preference. Previously this facet was interpreted as evidence, that *C. antiquitatis* used its nasal horn to brush away snow from the ground while feeding in the winter (Fortelius, 1983; Haase, 1914). A more plausible cause of this wear pattern can be more physically demanding activities, such as breaking of the snow crust and/or ice coating (*dzud*). The anteroposteriorly elongated core of the nasal horn gave the woolly rhinoceros a reserve of resistance to this kind of abrasion. We hypothesize that if the core part of the horn of the woolly rhinoceros had been narrower in the anteroposterior direction (as in extant rhinoceroses), the horn could have worn down to a fracture and thus lost its functionality with prolonged use.

Finally, we believe that the cranial features described above may help in the reconstruction of the shape of horns in other fossil rhinoceroses. If the rugosity type indicates the presence of the keratinous horn (see Hieronimus, 2009), then at the base, the horn is rather strictly repeating the shape of the rugosity area, while the presence and shape of additional outgrowths on the nasal bones (conical, longitudinal ridge etc.) may indicate the shape of the core part of the horn.

AUTHOR CONTRIBUTIONS

Ruslan I. Belyaev: Conceptualization; writing—original draft; visualization; investigation; formal analysis. **Gennady G. Boeskorov**: Conceptualization; investigation; writing—original draft; formal analysis. **Maksim Yu. Cheprasov**: Writing—original draft. **Natalya E. Prilepskaya**: Writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article.

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