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Ecomorphological patterns linking fossil *Coelodonta antiquitatis* and extant *Ceratotherium simum*: a review (Perissodactyla: Rhinocerotidae)

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Abstract. Relationships between morphological traits and their ecological function frequently result in patterns that are consistently observed within taxa. It was under this premise that the fossils of the cold-adapted, shaggy-coated fossil woolly rhinoceros *Coelodonta antiquitatis* was compared to those of other *Coelodonta* species, indicating that this genus originated in the Tibetan region during the Pliocene. It occurred throughout the Pleistocene mammoth steppe, covering the northern Iberian Peninsula, Great Britain, Central Europe, Russia, and Siberia, and was characterized by a diverse community of large herbivores. Plant fragments stuck in woolly rhino teeth (most typically inside the infundibula – the crescent-shaped recesses present in the middle of the molars) show that they were grazers, with grasses comprising about 96% of their diet, and mosses and forbs forming the remainder. Moreover, as the extant white rhinoceros *Ceratotherium simum* shares several common characters with *C. antiquitatis*, the animals likely originate from the same ancestors. These hypotheses are supported by a detailed analysis of their physical characters, distribution, habitat, and behaviour.

Key words. Woolly rhinoceros, white rhinoceros, Pleistocene, morphology, phylogeny, ecology, mammoth steppe, systematics.

INTRODUCTION

The study provides a detailed review of physical characteristics, distribution, habitat preferences, and behavioural traits, offering valuable insights into the fascinating interplay between form and function in two remarkable creatures, the fossil woolly rhinoceros *Coelodonta antiquitatis* and the extant white rhinoceros *Ceratotherium simum*.*

Coelodonta antiquitatis (Blumenbach, 1799)

The name *Coelodonta* Bronn, 1831 derives from the Greek words κοιλία (koilía) and οδούς (odoús), meaning "hollow tooth", in reference to the deep grooves in their molars, whereas *antiquitatis* originates from Latin and can be translated as "of the remote ages".

In the northern hemisphere, the Late Pleistocene glacial phases were characterized by the relatively cloudless mammoth steppe ecosystem, consisting of a mosaic of steppe-tundra and shrub vegetation with nutrient-rich soils suitable for the growth of plants that sustained grazing

* the views expressed are those of the author

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species (Guthrie 2001). The mammoth steppe extended from the northern Iberian Peninsula, across Great Britain and Central Europe, to Russia and Siberia, and was characterized by a diverse community of large herbivores (Schreve et al. 2013, Rey-Iglesia et al. 2021; Fig. 1).

The woolly rhinoceros, *Coelodonta antiquitatis* (Fig. 2) was one of the iconic inhabitants of this steppe-tundra ecosystem. Woolly rhinoceros fossils have been found across a vast area spanning from Spain in the west to Siberia in the east, and from Russia in the north to Italy and Greece in the south, it was one of the most abundant species and an indicator of the Eurasian megafauna (Boeskorov 2001, Garutt & Boeskorov 2001; Fig. 3). The species was well-adapted to cold environments, as it was covered with thick and long hair, as evident from its mummified remains. It is believed to not have been suitably equipped for moving across snow due to its massive body and short legs (Boeskorov et al. 2011). Further, analyses of its dentition and mesowear indicate a diet of a grazer (Stefaniak et al. 2021), which is supported by grass remains recovered from the diastemata of some specimens (Guthrie 1990; Fig. 4).

However, microwear analysis of woolly rhinoceroses conducted by van Geel et al. (2019) suggested periodical inclusion of woody components in their diet, while pollen analysis of stomach contents performed by Boeskorov et al. (2011) indicated that they mostly consumed grasses and sagebrushes. These results are in accordance with those yielded by genetic analysis of stomach and gut contents, supporting a diet in which short grasses predominated and were occasionally accompanied with forbs (Willerslev et al. 2014). *Coelodonta antiquitatis* was predominantly a grazer, rendering it evolutionarily closer to extreme grazers as *Bos bison* Linnaeus, 1758, *Equus quagga* Boddaert, 1785, *Equus grevyi* Oustalet, 1885, and *Ceratotherium simum* (Burchell, 1817) (Stefaniak et al. 2021).

The woolly rhinoceros is one of the first fossil species to be recognized. It was described by Blumenbach (1799), who noted that it became extinct after the last glacial maximum, i.e., by the Latest Pleistocene. No further contributions to this field were made until the 1960s when two new species – the Tologoyan woolly rhinoceros *Coelodonta tologoijensis* Beliajeva, 1966

Fig. 1. Ukok Plateau, one of the last remnants of the mammoth steppe. Photo by M. Chytrý.

Fig. 2. Woolly rhinoceros *Coelodonta antiquitatis*. – Embalmed specimen at the Natural History Museum, Kraków, Poland. It is a complete – i.e. with preserved skeleton, but also soft parts: tongue, part of the guts, muscles, skin – specimen of the extinct woolly rhino species from the Pleistocene epoch, discovered near the village of Starunia, Ukraine (at that time south-eastern Poland) in 1929. Photo by K. Rudloff.

from north-eastern Russia that lived in the Early-Middle Pleistocene, and the Nihewan woolly rhinoceros *Coelodonta nihowanensis* Chow, 1978 from northern China that lived during the Early Pleistocene – were described by Belâeva (1966) and Kahlke (1969), respectively. More than four decades later, Deng et al. (2011) provided a description of the oldest undisputable representative of the genus, the Tibetan woolly rhinoceros *Coelodonta thibetana* Deng, 2011 based on the evidence found in the upper Pliocene deposits in the Zanda Basin, south-western Tibet (Uzunidis et al. 2022).

Three decades earlier, guided by new information available at the time, Guérin (1980) suggested splitting *C. antiquitatis* into two subspecies, whereby the more slender and taller form from the Middle Pleistocene would be denoted as *Coelodonta a. praecursor* differentiating it from the Late Pleistocene nominal subspecies, *C. a. antiquitatis*. The author argued that this distinction would match a general trend within the species, from cursorial to fully graviportal locomotor adaptations. Consequently, in subsequent publications, references to *Coelodonta a. praecursor* were made based on the remains uncovered at several European sites, suggesting slenderness of postcranial limb bones (Uzunidis et al. 2022).

All known species of the woolly rhinoceros lived in cold conditions in northern Eurasia, Siberia in particular (Kahlke 1999), and a few rare southern forms dwelled in high-elevation regions, such as Aba (Vangengejm et al. 1966), Gonghe (Zheng et al. 1985), and Linxia (Qiu et al. 2004), in or along the eastern margin of the Tibetan Plateau. Based on this zoogeographic pattern of progressive expansion from Tibet, as well as the congruence between phylogeny and chronology, it can be postulated that, as global climate cooled and cold habitats expanded,

ancestral woolly rhinoceros descended from Tibet to Siberia, eventually turning to grazing in the Late Pleistocene (Kahlke & Lacombat 2008). It is this ability to adapt to different altitudes and latitudes that likely contributed to their superior success relative to other Ice Age megaherbivores.

According to the available fossil records, the woolly rhinoceros evolved in Asia, but its early ancestry cannot be established (Qiu et al. 2004, Kahlke & Lacombat 2008). Nonetheless, Deng et al. (2011) assert that the Tibetan woolly rhinoceros, *Coelodonta thibetana*, found in the high-altitude Zanda Basin in the foothills of the Himalayas in south-western Tibet, occupies the most basal position of the *Coelodonta* lineage and, having been dated to the middle Pliocene (~3.7 Ma), is the earliest representative of the genus. As the Ice Age began about 2.8 Ma, it is speculated that the Tibetan woolly rhinoceros descended, through intermediate forms, to low-altitude, high-latitude regions in northern Eurasia. It is in this territory that – along with the Tibetan yak *Bos mutus* (Przewalski, 1883), argali *Ovis ammon* (Linnaeus, 1758), and bharal *Pseudois nayaur* (Hodgson, 1833) – it became part of the emerging *Mammuthus-Coelodonta* fauna in the Middle to Late Pleistocene (Deng et al. 2011).

Most of the findings pertaining to the Tologoi woolly rhinoceros *Coelodonta tologoijensis* in the Asian part of its range were located in the Trans-Baikal region (Vangengeim 1967), which mostly comprised dry steppes with small semi-desert areas during the Pleistocene. As the number of rhinoceros finds decreases toward the north, this observation coincides with the fact that no remains of this species were found in Europe beyond 63°N (Smirnov 1937, Gromova 1965).

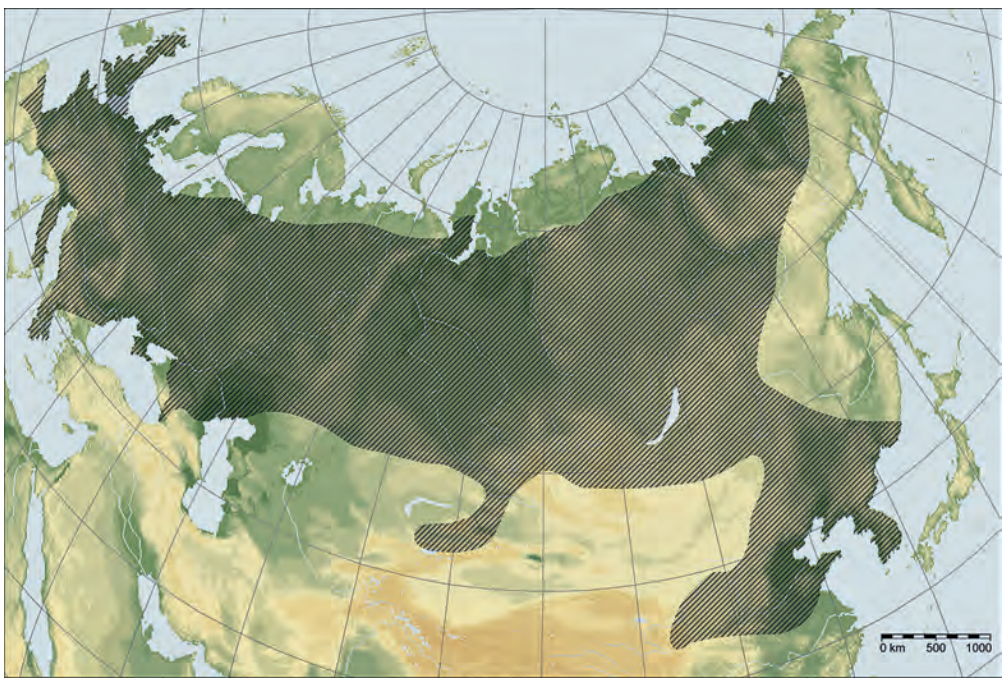

Fig. 3. The distribution map of the genus *Coelodonta*. Credit: R.-D. Kahlke.

Fig. 4. Right upper dentition of *Coelodonta antiquitatis*, showing embedded plant remains within the dental fossae. After Pandolfi & Maiorino (2016).

This finding is not surprising, given that the vegetation cover in the Trans-Baikal region was dominated by xerophytic groups, followed by tundra elements, with minimal contribution of woody vegetation (mostly birch and larch), whereas the southern part of Siberia was occupied by periglacial steppes.

Given that very few woolly rhinoceros carcasses have been uncovered, conclusions regarding specific morphological features are typically reached based on the bone remains (Boeskorov 2012). As a rare exception, one carcass was found near the village of Verhneviûjsk (Верхневиюйск, Yakutia) while another was located in the basin of the Âna River, near the Halabuj River, a tributary of the Bytantaj River. However, only two legs and the head were taken from the former carcass and the head and one leg were taken from the latter one, thus limiting the extent of analyses that could be performed (Brandt 1849, Čerskij 1874, Schrenck 1880). In the early 20th century, two mummified carcasses were found in ozocerite deposits near the town of Starunia, south-eastern Galicia, later Poland, today Ukraine (Bayger et al. 1914, Nowak et al. 1930). The first finding, made in 1907, comprised head and horns and is presently displayed at the Natural History Museum of Lviv (Ukraine), whereas the second, discovered in 1929, was a complete female carcass without horns, and is held at the Natural History Museum, Kraków, Poland (Fig. 5). Unfortunately, complete skeletons of the woolly rhinoceros with retained soft tissues are equally rare. The best known one was found in 1972 in the village of Čurapča (Чурапча), 200 km east of Âkutsk. The right femur was partially covered by skin and fur coat, and stomach remains were preserved (Lazarev et al. 1998).

Although these findings cannot provide a full picture of the specific morphological and ecological features of *C. antiquitatis*, they were sufficient for confirming the presence of a thick woolly coat and thick skin, flattened front horn, full bony nasal septum (providing additional support for the nasal bones carrying the front horn), predominantly herbaceous diet, and specific body type (elongated trunk and relatively short legs). They also pointed to a massive hump between the shoulder blades (Boeskorov 2012). The palaeobotanical data are available from four frozen woolly rhinoceroses (Axmanová et al. 2020).

The most detailed morphological descriptions of woolly rhinoceroses are associated with two Starunia carcasses (Bayger et al. 1914, Nowak et al. 1930) and the so-called Kolyma rhinoceros (Boeskorov 2012).

The Kolyma woolly rhinoceros and its comparison with other rhinoceroses

In 2007, a well-preserved frozen mummy of a female woolly rhinoceros was discovered at a gold mine in Yakutia, which was estimated to be 39,000 years old and have once weighed around 1.5 tons. The specimen had a thick brown fur and skin, a short fur-covered tail and narrow ears (Boeskorov et al. 2011; Fig. 6).

In 2015, a nearly complete frozen mummy of a woolly rhinoceros calf (named "Sasha") was also discovered in a gold mine on the lower reaches of the Kolyma River, north-eastern Siberia. This was the first find of the whole body of a woolly rhinoceros in permafrost and, based on its rib fragment, it was dated approximately 39,500 years ago (Fig. 7).

In the Kolyma specimen, the skull and mandible are completely preserved, with some tendon remains present. Moreover, mummified greyish-brown tongue of oval cross-section can be found at the bottom of the mouth cavity. The tongue root, body, and part of the tip are still

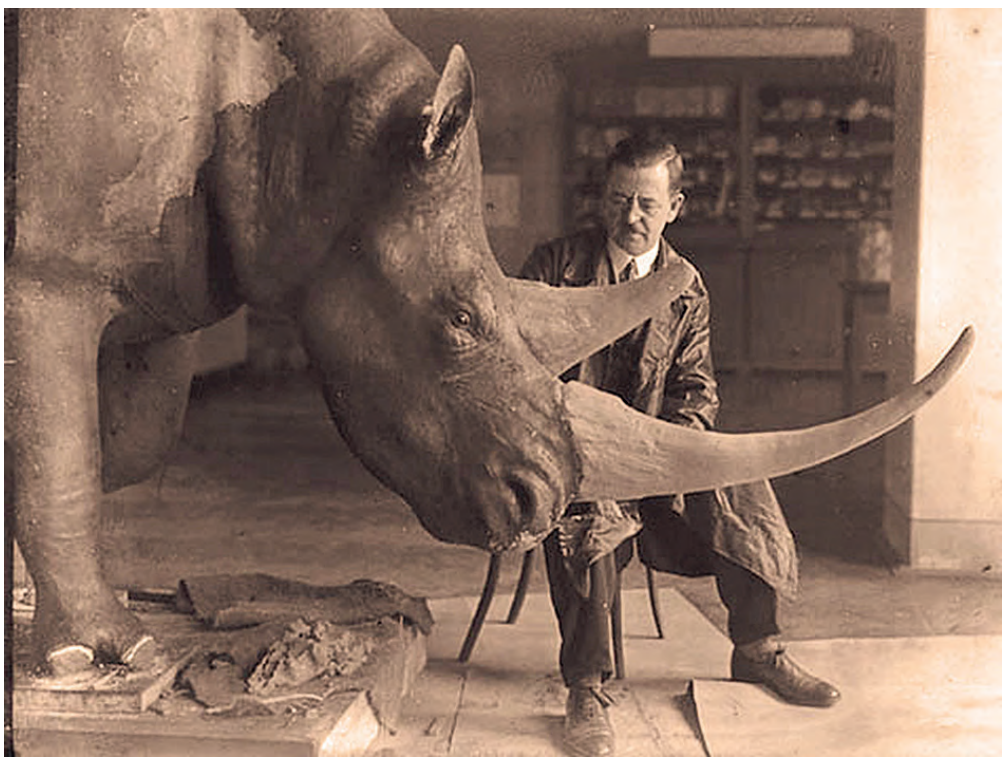

Fig. 5. Head of the embalmed specimen of *Coelodonta antiquitatis* from Starunia, Ukraine. The woolly rhinoceros was excavated on 17 December 1929 and on 22 December it was transported to Kraków, where it is still today and is on display at the Natural History Museum. The final preparation and conservation was carried out by a sculptor by training, and a taxidermist by profession, Franciszek Kalkus. (Public domain image.).

Fig. 6. Very well preserved woolly rhino from Kolyma, Russia. Photo by V. Filippov.

present, whereas the ventral part and the papillae have been destroyed. From its root to the ventral part of the retained tip, the tongue measures 310 mm in length. Its height at the maximum cross-sectional width of 68 mm is 82 mm. The right hyoid bone (*os hyoideum*) measuring 208 mm in length is also well preserved. The muscular process (*processus muscularis*) width is 74 mm, and that of the stylohyoid is 25 mm. In terms of shape, the rhinoceros tongue is closest to the horse tongue according to Boeskorov (2012), but this study did not contain a detailed comparison with extant rhinoceroses, available e.g. in Cave (1977). The permanent teeth in woolly rhinos can be described by the following formula: I 0/0; C 0/0; P 3/3; M 3/3. Its skull measures 653 mm in length, with 332 mm zygomatic breadth, and 178 mm maximum height in the frontal horn region. These dimensions are rather large in comparison with the corresponding measurements of the *C. antiquitatis* skull provided by Borsuk-Bialynicka (1973): 580–685 mm (M=634.06 mm), 300–386 mm (M=335.08 mm), and 155–190 mm (M=169.9 mm).

Garutt (1994) reported on a *Coelodonta antiquitatis* study involving 267 skulls and 160 mandibles, revealing a notable similarity with the dentition of the extant African rhinoceroses *Diceros bicornis* and *Ceratotherium simum*. According to this author, the presence of the deciduous tooth D1, the condition of D2−D4, and some morphological characteristics of the maxillary molar rudiments point to the similarities in the development of deciduous dentition among *C. antiquitatis*, *D. bicornis*, and *C. simum*. Based on the findings subsequently provided by Pandolfi (2015), two groups located in different areas of the morphospace can be distinguished within Dicerotina, which are respectively represented by the skulls of *Diceros bicornis* and those of the genus *Ceratotherium*. According to the latter author, "the cranial shape of the latter group is close to that of Coelodontina" (p. iv).

The rudimentary incisors dI1 and dI2 in adult woolly rhinoceros individuals and their contemporary African counterparts also share many similarities. Likewise, the initiation, development and eruption of P4 and M3 in the two species are identical. According to the morphological analyses performed by Garutt (1994), even the abnormalities, such as irregular eruption of P4 and supernumerary P4 and M3, are found both in recent and fossil rhinoceros of the genera *Coelodonta* and *Dicerorhinus*. These findings suggest that, during evolution, the dentition of the family Rhinocerotidae was not subject to rigid specialization, but rather exhibited considerable plasticity and ability for rapid reconstruction.

Some similarities are also noted in the elements which are absent, as is the case of incisors, which are rarely present in the maxillae of adult individuals of the African rhinoceroses as well as woolly rhinoceroses. Likewise, the crown form, the development and orientation of parastyle and metastyle fold, and the degree of inclination of transversal crests in the deciduous molars of *C. antiquitatis* are comparable to those in fossil rhinoceroses of the genus *Dicerorhinus*

Fig. 7. Woolly rhinoceros calf "Sasha"– A lifelike restoration using the remains of a baby woolly rhinoceros recovered from the Siberian permafrost. The specimen was nicknamed Sasha after the hunter who discovered it. Photo by A. Banderov.

Fig. 8. Southern white rhinoceros *Ceratotherium simum simum*. Photo by C. Nienaber.

(Garutt 1994) which would be fully concordant with the consensual phylogeny of Rhinocerotidae (Liu et al. 2021), however not concordant with Garutt (1994) who considered these features, rather than serving as evidence of their phylogenetic propinquity, as indications of ancestral forms of Rhinocerotidae. In an earlier study, Garutt et al. (1970) noted that, based on the information provided in popular science literature, given its long trunk and short legs, *Coelodonta antiquitatis* can barely be differentiated from the herbivorous steppe-dwelling rhinoceros *Ceratotherium simum* (Figs. 8, 9).

The information pertaining to the woolly rhinoceros neck is based on the analysis of the specimen excavated in Starunia in 1907. Its particularly interesting feature is a small bulgy protuberance in the middle (about 44 cm from the occiput) that is disconnected from the bony protuberances of the vertebrae, coinciding with the descriptions provided for the neck of the white rhinoceros *Ceratotherium simum* by Roosevelt (1911). The Starunia specimen also exhibited a hump in the scapula, bearing a close connection with the very long spinous processes of the vertebrae of this part of the neck. Likewise, *Ceratotherium simum* possesses very distinct humping of the skin on the neck (Nowak et al. 1930).

A detailed examination of the female mummy discovered in 2007 revealed a characteristic sabre-shaped bend in the front (nasal) horn which is flattened from its sides. The horn anterior surface is considerably abraded, with the abraded region measuring 510 mm in length. According to its internal and external curvature, the horn is 627 mm and 845 mm long, respectively, whereby the antero-posterior length of its base is 229 mm. The transverse breadth and thickness in the middle part are 123 mm and 26 mm, respectively. Such nasal horn measurements are characteristic of a young

adult rhinoceros, aged about 14–20 years. Given that the Kolyma rhinoceros horn has 17–19 transverse bands of annual growth, the individual's age can be estimated at about 20 years (Fortelius 1983, Garutt 1998, Lazarev et al. 1998). These assertions are supported by the evidence provided in pertinent literature, indicating that *C. antiquitatis* individuals exhibit larger horns at an age of 25–35 years, with an external curvature length of 100–1350 mm (Černova et al. 1998, Garutt 1998, Lazarev et al. 1998, Boeskorov & Isakova 1999; Fig. 10).

Fig. 9. White rhinoceros calf. Photo by D. Noakes.

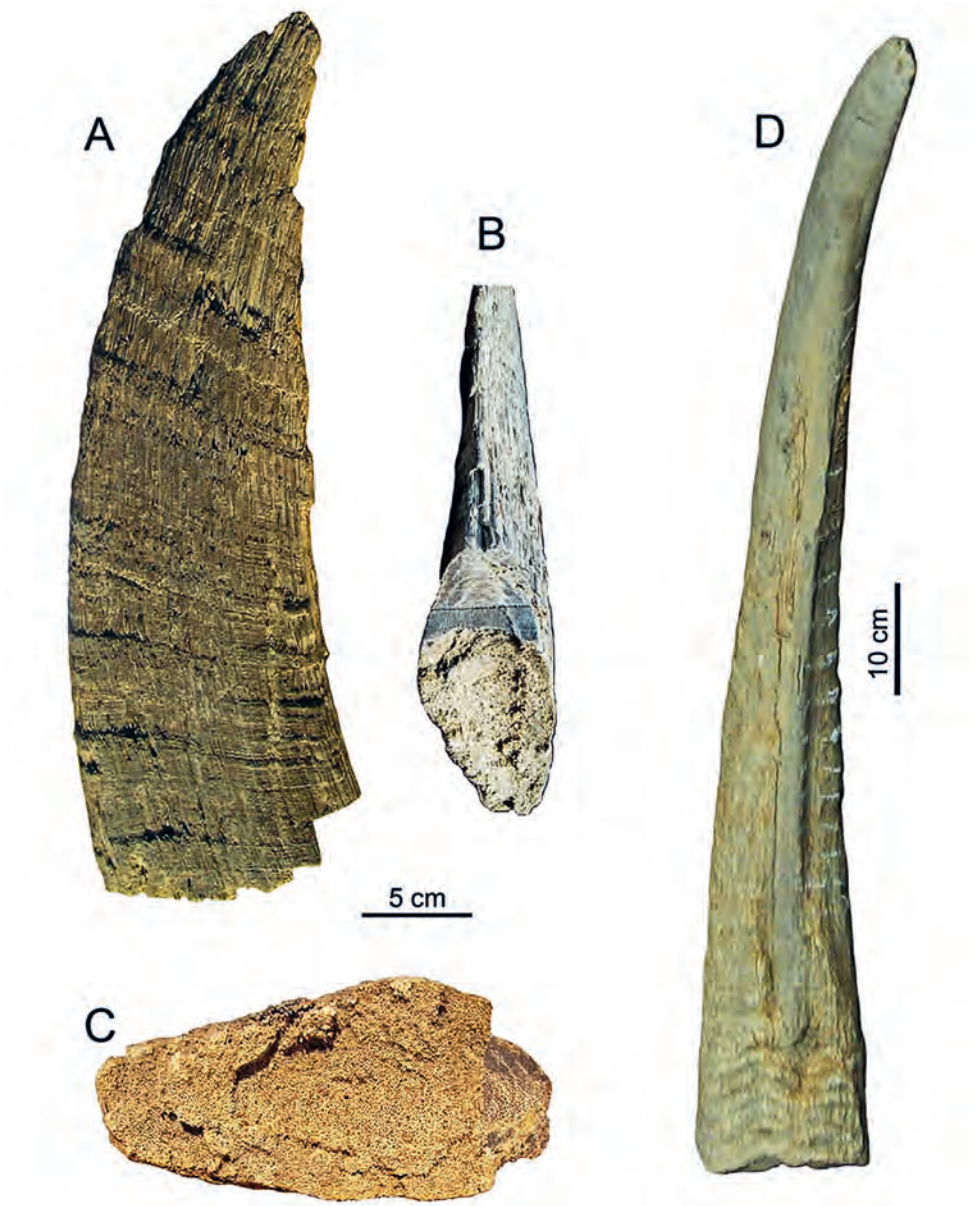

Fig. 10. The horns of the woolly rhinoceros *Coelodonta antiquitatis*: A – left lateral side; B – ventral side of the horn base: longitudinal and transversal sections of the horn are shown; C – the porous "sole" of the horn base in a place of growing layer's boundary (in this case – it is also a place of natural break); D – back view: the prominent central hardening is visible. Scale bars: A–C = 5 cm; D – 10 cm. Credit: O. Černova & I. Kirillova.

The frontal (back) horn measures 150 mm in length, whereby the length of its base is 146 mm, and its width in the middle part is about 80 mm. Moreover, the horn breadth and thickness in the middle part are 78 mm and 48 mm, respectively. The intact horn is 170 mm long, displays at least 10–11 detectable transverse bands, and its tip is abraded. While the measurements of woolly rhinoceros frontal horns are based on very few available samples, the greatest reported length (475 mm) belongs to the specimen recovered from the Ojmâkon Upland. Thus, based on the frontal horn dimensions, the Kolyma rhinoceros was sexually mature and relatively young (Garutt 1998, Lazarev et al. 1998).

The Kolyma rhinoceros mummy skin is mummified and hardened (its thickness ranging from 5 to 15 mm), and is mostly dark brown, with occasional patches of blue vivianite crystals. The skin on the lateral side of its head is the thinnest (measuring on average 5.5 mm), and that on the rump is the thickest (measuring on average 11.2 mm), followed by thorax (10.5 mm on average), and back (10.4 mm on average).

Based on the measurements performed by Nowak et al. (1930), the Starunia female rhinoceros found in 1929 had the thickest skin on the lower lip, measuring at 28 mm. In this specimen, only hair on the lower parts of the legs is preserved, while tawny brushes are found over the nail plates of the hoof phalanges. These findings are typical of the carcasses of fossil animals buried in the upper layers of permafrost, as repeated freezing-thawing cycles tend to destroy the hair coat over time. However, as skin is less susceptible to these conditions, a large patch of skin has been preserved, comprising the left ear, eye pit, and part of the anterior snout edge.

As would be expected, the ear has lost its natural shape, and is flattened from the sides, taking a lancet form (in comparison, the ear of the extant rhinoceros has a widened upper part). Its length measured from the base and the edge of the auricular notch is 215 mm and 185 mm, respectively. The antero-posterior length of the left eye pit is 36 mm and is comparable to 40 mm measured for the Starunia rhinoceros found in 1907 (Bayger et al. 1914). The eyeball with mummified eye muscles and fasciae is preserved on the inner part of the eye pit skin. Its antero-posterior diameter is 51 mm, and the transverse diameter is 31 mm, with 315 mm distance from the posterior eye pit edge to the anterior ear edge.

The rhinoceros body is deformed, with the front and hind legs pressed closely against the trunk. As is characteristic of the extant rhinoceroses, large skin fold is present between the hind leg and the abdomen. Although the trunk on the left side is almost intact, a considerable part of the skin is absent from the right side and the legs are torn off, and the skin covers only the dorsal part of the back and part of the abdomen. The abdominal cavity contains the remains of mummified stomach bags (measuring 70 cm in length) with their contents, which are identified as hardened grout of half-digested plant remains. Fragments of mummified intestines are also present.

The left legs are completely retained, whereas only the distal part of the right hind leg is present (comprising a fragment of the gaskin above the hock to the sole). The legs are pillar-like, as is characteristic of the rhinoceros. Only the remains of the humerus, cubitus, pastern and carpus bones of the front right leg are retained, along with two hoof phalanges. Each of the three preserved legs has three "claw horns" (nail plates of hoof phalanges). Concurring with the findings reported for the Churapcha rhinoceros, the level of the elbow joint in this individual is slightly above the ventral abdominal surface. Conversely, in the Starunia rhinoceros found in 1929, these body parts are approximately at the same level. These features are also present in the extant rhinoceros, whose ventral abdominal surface is either around the same level with the elbow joint or slightly above the latter (Walker et al. 1964, Zukowsky 1964, Groves 1982, Laurie et al. 1984).

Based on the bearing surface area of the left legs (230 cm^2) and 185 cm^2 measured for the hind leg, the total bearing surface area of all four legs for this individual is estimated at about 830 cm^2. As the hoofs on the right foot are well preserved, exact measurements can be made, yielding the middle hoof width of 96 mm and 54.5 mm height in the middle part. The corresponding measurements for the right and left hoof are 74 and 57.5 mm, and 71 and 53 mm, respectively.

The tail, albeit without hair, is completely preserved and measures 47 cm in length, being the thickest at the base and gradually tapering toward the tip. Its circumference at the base is 30 cm, reducing to 23 cm in the middle, while the dorsal breadth of the tail base is 13 cm. In comparison, the tail of the Starunia rhinoceros found in 1929 is 2 cm longer and its circumference at the base and mid-length is 29 cm and about 20 cm, respectively, with 15.5 cm reported for the dorsal breadth of the tail base (Nowak et al. 1930). Given that the orifices of hair follicles are present across the entire tail skin surface and their diameter increases at the tail tip, the tail of the Kolyma rhinoceros is expected to have been completely covered with hair. In comparison, the tail of extant rhinoceroses is long with free dock covered by tufts of long and thick hair from both the outer and inner sides, especially at the end, allowing animals to efficiently whisk away biting insects from their hips and groin. The Kolyma rhinoceros is also likely to have had a switch of bristly hair at the tip of its tail.

According to the descriptions provided by Nowak et al. (1930), the Starunia female found in 1929 has two nipples in the inguinal region of its abdomen, which is characteristic of the odd-toed ungulates in general and the rhinoceros in particular. The right (left) nipple measures 20 mm (18 cm) in length with the largest breadth of 17 mm (16 mm). The inner sides of the nipple bases are 31 mm apart.

The total weight of the mummified Kolyma rhinoceros carcass is 875 kg, while the skull, horns, remains of two right legs, and other bones found separately weigh further 75 kg. Given that most of the viscera are absent and not all the muscle tissue and skin have been preserved, as well as that the soft tissues have been subject to cryogenic sublimation, the intravital weight of this individual can be estimated at 1.5 tons at the minimum. This also coincides with the greater body weight of adult males, reaching up to 2 tons. Due to its relatively low height, the rhinoceros had a long ponderous trunk and short legs. Thus, based on the body weight of 1.5 tons and the bearing surface area estimated at 830 cm^2, the load per cm^2 of the foot bearing surface was approximately 1800 g, considerably exceeding 420–560 g/cm^2 for the extant elk *Alces alces* (Linnaeus, 1758) and 1000–1300 g/cm^2 for the European bison *Bos bonasus* Linnaeus, 1758 (Formozov 1946, Kuz′mina 1977).

These descriptions pertaining to the Kolyma rhinoceros measurements performed on the carcass remains of other rhinoceroses near the Malaâ Filippova (Малая Филиппова) River and the data reported by other authors allow these and other specific morphological and ecological features of the woolly rhinoceros to be better understood.

For example, as the udder of the woolly rhinoceros had two nipples, it is unlikely that they bore more than two calves, with one being most common. Moreover, based on the data pertaining to the extant rhinoceroses (Walker et al. 1964), they would have a 2–3 year reproductive cycle, as is typical of the family.

However, given that the body dimensions are based on the measurements of only one female *Coelodonta antiquitatis*, any conclusions regarding the species size are only tentative. This particular individual was very large, with only the mammoth having greater dimensions among the North Eurasian mammoth fauna. In terms of its 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 white rhinoceros species. The largest in this group is the African white rhinoceros *Ceratotherium simum*, with a body length reaching up to 350 cm, shoulder height measuring 185 cm, and body weighing about 1700−2400 kg. Similarly, the Indian rhinoceros *Rhinoceros unicornis* Linnaeus, 1758, has a body length of up to 340 cm, shoulder height of 170 cm, and body weight of 1600−2200 kg. In comparison, females of the African black rhinoceros *Diceros bicornis* (Linnaeus, 1758) have a somewhat shorter body (up to 300 cm), as well as a smaller height (150 cm shoulder height) and weight (1200–1500 kg). The Javan rhinoceros *Rhinoceros sondaicus* Desmarest, 1822 has a comparable body length (up to 300 cm) but is rather tall (to 170 cm) and heavy (to 1500 kg). The smallest of the extant rhinoceroses is the Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fischer, 1814), with a body length not exceeding 280 cm, shoulder height below 140 cm, and body weight below 950 kg (Walker et al. 1964, Zukowsky 1964, Groves & Kurt 1972, Groves 1982, Laurie et al. 1984).

The drawings made by Paleolithic humans show the woolly rhinoceros with relatively short narrow lancet-shaped or sharp ears, and this depiction coincides with the characteristics of preserved mummified *Coelodonta antiquitatis* ears. Although the ears of the Halabuj, Starunia, and Kolyma rhinoceroses are to a certain degree deformed, it is nonetheless evident that they differ from the ears of the extant rhinoceroses. According to the available data, the ears of the woolly rhinoceros measured 18.5–24 cm in length, exceeding considerably 14.1 cm measured for the woolly rhinoceros mummy found near the Halabuj River in 1877, while being comparable to 18–22 cm characterizing the modern black, Indian, Javan, and Sumatran rhinoceroses (Walker et al. 1964, Zukowsky 1964). Indeed, only the white rhinoceros has longer ears, reaching 25–26 cm (Heller 1913). On the other hand, the ears are considerably wider in most extant species and the auricle area is significantly larger relative to that measured for the woolly rhinoceros.

At about 50 cm, the tail of the woolly rhinoceros was rather short compared to 75–85 cm measured for the modern white, black, and Indian rhinoceroses (Heller 1913, Walker et al. 1964, Zukowsky 1964).

The woolly rhinoceros can also be differentiated from the extant tropical species by its shortened (or decreased in area) protruding body parts (ears and tail). These characteristics likely reflect Allen's ecological rule, implying that in warm-blooded animal species having distinct geographic populations, the limbs, ears, and other appendages of the animals living in cold climates tend to be shorter than in those living in warm climates. While this is a general principle applicable to all mammals, it is a known adaptation to cold climate of the North Eurasian Ice Age. Accordingly, the mammoth had a shorter tail and smaller ears than the extant elephants (Garutt 1964, Vereŝagin & Tihonov 1990).

The specific landscape (grass and shrub vegetation covering large open areas) and climate (sharply continental, mostly arid) features of the Pleistocene were rather adverse, as very little snow would fall in the winter, like many other extant herbivores, whereby soil would solidify (cf. Pavelková Řičánková et al. 2018). Specifically, due to a considerable body weight combined with short legs and a relatively small bearing surface area – three to four fold larger relative to the moose *Alces alces* and almost 1.5 fold larger as compared with the bison – its movements (and, correspondingly, grazing from under snow) would be considerably hindered by deep snow. For example, the extant ungulates struggle to feed when the snow layer is higher than the carpal and hock joints, and become almost helpless when it reaches their abdomen and thorax (Formozov 1946, Nasimovič 1955). Nonetheless, the mammoth and other animals living in that period, including the woolly rhinoceros, were adapted to such harsh conditions (Veličko 1973, Vereŝagin 1977, Šer 1997, Veličko & Zelikson 2001).

As the woolly rhinoceros had a thick and long coat and very thick skin, it was well adapted to the cold and dry climate of the late Pleistocene. Based on their recent study, Lord et al. (2020) concurred with the findings reported by Vangengejm (1961) and Vangengejm & Ravskij (1965), suggesting that the ecology of the woolly rhinoceros was primarily determined by climate warming, rather than low temperatures and hunting opportunities, as purported by Weyrich et al. (2017). Therefore, these authors suggested that physical and geographical conditions should be examined to better understand the reasons for the extinction of many Pleistocene mammals, large ungulates in particular. Given that the snow cover thickness would inevitably increase with greater temperatures and humidity in winter, while the ground would become swampy in summer, and that the first woolly rhinoceros was not adapted to such conditions that prevailed at the end of the Pleistocene and the beginning of the Holocene, unlike the mammoth, steppe bison *Bos priscus* Bojanus, 1827, aurochs *Bos primigenius* Bojanus, 1827 and others, it became extinct.

In addition, being heavy and having short legs would expose it to dangers posed by the natural traps formed by the thermokarst processes of that time, including cavities after melting of ice veins, deep thermal erosion washouts, boggy banks of thermokarst lakes and streams, etc. (Boeskorov et al. 2009). Thus, based on its carcass position (lying on its left side with its head stretched up), it is likely that the rhinoceros from the Kolyma slumped, bogged down in icy yedoma deposits, and drowned. This position may indicate that, with its body trapped in thixotropic liquid and viscous soils of melted yedoma deposits, the rhinoceros started suffocating, and lifted up its head in an attempt to breathe. Some carcasses of dead animals of the mammoth fauna displayed similar postures, including the Cherskij horse *Equus lenensis* Rusanov, 1968, as reported by Vereŝagin (1977) and the Yukagir mammoth (Mol et al. 2006).

Notwithstanding, a very recent study by Bergman et al. (2023) considers *Homo sapiens* the main perpetrator of the worldwide loss of large animal species over the past 100,000 years.

Diet and feeding adaptations

As a part of investigation, palynological analysis of the Kolyma rhinoceros stomach remains was performed, and the findings concur with those reported by Garutt et al. (1970) and Lazarev & Tirskaâ (1975), suggesting that *Coelodonta antiquitatis* inhabiting eastern and north-eastern Siberia was mainly herbivorous, with diet comprising mostly of cereals and wormwoods. The elongated head shape of this rhinoceros, the low set of the head, and the short and wide upper lip are also indicative of this specialization, and are also characteristic of the white rhinoceros that primarily feeds on short grasses.

Such specialization is also indicated by the elongated head of this rhinoceros, its low carriage (Uzunidis et al. 2022), loss of incisors and high-crowned teeth. It is also supported by the food remains in the deep folds of the enamel of molars often found in mummified rhinoceros heads or skulls preserved in the permafrost of Siberia**.**

Schmalhausen (1876) conducted the first detailed study of food residues from the teeth of a woolly rhinoceros, using the material obtained from I. D. Čerskij and B. I. Dybowski on behalf of the Irkutsk Museum. Based on their state of preservation, Schmalhausen concluded that the plant remains must have undergone prolonged maceration, suggesting that these were food remains, rather than plant particles accidentally introduced into the tooth cavity. His analyses further revealed predominant presence of leaves of monocotyledonous grasses (most likely cereals) and dicotyledonous herbaceous plants, along with sprigs of spruce (*Picea*), larch

(*Larix*), willow (*Salix*), and ephedra (*Ephedra*) from the Gnetaceae family. As spruce, fir, and larch have a different ecology and therefore cannot be found in the same habitat, it is likely that these food residues accumulated over time, during a transition across different habitats. It is also possible that the food residues Schmalhausen (1876) analyzed had been extracted from several rhinoceros skulls.

To address these ambiguities, Boeskorov et al. (2009) conducted palynological analysis of the host deposits where the rhinoceros carcass was buried. Their findings revealed that herb and shrub pollen predominated in the soil sample (accounting for 61.0%), with cereal pollen accounting for 23.9%, and wormwood and caryophyllaceous pollen contributing by 15.3% and 7.3%, respectively, followed by sedge (4.9%) and aster (1.4%). As these 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.), this evidence supports the previous assumption regarding prolonged food residue accumulation. Analysis further revealed pollen of trees and bushes (23.7%), which was primarily ascribed to small leaved angiosperms (18.0%), among which dwarf birches (9.7%), alders (3.8%), willow (solitary cases), and birch trees (3.4%) predominated. On the other hand, only solitary pollen grains of the coniferous larch *Larix* sp., pine *Pinus* sp., *Betula* sp., and *Quercus* sp. were identified (Schreve et al. 2013). According to Boeskorov (2012), this vegetation composition is characteristic of sharply continental and dry climate that would be found in open steppificated landscapes during the cold phases of Karginian interglaciation. In comparison, the current plant composition at the right bank of the lower reaches of the Kolyma River where the rhinoceros carcass was found is markedly different. This area presently belongs to the northern thin larch forest subzone, comprised of scrubs, marshes, and near-lake herb communities.

Compared to the percentage identified in the soil sample (61.0%), herb pollen was much more represented (98.5%) in the food remains (Boeskorov et al. 2011), and comprised primarily of cereals (45.9%) and the composite family (40.6%), which was mostly represented by wormwood pollen (40.1%). Forb pollen mainly originated from the steppe and meadow-steppe plants belonging to the caryophyllaceous (3.4%), plantain (2.3%), and rosales (3.2%) families. On the other hand, only small amounts of pollen of papaveraceous, ranunculaceous, buckwheat, cruciferous, goosefoot, leguminous, polemonium, valerian, chicory, aster, and sedge species was noted, while pollen of trees and bushes accounted for 0.9%, and spores contributed by only 0.6%.

Further analyses revealed presence of solitary pollen grains of spruce (*Picea* sp. and *P. omorica*), haploid and diploid pines, dwarf pine, and willow. As spruce and pine pollen grains were poorly preserved, it is possible that they were not part of the rhinoceros diet and were introduced to the oral cavity by accident. Likewise, only solitary spores of liverworts, horsetail, Siberian spike moss, and Arctic fir moss were identified (Boeskorov 2012), suggesting that the woolly rhinoceros diet was mostly comprised of cereal species and forbs, which is consistent with the observations pertaining to the feed remains from the teeth of the woolly rhinoceros from the Halabuj River in Verhoânsk (Garutt et al. 1970) and the analysis of the gastrointestinal contents of the Čurapča rhinoceros (Lazarev & Tirskaâ 1975).

In summary, the available literature and findings related to the woolly rhinoceros indicates that this animal was a herbivore that occasionally fed on shrub and tree sprouts. These assertions are also supported by a number of its anatomical and morphological features. They also concur with the findings yielded by studies on rhinoceroses living now, confirming a link between bodily proportions and nutrition. Specifically, rhinoceroses that primarily feed on the branches and

leaves of shrubs and trees have relatively long limbs and a short body. In contrast, the grass-eating white African rhinoceros has relatively short limbs, due to which the torso appears to be very elongated. Thus, as the woolly rhinoceros studied by Garutt et al. (1970) also had short limbs and a long body, its proportions correspond to those of the grazing rhinoceros of Africa.

In rhinoceroses, the occiput plane forms an angle with the skull base, which differs across different forms, allowing the lifestyle and diet of these animals to be compared (Zeuner 1934, 1936). For example, this angle is smaller in forest and forest-steppe rhinoceroses, such as the Sumatran and African black rhinoceroses, relative to grass-eating white rhinoceroses and woolly rhinoceroses. Likewise, an obtuse angle between the nape of the woolly rhinoceros and the skull base testifies to the inclined position of its head in relation to the body, corresponding to a diet rich in herbaceous vegetation.

Unlike all extant rhinoceroses, the woolly rhinoceros had a skull with a solid and fully developed bony nasal septum fused with highly developed nasal and intermaxillary bones – Pocock (1945) noticed the nasal septum in *R. sondaicus* and D. *sumatrensis*, but its occurrence is irregular. As the ossification of the nasal septum is not entirely completed, this information can be used to determine the animal's age. The woolly rhinoceros also had a nasal (front) and frontal (rear) horn. Evidence of strong abrasion on the leading edge of the nasal horn may indicate that this horn, along with hooves, was used to forage from under the snow in winter. This argument is supported by the presence of a powerful ossified nasal septum, as in other rhinoceroses it is comprised solely of cartilage**.**

In forest and forest-steppe species of modern rhinoceroses that primarily feed on branches and leaves, the upper lip is strongly developed, rather long, hanging down and very mobile, allowing them to grab branches, gnaw at the bark and tear off the leaves. This stands in sharp contrast to the upper lip of the steppe rhinoceros, which is short and wide, as it is adapted for grasping grass. In this respect, the woolly rhinoceros is similar to the white rhinoceros of Africa, as it has a wide short lip, providing further evidence that it mostly fed on grass. Woolly rhinos had very well-developed areas for muscle attachment on the skull, a low-slung head posture, and the large diastema to accommodate substantial mouthfuls of fodder (Schreve, pers.comm.).

Since some authors (Guérin 1982, Garutt 1994, Boeskorov 2012) recognised similarities between the woolly rhinoceros and white rhinoceroses, it is worth to specify peculiarties of white rhinoceroses as well.

Ceratotherium simum (Burchell, 1817)

Based on the available skeletal remains and rock art, the white rhinoceros *Ceratotherium simum* at one time covered a considerable range, spanning from the coastal areas of Morocco, Algeria, and Tunisia, through the Sahara and East Africa to South Africa (Skinner & Smithers 1990). Unfortunately, it is presently represented by a single subspecies, the northern white rhino *Ceratotherium simum cottoni* (Lydekker, 1908), which is on the verge of extinction.

As it can be seen from Figs. 8 and 9, based on its external appearance – larger size, presence of a nuchal hump (more obvious when head is held up), long and rectangular head, square lip, enlarged horn bases, and straight back with marked presacral as well as sacral eminence – the white rhinoceros is distinguished from the sympatric black rhinoceros *Diceros bicornis*.

The head is normally held low and the lips are squared and suitable for grazing (Groves 1972), as the lower lip bears a hardened pad (Van den Bergh 1955; Fig. 11). Its skin color is generally pale gray, with underdeveloped skin folds, likely due to the large amount of subcuta-

neous fat (Cave & Allbrook 1959). The skin is covered by sweat glands, and is the thickest (about 20 mm) on the shoulders (Skinner & Smithers 1990). Although hair follicles abound in most regions of the skin, hair shafts may only be evident on the tail, muzzle at the base of the nasal horn, and ear rims, while it tends to be sparse on the belly, throat, distal parts of both limbs, and hump apex (Alexander & Player 1965, Cave 1969, Groves et al. 2010). On the other hand, based on the analysis of a 3.5 month old female of *C. simum* "Zuluana", Bigalke et al. (1950) reported a sparse distribution of short, black hair over most of her body.

In terms of its size, white rhinoceros is larger than the woolly rhinoceros, as Macdonald (2001) indicated that its head and body length ranges from 3.4 to 3.8 m, while shoulder height

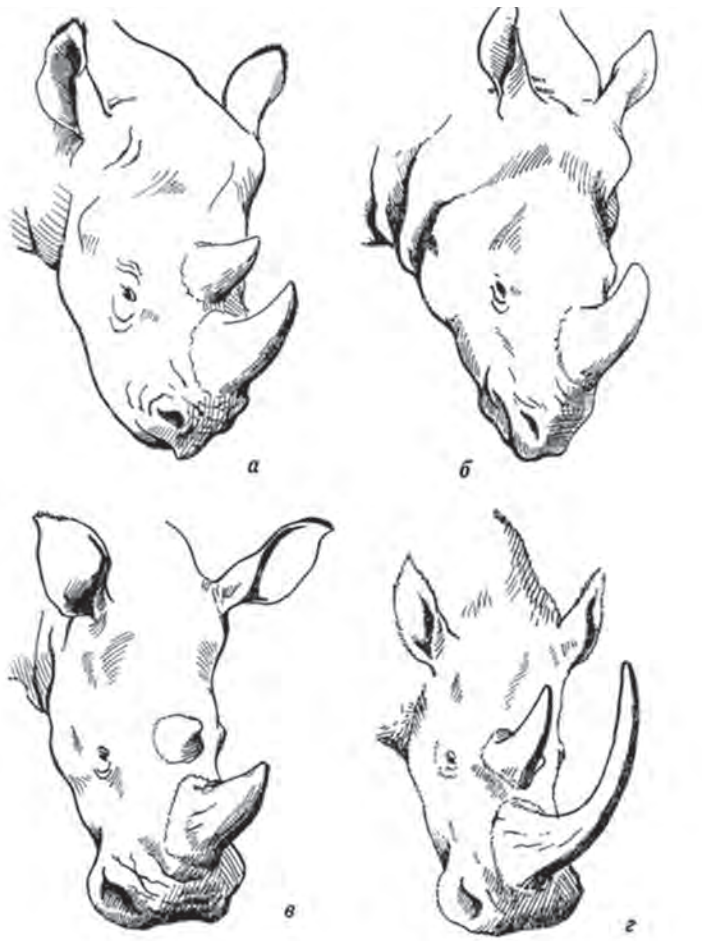

Fig. 11. Structure of the upper lip of rhinoceroses: *а – Diceros bicornis*; *б – Rhinoceros unicornis*; *в – Ceratotherium simum*; *г – Coelodonta antiquitatis*. Drawing by V. M. Smirin (after Garutt et al. 1970, 1982).

Fig. 12. *Ceratotherium simum* scraping soil with the horn. Photo by J. Corson.

and girth are 1.70−1.85 m and 2.80−2.90 m, respectively, with weight in the 1800−2500 kg range. Its horns are not joined at the base and have an enlarged and squared base and a thick, massive stem, whereby the nasal horn tapers without pronounced back-curvature. Its frontal horn is short and conical. According to the measurements (1660 mm) reported by Heller (1913), the nasal horn is considerably longer and thinner in the female, whereas males unusually have heavy horns, which may lean forward and scrape during grazing, as it can be seen from Fig. 12. They are also rarely as curved or as backward-pointing as in many *Diceros*.

The permanent teeth in white rhinos can be described by the following formula: I 0/0; C 0/0; P 3/3; M 3/3. The maxillary and mandibular second molars are the largest of the cheekteeth, which are broad-faced and have convoluted enamel layers on their biting surfaces, making them suitable for grinding up the food (Fig. 13). This dentition also allows feeding on short grass (Owen-Smith 1988), while in the absence of incisors, the animal would rely on the highly mobile movable and sensitive upper lip, assisted by a slight movement of the head, for extracting grass from the ground. As this would require head to be held low, the wide nostrils would remain in contact with the grass.

In South Africa, white rhinoceroses associate in crashes comprising 10–14 individuals, while crashes of more than four are rare in East Africa (Micha 1958, Guggisberg 1966). On the other hand, according to the data reported by Foster (1967), the most common grouping (38% of all encounters) in Uganda (where the sex ratio is 1:1) is one or two cows with their calves, or one or more males with a female (perhaps accompanied by a calf), while males are usually solitary. In the Congo, however, it is not uncommon for *ad hoc* groups to be formed

Fig. 13. Upper dentition of *Ceratotherium simum*. After Pandolfi & Maiorino (2016).

while grazing or resting, which later separate into their component parts (Backhaus 1964). The white rhinoceros trots at 24 km/h but can gallop over short distances at 40 km/h (Player & Feely 1960). As noted by Van den Bergh (1955), it runs with the head down, with the hind feet rapidly striking the ground.

Fig. 14. *Coelodonta antiquitatis* fighting – Chauvet cave, France. (Public domain image.)

The general appearance of the species is distinguished by a prominent hump between ears and shoulders, relatively longer head, normal head position (with mouth close to the ground), wide and straight-edged lips, straight-edged base of the anterior horn in front, and relatively larger ears, prominently tipped with hairs. The African white rhinoceroses – as the most ecologically similar to the woolly rhinoceros – live in open steppe-like regions and likely form crashes, as this would provide a degree of protection against predators.

In contrast, as African black rhinoceroses feed in dense, thorny acacia scrub, they are hidden from large predators, and do not need to form large groups, which thus rarely exceed five individuals. While a female with a calf or two males are not uncommon, white rhinoceroses may congregate in greater numbers around a watering hole. According to the available cave drawings, a similar behaviour was likely present in the woolly rhinoceros.

It is also worth noting that some Late Palaeolithic cave murals feature woolly rhinoceroses fighting by horns that is typical for African species, not the Asiatic ones which use their lower outer incisors as weapons (e.g. Dinerstein 2003). In particular, a woolly rhinoceros image discovered in the Chauvet cave in 1994 depicts such conflict, suggesting that males rarely lived in groups (Fig. 14).

Summarizing all specified evidence, both genera exhibit quite a number of similar characters. Although these features could be considered convergent due to the similar habitat and diet, they could alternatively indicate an ancestral condition, when the phylogenetic relationships are considered (Liu et al. 2021), because the grazer species (*Ceratotherium* spp., *Elasmotherium* sp., *Coelodonta* spp., *Rhinoceros unicornis*) occupy all basic phylogenetic lineages detected by Liu et al. (2021). It could be also mentioned in this context, that *Diceros* is considered a derived genus in contrast to *Ceratotherium* (Geraads 2005).

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