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Reshaping a woolly rhinoceros: Discovery of a fat hump on its back

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ABSTRACT

Until now, a key question in reconstructing the appearance of the woolly rhinoceros has remained open: why did various Paleolithic artists often depict this animal with a hump on its back? Previous findings of mummies of this rhinoceros either had no hump or this area of the carcass was damaged. In this study, we describe the discovery of a subadult *Coelodonta antiquitatis* mummy (4–4.5 years old) from the permafrost of Yakutia. This is the first time that the presence of a hump in the neck and withers area has been reliably established. The hump of the studied rhinoceros measures 36 cm in length, 13 cm in height, and 14 cm in thickness, and is filled with adipose tissue. The dimensions of the subcutaneous and hump adipocytes probably indicate that the hump was filled with white fat. The presence of a fat hump in the woolly rhinoceros represents a distinctive adaptation that is not typical of the extant large mammals in the northern latitudes and likely contributed to their survival during the harsh winters of the Ice Age. This discovery shows that Paleolithic artists from Chauvet Cave made strikingly accurate depictions of the exterior of a woolly rhinoceros.

1. Introduction

Adipose tissue, also known as fat deposits, is crucial in living organisms. Its primary function is to store energy and provide thermal insulation for the body. Additionally, adipose tissue produces various hormones, including estrogen, leptin, etc., and has been recognized as an important part of the endocrine system (Cinti, 2005; Gesta et al., 2007; Zhang et al., 2018). In adult humans, adipose tissue is located under the skin, around internal organs (visceral fat), within bones (marrow adipose tissue), between muscle fibers, and in the mammary glands (Aarsland et al., 1997). Adipose tissue develops and deposits similarly in various mammals. Many hibernating species accumulate a large amount of fat. So, in the brown bear (*Ursus arctos* Linnaeus, 1758) in the fall, before hibernation, fat can reach 20% or more of the total body mass (Heptner et al., 1967), in marmots (genus *Marmota*) up to 25% (Kolosov et al., 1979), and in susliks (genus *Spermophilus*) up to 41% (Avetisyan, 1970).

Among ungulates, in the Yakutian domestic horse (*Equus caballus* Linnaeus, 1758), which does not hibernate during winter, but lives in harsh climate, the fat may reach 20–23% of body mass by the beginning of winter (Gabyshev, 1957). In many large mammals, fat is rather evenly deposited in subcutaneous fatty tissue, internal organs, and muscles (this fat determines the "marbling" of meat in cattle). In cattle, subcutaneous adipose tissue is concentrated around the root of the tail, rump, ischial tuberosity area, groin, lumbar region, flanks along the ribs, behind the shoulder blades, and sternum. Sometimes fat deposits in cattle reach a thickness of 4–6 cm or more (Hardin, 1990; Khakimov and Salimova, 2009). In the muskox (*Ovibos moschatus* Zimmermann, 1780), fat can reach 20% of the total body mass and its thickness on the back may reach up to 4–5 cm by November (Adamczewski et al., 1997). In the domestic horse, fat is mainly deposited on the flanks, rump, back, withers, and neck (Henneke et al., 1983); in the Yakutian horse its thickness on the belly can reach 4.5 cm, and on the back and withers up to 8–9 cm (Gabyshev, 1957).

Some artiodactyls have a unique feature of accumulating fat in humps on their backs. For instance, the two-humped camel (*Camelus bactrianus* Linnaeus, 1758) and the one-humped camel (*Camelus dromedarius* Linnaeus, 1758) has fat humps, and the zebu breed of cattle (*Bos taurus indicus* Linnaeus, 1758) has a muscle-fat hump. In camels, the fat in the humps serves as a source of energy contained in lipids.

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Additionally, the fat deposits in camels act as insulation, accumulating primarily on their backs, which are most exposed to sunlight. If camels had fat distributed evenly over their bodies, it would prevent heat from escaping (Macfarlane, 1977; Kohler-Rollefson, 1991). Another example of the fat concentration is seen in domestic "kurdyuk" sheep (*Ovis aries* Linnaeus, 1758), which have large fat reserves at the root of the tail, forming the so-called "kurdyuk" (tail fat) weighing up to 13–14 kg (Liskun, 1949). Extant mammals in the northern latitudes were observed to lack specific fat concentrations in particular parts of their bodies. They do not have a fat hump, and their adipose tissue is quite evenly distributed throughout the body, often performing a thermo-insulating function (Garutt, 1964).

The question of how mammals of the Mammoth fauna adapted to the harsh conditions of the Ice Age has a long history of study. This includes the peculiarities of their accumulation of fat reserves to survive the cold winter periods of the Late Pleistocene. The investigation of frozen mummies of fossil animals found in the permafrost of Yakutia provides unique information on this issue. The subject of this study will be the recently discovered mummy of a subadult woolly rhinoceros from the permafrost of Yakutia (Fig. 1; Boeskorov et al., 2024). This specimen is characterized by the presence of a fat hump, which was previously unknown for *Coelodonta antiquitatis* Blumenbach, 1799. Until now, the presence of a hump in the woolly rhinoceros was suggested only by cave paintings of these animals by Paleolithic artists. In this study, we describe the anatomy of the hump, compare the fat hump of the woolly rhinoceros with nuchal hump of the white rhinoceros, describe the histology of the adipose tissue, and propose hypotheses about its functional purpose.

2. Material and methods

The mummy of the studied rhinoceros was discovered in August 2020 on the bank of the Tirekhtyakh River, the right tributary of the Indigirka River (Abyisky District of Yakutia; geographic coordinates: 68°35′18.19″N, 147°7′13.21″E). It is a relatively well-preserved frozen carcass of a *C. antiquitatis* with soft tissues, skin, and fur (Fig. 1). The details of the rhinoceros' discovery are described by Plotnikov (2021). The mummy was buried at a depth of 3–4 m on the slope of a ravine in loess-like loam and vein ice (Fig. 1b). The rhinoceros was found on the "adit" (artificial formation in the permafrost) top, after a collapse of the upper layers of soil (Tumskaya et al., 2024). The composition of the chitinous remains of various arthropods found in the fur of the rhinoceros suggests that the carcass was buried in a shallow, apparently temporary, fishless reservoir (Boeskorov et al., 2024). The rhinoceros' carcass is currently frozen at the Department for the Study of Mammoth Fauna of the Academy of Sciences of the Republic of Sakha (Yakutia) and has the temporary collection number DMFS-2020-01. To conduct anatomical and morphological studies, the rhinoceros mummy was temporarily defrosted, and the surface of its body was cleaned of sediments. Various samples of soft tissues were taken for analysis.

The individual age of the Abyisky rhinoceros (Figs. 1 and 2) was established by the development of the dental system and nasal horn. The development of the dentition in the woolly rhinoceros is elaborated in comparison with modern-day rhinoceroses. The order of tooth eruption and replacement, as well as their wear process, are best established in African species (Hitchins, 1978; Hillman-Smith et al., 1986). Based on these data Garutt (1992, 1994) established the age gradations of *C. antiquitatis*. Horn development is another valuable indicator of an individual's age. The growth of the rhinoceros keratinous horn occurs at its base. The smallest structure of the horn is presented by a horn lamina (layer ~1−2 mm thick), which appears as a band in the sagittal or transverse section (Hieronymus et al., 2006). Along the length of the horn, fairly wide transverse layers of lighter keratin and narrower transverse patches of darker keratin alternate. As was shown in the white rhinoceros, the distance between these dark patches corresponds very well with the annual growth rates of horns (Hieronymus et al., 2006). Thus, the number of transverse dark patches on the horn roughly corresponds to the number of winters that animal survive (Fortelius, 1983; Garutt, 1998; Chernova et al., 1998; Chernova and Kirillova, 2010; Kirillova and Shidlovskiy, 2010).

The hump and subcutaneous fat of *C. antiquitatis* were examined for histological studies. A sample from the hump was taken from a depth of about 9 cm from the body surface, and subcutaneous fat from a depth of about 1.5 cm. We get the intermuscular fat of the cow and the subcutaneous fat of the pig (*Sus scrofa domestica* Linnaeus, 1758) for comparison. Cryosections 10 µm thickness (Leica CM1850) were obtained from each sample. The tissue samples taken from the rhinoceros mummy were severely dried, especially the subcutaneous one (probably because of the higher amount of collagen fibers and its more superficial location). Rehydration in water with thymol at 4 °C and using routine cryoprotection protocol (three steps – 10%, 20%, 30% m/m sucrose solutions) facilitated the subsequent sectioning. The sections of

Fig. 1. The remains of the Abyisky rhinoceros: (a) lateroventral view from the right side, (b) laterodorsal view from the left side, (c) posterior view from the right side. Photos by V.V. Plotnikov (adapted from https://nplus1.ru/news/2020/12/31/old-young-rhino).

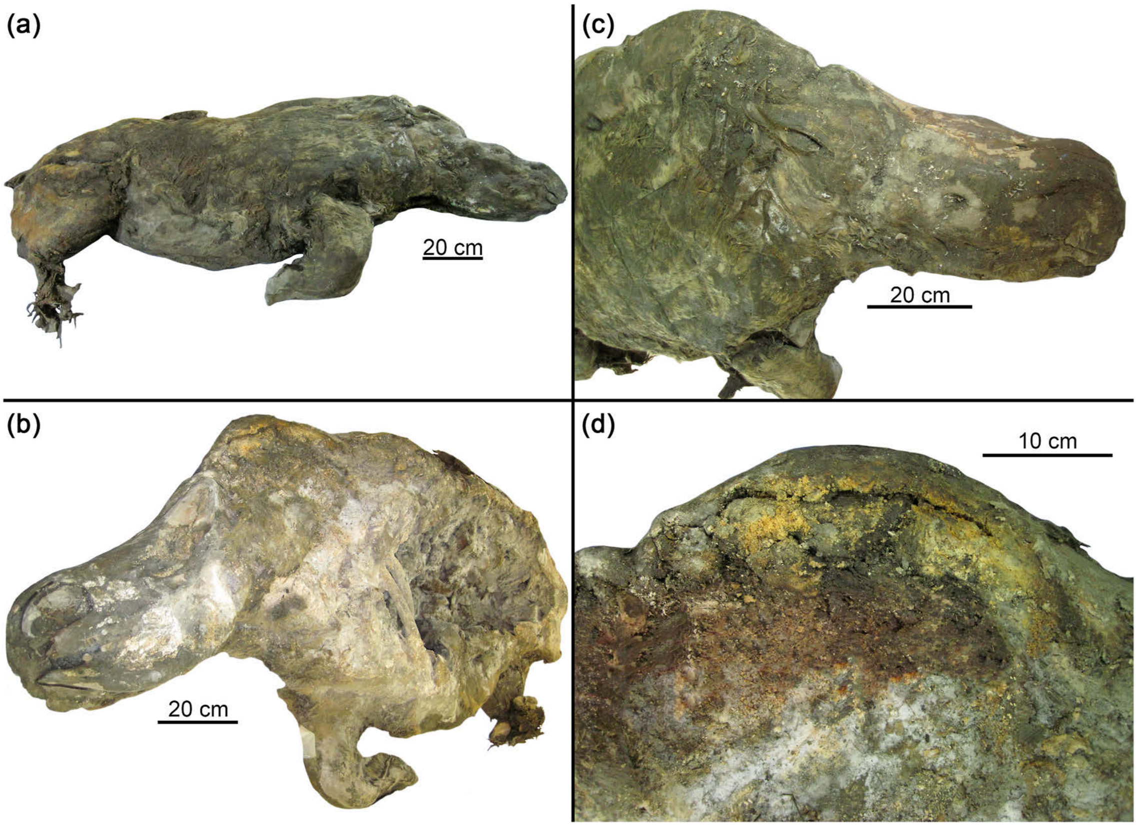

Fig. 2. The mummy of the Abyisky rhinoceros: (a) lateroventral view from the right side, (b) anterolateral view of the left half of the carcass, (c) right side view of the rhinoceros hump, (d) left side view of the rhinoceros' hump.

rhinoceros adipose tissue obtained did not adhere well to the slide and floated off the surface even when stained horizontally. To address this, we used chrome alum gelatin coating slides. Even with all these preparations, only a few acceptable sections (out of ~300) were obtained.

Tissue sections were stained with Ehrlich's hematoxylin, Mallory's trichrome, and Nile blue (0.1% aqueous solution). Hematoxylin stains tissues pale, even with prolonged exposure (30 min or longer). We were unable to successfully stain rhinoceros fat with eosin. Nile blue stained the rhinoceros' adipose tissue only blue, while the cow and pig tissue were stained pale salmon pink and bright azure blue colors. However, luminescence was observed where we would expect to see pink under light microscopy in rhinoceros. The staining results were not noticeably affected by fixation with formalin-$CaCl_2$; non-fixed samples and samples fixed before and after cryosectioning were stained approximately equally.

We selected 15 micrographs of adipose tissue, with one micrograph from each section (3 from the pig, 4 from the other samples). Adipocyte size was defined as the median longest (length) and median shortest (width) linear dimensions of cells measured in each selected micrograph within 591.91 × 591.91 μm (1024 × 1024 px) square area. We used ImageJ (Schindelin et al., 2012; fiji.sc) for image calibration and cell size measurement, SPSS for data analysis, and Inkscape (inkscape.org) for preparing figures.

3. Results

The precise age of the discovery was determined using radiocarbon dating of the rhinoceros' fur at the Center for Applied Isotope Studies (CAIS) at the University of Georgia (USA). The analysis indicated an age of 32,440 ± 140 years uncal BP (UGAMS 65491; Boeskorov et al., 2024) or 36,543–36,938 years cal BP; calibration was performed in CALIB REV8.2 packet (Stuiver and Reimer, 1993) using the calibration dataset of Reimer et al. (2020). This date corresponds to the Karginian Interstadial of the Late Pleistocene, the same period to which most of the frozen mummies of animals of the Mammoth fauna in Yakutia belong.

3.1. Anatomical aspect

The dentition of the studied individual consists of slightly worn P2, unworn P3, dP4, M1, and unerupted M2 and M3. This corresponds to group C-IV, according to the age gradations of *C. antiquitatis* (Garutt, 1992, 1994). The nasal horn length across the outer side is ~240 mm,

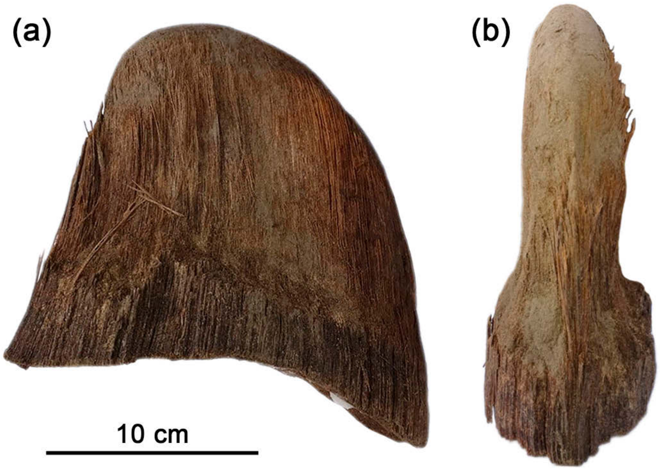

Fig. 3. The Abyisky rhinoceros' nasal horn: (a) right-side view, (b) anterior view. Photos by V.V. Plotnikov (adapted from https://nplus1.ru/news/2020/12/31/old-young-rhino).

the height from its base is ~160 mm, and the number of dark transverse patches on the horn is 3–4 (Plotnikov, 2021, Fig. 3). Thus, the annual growth rates of the Abyisky rhinoceros' nasal horn are ~4 cm/year. Based on the combination of development of the dental system and nasal horn, we estimate the individual age of the Abyisky rhinoceros to be 4–4.5 years.

The shape of the Abyisky rhinoceros' nasal horn is consistent with recently described specimen from the Suruktakh site (Belyaev et al., 2023a). The horn is wide at its base, at about 5–8 cm above the base the horn exhibited rapid wear and destruction of the peripheral layer of keratin and rapidly narrowed until the smooth part (Fig. 3). This part corresponds to the strongly melanized and calcified core part of the horn (Hieronymus et al., 2006), unlike modern-day rhinoceroses, which has conical core part of the horn, in *Coelodonta* this part was elongated anteroposteriorly and saber-shaped (Belyaev et al., 2023a).

The Abyisky rhinoceros was not yet sexually mature. Nevertheless, this specimen reached rather a large size: body length from the tip of the snout to the base of the tail (along the curvature of the body) is 236.5 cm and height at the shoulders is 131 cm. For comparison, the similar body measurements for adult individuals of *C. antiquitatis* are 323–358 cm (average 346.5 cm) and 145–155 cm (average 151 cm; Boeskorov, 2012; Boeskorov et al., 2024).

The mummy's right side is well preserved, represented by soft tissues, skin, and fur (Fig. 1a, c, 2a, c). On the left side, the internal cavity of the body is exposed, the left fore- and hindlimb are eaten, and most of the viscera are missing (Figs. 1b and 2b). We can assume that the

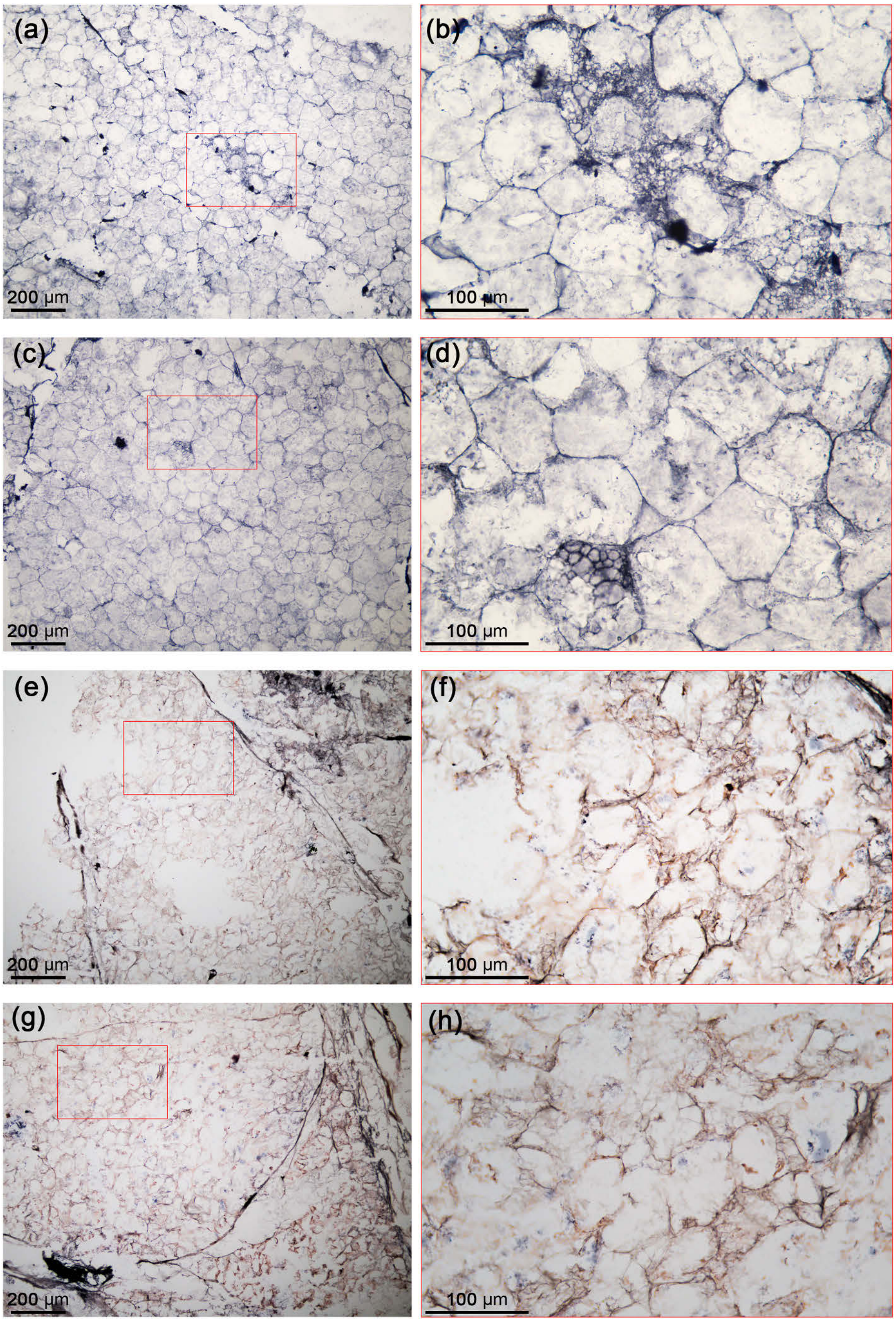

Fig. 4. Microstructure of the adipose tissue of the Abyisky rhinoceros: (a–d) hump fat; (e–h) subcutaneous fat. The left column is at 10× magnification, and the right column is at 40× magnification.

rhinoceros' carcass was not buried immediately after its death and was accessible to predators. We can hypothesize that the rhinoceros died during the cold season of the year or at the end of the warm season. This might explain why only the bottom (right) side of the carcass, which was probably frozen in ice or snow, was preserved. However, this assumption requires further verification.

The neck and withers area of the Abyisky rhinoceros is well-preserved and represents a distinct hump (Figs. 1 and 2). The hump measures 44 cm anteroposterior length across the outer surface of the body and 36 cm in a straight line, the height of the hump is 13 cm, thickness is 14 cm. On the left side of the mummy, the skin around the hump is partially absent, the hump appears to be filled with a light-yellow, finely lumpy substance (Fig. 2d). To confirm the adipose nature of the tissue from the neck and withers area, standard qualitative chemical reactions (Stroev et al., 2012) were carried out on the components of fat—fatty acids and glycerol. To do this, hydrolysis of the tissue under study was carried out in an alcoholic solution of potassium hydroxide. As a result of the hydrolysis of tissue from the hump, soluble potassium soap, insoluble lead soap (fatty acid salts), fatty acids (in the reaction of soap decomposition with mineral acids), and glycerin (in reaction with sodium hydroxide and copper sulfate) were detected in the hydrolysate, which confirms lipid nature of the tissue studied (Boeskorov et al., 2024).

Subcutaneous fat was also found in this specimen and is present on the head, neck, chest, flanks, and back. The thickness of subcutaneous fat reaches 1–1.5 cm on the lower jaw, rear part of the back, and 1.5–3 cm on the chest. Thus, the thickest fat deposits in the studied rhinoceros are localized in the neck and withers area.

3.2. *Adipose tissue histology*

The fat tissue from the hump is light brownish yellow, while the subcutaneous one is very pale yellowish beige with a large amount of collagen fibers from the associated dermis. Fat from the hump holds its shape under manipulation, while subcutaneous fat is drier and crumbles easily. Both ones show the expected histological design.

The major part of the rhinoceros hump fat sample is represented by relatively large cells in the form of polynomes and ellipses (Figs. 4 and 5). Visually, the size and shape of the adipocytes appear homogeneous. Among the large adipocytes, there are occasionally islets of small cells, their size is much (4–5 and more times) smaller than the surrounding cells (Fig. 4a–d).

The subcutaneous fat of rhinoceros has typical dermal collagenous fibers inclinations. The preservation of the cellular structure in these samples is much worse, probably due to the much worse preservation of the material (Fig. 4e–h, Fig. 5a and b). The adipocytes in subcutaneous fat are generally similar to those in the hump, but the cells are visually more oval in shape. It is very similar to the white fat of Malolyakhovski mammoth (Garmaeva et al., 2014, 2023: Fig. 1) In contrast to the sections of the hump fat, islets of small cells could not be detected in subcutaneous fat (Fig. 4e–h).

In general, the adipose tissue of rhinoceros, cow, and pig appear similar (Fig. 5). The staining results do not allow us to establish the presence of multilocular adipocytes in the Abyisky rhinoceros. This does not allow us to draw a reliable conclusion about the presence or absence of brown adipocytes in the studied tissues.

A summary of the dimensions of adipocytes is presented in Table 1. Among the 4 samples studied, the largest adipocytes are characteristic of pig subcutaneous fat (median 86.1 × 58.6 μm), slightly smaller cells are characteristic of cow intermuscular fat (83 × 54.1 μm), and rhinoceros hump fat (73.4 × 55.5 μm), and the smallest cells are found in rhinoceros subcutaneous fat (47.6 × 32.1 μm). The most isometric shape (length/width ratio) of adipocytes is observed in the hump of the woolly rhinoceros (mean = 1.41), whereas in other samples adipocytes have a more oval shape (mean from 1.49 to 1.57).

The range of adipocyte size variability in pig subcutaneous fat, cow intermuscular fat, and rhinoceros hump fat overlap almost completely with each other (min length from 28 to 32 μm; max length from 147 to 174 μm). Only the adipocytes in the subcutaneous fat of the woolly rhinoceros are noticeably smaller in size. The postmortem changes in rhinoceros fat, especially the high degree of dehydration of subcutaneous fat, make more detailed statistical comparisons unreliable.

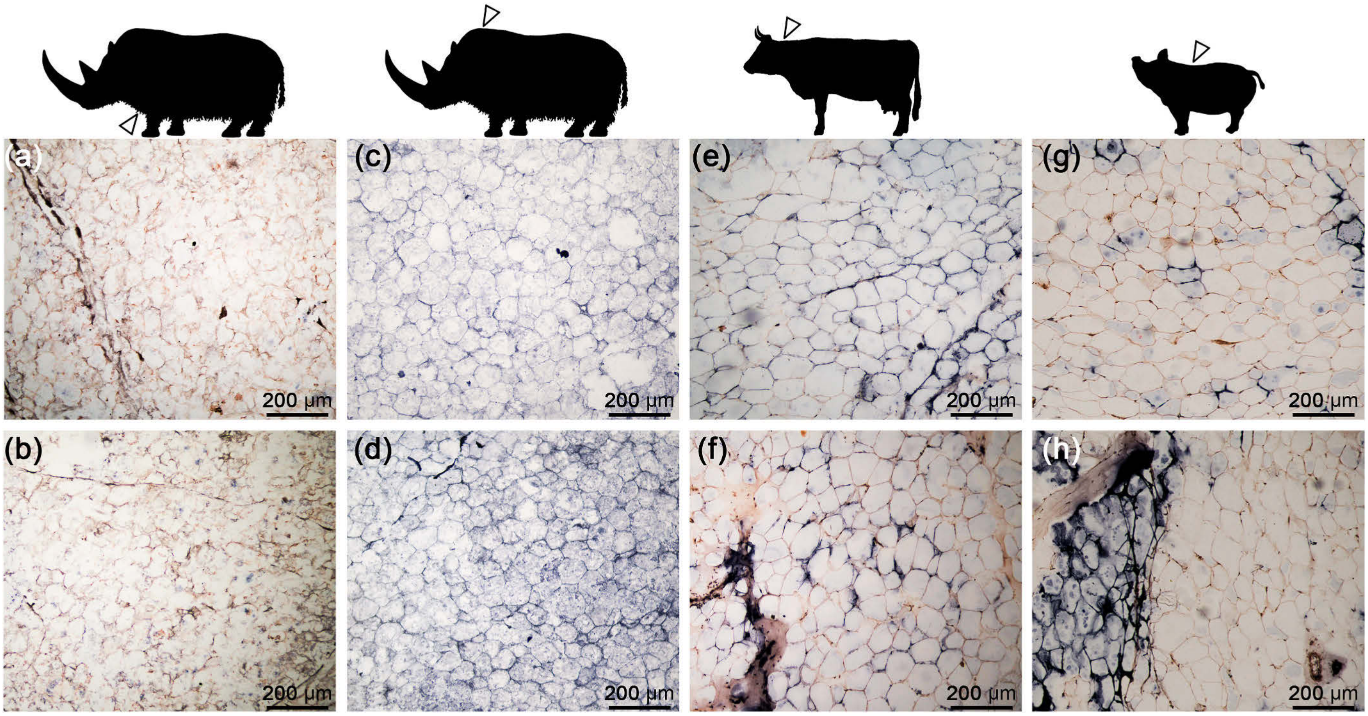

Fig. 5. Comparison of the adipose tissue microstructure between the Abyisky rhinoceros and other large ungulates: (a, b) subcutaneous fat of the woolly rhino; (c, d) hump fat of the woolly rhino; (e, f) intermuscular fat of the cow; (g, h) subcutaneous fat of the domestic pig.

Table 1
Adipocytes dimensions in the woolly rhinoceros, cow, and pig.

Sample of fat	n	Long dimension (um)				Short dimension (um)			
		Min	Max	Mean	SD	Min	Max	Mean	SD
Woolly rhinoceros hump	225	30	162	74.4	19.5	18	101	54.9	17.2
Woolly rhinoceros subcutaneous	264	16	103	49.3	15.5	13	72	33.1	11.3
Bos taurus intermuscular	265	28	174	81.7	23.7	16	109	55	19.1
Sus scrofa subcutaneous	188	32	147	84.2	23.7	25	101	59.4	17.5

4. Discussion

4.1. Comparison with other rhinoceroses and woolly mammoth

Among the numerous previous discoveries of woolly rhinoceros remains, only two represented by sufficiently well-preserved mummies that allow us to evaluate the anatomy of their neck and withers area: the Starunia rhinoceros and Kolyma rhinoceros (Niezabitowski et al., 1914; Boeskorov et al., 2011; Boeskorov, 2012). Both mummies represent the remains of adult animals and neither of them show any evidence of a fat hump. It should be noted that the neck area of the Kolyma rhinoceros is damaged, so a definite conclusion about the presence of a hump in this individual is not clear.

Among extant rhinoceroses, only the white rhinoceros (*Ceratotherium simum* Burchell, 1817) has a hump (Fig. 6a). The hump in this species is located on the dorsal part of its neck and is often called a nuchal hump (Cave and Allbrook, 1959). The anatomy of the white rhinoceros hump is very different from that we have described here for the subadult woolly rhinoceros. The nuchal hump of *C. simum* consists of three parts: (1) dermal and epidermal covering; (2) a layer of subcutaneous fat; (3) dorsal neck muscles and nuchal ligament (Alexander and Player, 1965). The skin cover (1) is characterized by significant thickening in the hump area, so the thickness of the skin reaches 49 mm, which is three times the thickness of the skin on the lateral surface of the neck. The adipose tissue (2) in the hump, on the contrary, is rather thin and reaches a thickness of only ~30 mm in the midline; it is thinning and disappearing to the sides, back, and front of the nuchal hump. Finally, the main volume of the hump is formed by the hypertrophied nuchal ligament and dorsal muscles of the neck (3). Alexander and Player (1965) suggested that nuchal hump evolution in the white rhinoceros is related to feeding patterns. Unlike other extant rhinoceroses, *C. simum* feeds at the ground level. Additionally, this species has bigger and heavier heads (Groves, 1972; Wilson and Mittermeier, 2011). This feeding behavior could explain the hypertrophy of the nuchal ligament stretching between the head and withers and relatively better-developed head elevator muscles (Alexander and Player, 1965).

The presence of a hump is not characteristic of other modern-day rhinoceroses. There is only data on subcutaneous fat in some species.

Fig. 6. Rhinoceros humps: (a) left-side view of the *Ceratotherium simum* in the ZooParc de Beauval in Saint-Aignan-sur-Cher, France (adapted from https://commons.wikimedia.org/wiki/File:Ceratotherium_simum_simum_(Rhinoc%C3%A9ros_blanc_du_Sud)_-_385.jpg; Credit: William Crochot, CC-BY-SA 4.0, via Wikimedia Commons); (b) group of the woolly rhinoceroses from the Chauvet Cave, Ardèche, France (adapted from https://en.wikipedia.org/wiki/File:16_PanneauDesLions(CentreGauche)Rhinoc%C3%A9rosEnFuite.jpg; Credit: Claude Valette); (c) woolly rhinoceros from the Rouffignac Cave, Dordogne, France (Photograph courtesy of Jean Plassard/Bradshaw Foundation); (d) woolly rhinoceros from the Chauvet Cave, Ardèche, France (adapted from https://commons.wikimedia.org/wiki/File:Rhinoc%C3%A9ros_grotte_Chauvet.jpg; Credit: Inocybe, via Wikimedia Commons). The photograph from Rouffignac Cave has been mirrored to match other images.

The thickness of subcutaneous fat in the white rhinoceros can reach 2.5 cm on the back and 5 cm on the abdomen (Cave and Allbrook, 1959). It has been noted that wild individuals of the Sumatran rhinoceros (*Dicerorhinus sumatrensis* Fischer, 1814) do not have significant deposits of the subcutaneous fat, but it may accumulate in individuals kept in zoos (van Strien, 2005). Subcutaneous fat is deposited in the black rhinoceros (*Diceros bicornis* Linnaeus, 1758) and Indian rhinoceros (*Rhinoceros unicornis* Linnaeus, 1758) in the neck area, shoulder region (not forming a fat hump), ribs, along the backbone, rump, and at the base of the tail (Reuter and Adcock, 1998; Heidegger et al., 2016). In the Indian rhinoceros, subcutaneous fat reaches a thickness of 2–5 cm and is well supplied with blood vessels that contribute to thermoregulation (von Houwald, 2005).

The woolly rhinoceros and extant white rhinoceros have both similarities and differences in their appearance and hump morphology. Both species have a hump located in the neck and withers area. Also, the woolly rhinoceros, like the modern-day white rhinoceros, is a grazer feeding at the substrate level, characterized by a large and heavy head and squared-shaped lips. Thus, a woolly rhinoceros may have had a relatively increased mass of the dorsal extensors of the neck and elevators of the head. However, the hump morphology of the *C. antiquitatis* differs significantly from that of the *C. simum*. First, the woolly rhinoceroses have thick deposits of subcutaneous fat, which significantly exceed those of the African species (13 cm *vs* 3 cm). Second, in the study of two individuals (calf and adult), Alexander and Player (1965) noted that the fat layer was observed only in the adult white rhinoceros, while in the woolly rhinoceros, a fat hump was found only in the described here subadult individual, thus far. White and woolly rhinoceroses are not close relatives, they are divided by millions of years of separate evolution (Liu et al., 2021) and the occurrence of a hump (uncharacteristic of other rhinoceroses) of these species is homoplasy.

The next line of comparisons is related to another large representative of the Mammoth fauna of Yakutia, the woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799). Studies of frozen mummies of woolly mammoths first revealed that adult mammoths had a thick layer of subcutaneous fat (~8–9 cm) evenly covering their entire body. This fat was not concentrated in any particular part of the body (Berezovsky mammoth – Hertz, 1902; Taimyr mammoth – Garutt, 1964). This suggests that subcutaneous fat in mammoths had a thermo-insulating function somewhat similar to marine mammals (Sokolov, 1979b). Subsequent studies of a juvenile mammoth (1.2–1.3-year-old) from the Oymyakonsky District of Yakutia revealed subcutaneous fat deposits about 2 cm thick on the lateral surfaces of its body, with the most significant fat deposits, up to 7 cm thick, found in its neck and withers area. The latter formed an actual fat hump in this individual (Boeskorov et al., 2007). A similar fat hump was discovered in the neck area of the juvenile Lyuba mammoth (~1 month old). Furthermore, Fisher et al. (2012) state that fat histology revealed the presence of cells with a multilocular structure (probably brown adipose tissue) accumulated in the hump, yet they provide no substantiating evidence for this fact. Notable fat deposits were found in the wither area of the subadult Sopkarginsky mammoth (8–10 years old; Maschenko et al., 2017). In this mammoth specimen, fat deposits covered the entire neck region with a layer up to 5 cm thick, and in the wither's area, their thickness exceeded 15 cm. The soft tissues in the withers area of the adult Berezovsky and Taimyr mammoths were not preserved, which could explain why fat humps were not found in these individuals. Thus, mammoths could accumulate a significant amount of fat in the neck and withers area, which served as an energy reserve (Boeskorov et al., 2007; Maschenko et al., 2013). This adaptation helped them to survive harsh winter conditions, food and water deficits. This characteristic sets the mammoth apart from modern-day elephants, which do not have large accumulations of subcutaneous fat (Vereshchagin and Tikhonov, 1990).

Recent studies have shown that subcutaneous fat is deposited in female African elephants on the ribs, back, loins, and pelvic region. In the pelvic region, the thickness of subcutaneous fat can reach 3 cm (Morfeld et al., 2014). The only significant accumulations of adipose tissue in modern-day elephants are located in the digital cushion of the fore- and hind feet. This allows them to lower peak foot pressures at the beginning of the contact phase, distributing the load from the individual bones to the fat pad (Gambaryan, 1974; Gambaryan and Ruhkyan, 1974).

The last line of arguments is based on the work of Paleolithic artists, who depicted silhouettes of woolly rhinoceroses on cave walls. Some of these depictions have a large hump on their backs and have an almost bison-like appearance (Fig. 6c and d). However, in other depictions of woolly rhinoceros, the humps in the neck and withers region resemble rather the nuchal hump of the white rhinoceros (Fig. 6a and b). Based on the appearance of the studied subadult rhinoceros, similar to other rhinoceros species (rather than large bovins) proportions of the body (our unpublished data and Belyaev et al., 2024), and length profile of the spinous processes along the thoracolumbar region of the backbone in adults (Sokolov, 1979a; Belyaev et al., 2021, 2023b), we find the bison-like depictions of the woolly rhinoceros (Fig. 6c and d) to be artistic overestimations. Surprisingly accurate illustrations of the *Coelodonta antiquitatis* were made by a Paleolithic artist from Chauvet Cave (Fig. 6b). Depictions of woolly rhinoceroses with hump and long horns, as well as scenes of fights (probably tournament fights between males) between long-horned individuals with humps (Chauvet et al., 1996), allow us to assume that this anatomical feature was presented in adults as well.

4.2. *The function of fat reserves in a hump*

Thus, it has been established that the largest representatives of the Mammoth fauna, the woolly mammoth and woolly rhinoceros, had a distinguishing feature from their extant relatives – a fat hump. To explain the function of the hump in these megaherbivores, it is necessary to note an important distinction between the two types of adipose tissue that mammals can store: white and brown fat. The main function of brown fat is thermogenesis, while white fat stores energy as lipid droplets (Zhang et al., 2018; Jung et al., 2019). Brown adipose tissue is most pronounced in newborn children and some animals (such as rodents and hibernating mammals). Typically, brown fat in animals is located in the interscapular region and on the neck (Gesta et al., 2007; Daly et al., 1997). During ontogenesis brown fat tends to transform into white fat, but adult mammals still have some brown fat, as shown in humans, rats, mice, and cats (Cinti, 2005; Clark et al., 2013; Zhang et al., 2018; Jung et al., 2019). It has been noted that under certain conditions, there is also a reverse process of white fat transforming to brown fat (such tissue is often called beige or brite fat; Cinti, 2005; Herz and Kiefer, 2019). Among the differences between brown and white adipocytes available for study on histological sections, the key ones are the number of fat droplets (one big lipid droplet in white and numerous small ones in brown adipocytes; Lafontan and Berlan, 1993) and the slightly smaller size of brown adipocytes (Sokolov, 1973; Maliszewska and Kretowski, 2021; Liu et al., 2023).

The fat deposits in the neck and withers area, combined with the statement of a multilocular adipocyte structure in the hump of the Lyuba mammoth (Fisher et al., 2012), indicate that the woolly mammoth and woolly rhinoceros may have had a hump of brown fat at a certain age. However, our data for the subadult Abyisky rhinoceros do not allow us to determine the number of fat droplets in the cells reliably, and the size of adipocytes in the hump notably exceeds that in the subcutaneous fat. Thus, the size of the adipocytes rather indicates that the hump is filled with white fat. Since islets of brown fat are found even in old animals (Clark et al., 2013) we think it is reasonable to expect to observe remnants of brown fat in the hump tissues of the Abyisky rhinoceros as well. We draw the reader's attention to the fact that the proposed assumption about the type of adipose tissue in the hump is preliminary and is subject to more careful verification. Possibly, newborn and juvenile woolly rhinoceroses and woolly mammoths had brown fat in the hump, which with age was partially or completely replaced by white fat. In the cold season, the white fat could partially turn brown (turning into beige), returning to its function of thermogenesis.

Based on the available data, we can offer two explanations for the presence of fat humps in woolly mammoths and rhinoceroses. The first explanation suggests that the humps were present in both juvenile and adult individuals and played an important role in thermoregulation and nutrient storage throughout their lifespan. In this case, the absence of fat humps in previously found adult specimens of both species may be related to the seasonal nature of fat storage in the hump. Fat could have been accumulated during the warm season and utilized during the cold season. The second explanation suggests that the fat hump was present only for juvenile/subadult individuals of woolly rhinoceroses and mammoths. In this case, the fat hump could be an “organ of heat generation”. Such an organ would theoretically be especially beneficial for young animals because of the ratio of body surface area to body volume. With an increase in body size the volume, mass, and weight of the animal would grow proportionally to the linear dimensions (lengths) cubed, but the surface area of skin only to the lengths squared. Therefore, the larger an animal becomes, the smaller (relatively its body mass and volume) the area of the body surface through which it loses heat. Consequently, larger animals can more efficiently retain internal heat (Lindstedt and Boyce, 1985). With this explanation, the fat hump can be viewed as a structure that supports juveniles during the coldest times of the year and which disappears as they mature. Such adaptation is found in juveniles of the muskox, which have a large amount of brown fat at birth (Lent, 1988), providing them with an “organ of heat generation”. Mixed explanations are also possible, such as the seasonal presence of the fat hump, but only in juvenile individuals; the presence of the fat hump throughout the lifespan in woolly rhinoceroses and only in juvenile/subadult mammoths; the transition from the brown fat hump, responsible for thermogenesis in juvenile individuals, to the white fat hump, storing nutrient in adults, etc.

5. Conclusion

In this paper, we describe a recently discovered mummy of a subadult woolly rhinoceros in the permafrost of Yakutia. This discovery allowed us to confirm a unique feature of the woolly rhinoceros exterior – the presence of a hump in the neck and withers area. The hump made the appearance of the woolly rhinoceros similar to the extant white rhinoceros. However, unlike its modern-day relative, the hump of the *Coelodonta antiquitatis* was filled with adipose tissue. The histology of the rhinoceros fat indicates that the hump of the subadult Abyisky rhinoceros was probably filled with white fat tissue.

This study confirms the accuracy of numerous cave paintings by Paleolithic artists of a woolly rhinoceros with a hump in the neck and withers area. The most accurate illustrations of the *C. antiquitatis* were made by a Paleolithic artist from Chauvet Cave (Fig. 6b). This study also raises important questions for future research on woolly rhinoceroses, mammoths, and other large herbivorous mammals of the Mammoth fauna. Was the fat hump featured in all age groups of these animals? If so, is it becoming bigger with age? Was the hump seasonal? Did the type of adipose tissue in the hump transform from brown in juvenile individuals to white in adults? Could the white adipose tissue in the hump turn beige before cold season? Clear answers to these questions will be achieved through further discoveries and research of Mammoth fauna remains.

Author contributions

G.B. conceptualized the study; G.B., M.S., and A.P. worked with the mummy of the rhinoceros; G.B. and R.B. wrote the initial manuscript; M. S. performed a chemical reaction on the components of fat; N.K. performed a histological study of the adipose tissue, prepared figures, and took measurements of the adipocytes; R.B., G.B., and A.P. analyzed the data, prepare the table and figures. All authors edited, read, gave final approval for publication, and agreed to be held accountable for the work performed.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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