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Skull pathologies in *Coelodonta antiquitatis*: implications about social behaviour and ecology

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Injuries to skulls of the woolly rhinoceros *Coelodonta antiquitatis* may indicate social behaviour and suggest important characteristics of rhino interactions at the end of the Pleistocene. This paper offers some ideas about woolly rhino biology, based on study of fossil materials.

Pathologische schedels van de wolharige neushoorn Coelodonta antiquitatis*: implicaties met betrekking tot gedrag en ecologie* – Verwondingen aan de schedels van de wolharige neushoorn *Coelodonta antiquitatis* geven aanwijzingen omtrent het sociale gedrag en suggereren belangrijke kenmerken van interacties tussen de neushoorns aan het eind van het Pleistoceen. In dit artikel worden enkele gedachten omtrent de biologie van de wolharige neushoorn ontwikkeld, op basis van de studie aan fossielen.

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INTRODUCTION

In this paper I describe data from an examination of a large series of skeletal remains (more than 300 skulls and 200 postcranial bones) of the woolly rhinoceros, *Coelodonta antiquitatis* BLUMENBACH. In the sample nine skulls exhibited various kinds of injuries that occurred during the animals' lifetime, and I infer some features of woolly rhino biology and behavior from the traces of trauma.

OBSERVATIONS

One of these rare specimens - a woolly rhino skull with a pathology of the left maxillary joint (specimen GM 82/112) - is on exhibit in the Vertebrate Paleontology Hall of the Mining Museum of St. Petersburg (Figs. 1a,b, 2a,b). The skull, brought from the Perm province (West Siberia) at the end of the nineteenth century, was originally found with its mandible, indicating a quick burial of the carcass where it had died in the zone of intensive sedimentation. The rest of the skeleton probably lay close to the skull, but only the skull and mandible were collected. Only two teeth on each side (M2 and M3) are preserved in the upper jaw. The lower jaw has the left m2 and m3. While in the museum, the teeth were subjected to further destruction by drying and cracking.

Judging by the state of the alveoli, which are well developed, the animal had complete tooth rows, P2 to M3, both in the upper and lower jaw at the moment of death. Judging

Figure 1 Skull of *C. antiquitatis* (specimen GM 82/112, the Perm region, Ural). **a** side view, **b** palatal (ventral) view.

by the degree of wear of the teeth the age of the animal was about 30-35 years old (see Garutt 1992 for a discussion of age-determination methods and models). The left maxillary joint of the skull is pathologically deformed (Fig. 2a,b). Both the articulate cartilage and the bone itself were subjected to destruction during the animal's lifetime. The articulate head (*caput mandibulae*) of the left mandibular branch became flat and spread. The same happened with the joint prominence (*tuberculum articulare*) of the zygomatic process (*processus zygomaticus*) of the temporal bone. The bony tissue of the injured area became porous, which was caused by the degenerative dystrophic processes connected with deforming arthrosis. As a rule, deforming arthrosis emerges as a result of heavy mechanical damage, as was mentioned in a personal communication by V.P. Petrov, Head of the Department of Forensic Medicine and Criminal Law, St. Petersburg State University (1995). Possibly the animal caught a strong blow in this area of the skull in the course of a fight with a rival. Considerable bone expansions increased the size of the joint surface. Neither asymmetry nor any difference in the degree of tooth wear between the right and left sides can be observed. The teeth are equally worn, and the masticatory surfaces are even. Proceeding from these observations, one may conclude that the animal was traumatized at a mature age, lived with the pathology for a short time and soon died.

On the other skulls the pathologies are confined to the orbits, nasal and occipital bones. The primary cause in each case was a mechanical trauma, on the spot of which secondary post-traumatic diseases, most likely osteomyelitis, developed. The mentioned areas of the skull are of vital importance. They bear functionally significant groups of muscles, copulas, cartilages and numerous nerves and blood-vessels. The injuries of these areas must have led to the crushing of soft tissues and destruction of organs. The healing of such injuries was a long process, and therefore it probably became complicated with osteomyelitic infections, which could have led to rapid deaths of the animals concerned. As an example one may take the skull of a woolly rhinoceros kept in the collection of the Geological and Mineralogical Museum of Kazan State University (speci-

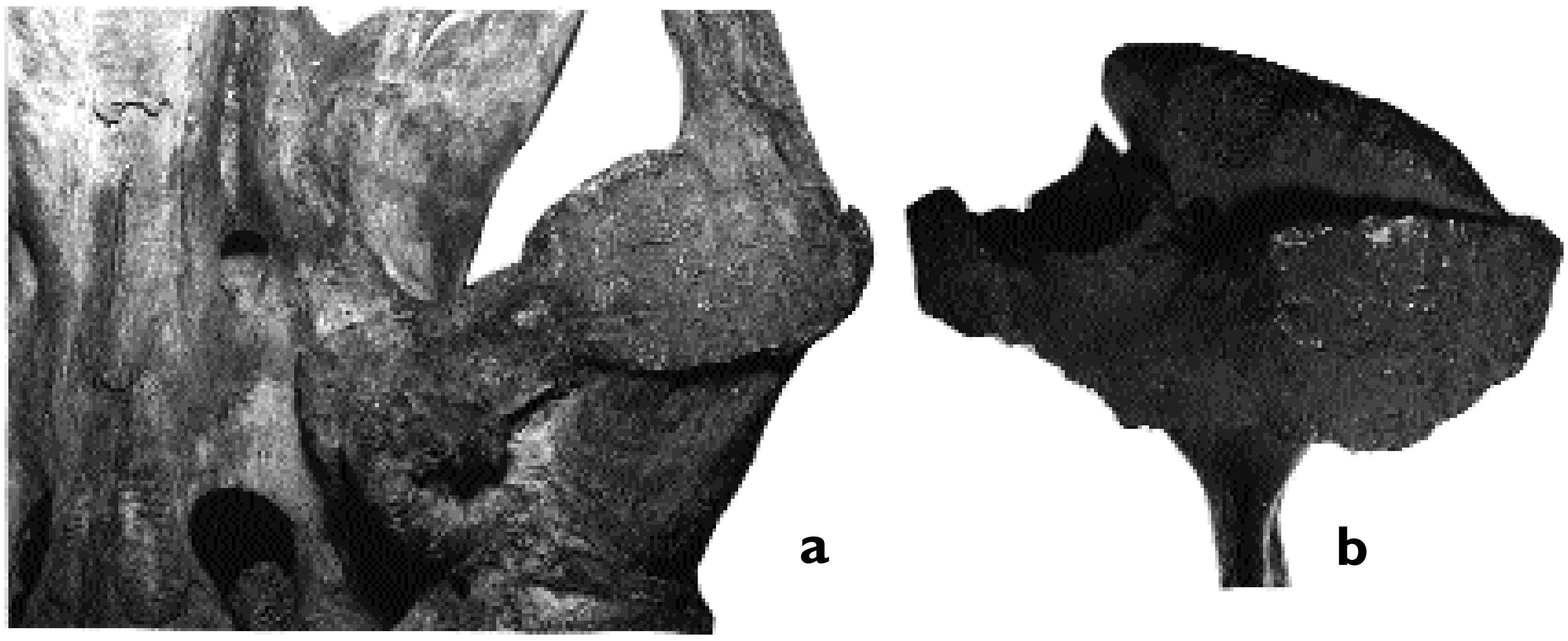

Figure 2 Maxillary joint damaged by deforming arthrosis (specimen GM 82/112, the Perm region, Ural). **a** the joint prominence of the zygomatic process of the temporal bone, **b** the articulate head of the left mandibular branch.

Figure 3 Skull of *C. antiquitatis* (specimen PIN RAN 170-8, the Middle Volga). **a** side view, **b** view from above (dorsal), an indentation is seen on the parietal bones.

men GMM KGU 742, from the Kazan province, Middle Volga). This skull lacks zygomatic arches and most of the facial bones. The maxillary bone between the orbit and infraorbital foramen is affected by osteomyelitis. Bones affected by osteomyelitis in its acute and subacute phases very likely would not preserve in soil for long. The destruction of the cancellous tissue (*substantia spongiosa*) is characteristic of these phases. It is only in the chronic phase that the bone becomes thicker because of the periostal formations accumulating on it. These formations protect the bone against destruction even in the presence of numerous cloacae. On these grounds one can suppose that the *Coelodonta* individual whose skull shows osteomyelitis survived the trauma and, although disabled, lived for a long time. The osteomyelitic bone tissue can be seen near the orbit. The animal was unable to see straight ahead out of its right eye.

There are also some skulls of *Coelodonta antiquitatis* with lifetime traumas of the parietal bones (Figs. 3ab, 4, 5, 6, 7). Such traumas look like one or several indentations of different depth, surrounded with a cylindrical projection of crushed and shifted bone tissue. Traumas of such a type did not lead to the destruction of vital functions, and the animals could have lived to an old age. The parietal bones of rhinoceros are very massive. Like armour, they seem designed by nature itself to protect the brain from strong traumatizing blows. The external compact tissue of the woolly rhino's parietal bones is 12-18 mm thick. Behind it there are spacious sinus cavities, then the inner compact tissue (no less solid). The thickness of the muscles in the parietal area is minimal, and so the wounds quickly cicatrized without being complicated by other diseases. It is known from the literature that the traumatic dama-

Figure 4 Parietal bone fragment with indentation, same specimen as Figure 3 (PIN RAN 170-8, the Middle Volga). Enlarged.

Figure 5 Skull of *C. antiquitatis* (specimen ZIN RAN 10.713, the environs of Krasnoyarsk, East Siberia). View from above (dorsal).

ges of skeletal bones by deforming arthrosis, osteomyelitis, and ankylosis are found in other large mammals (elephants, bison, horses, elk), too (Skorik 1979). In elephants such damage is often situated on the skull, while in the ungulates mainly the hind limbs are open to injury. It is likely that the traumas were received in the course of struggling for mates or forage. The localization of traumatic damage directly depends on fighting positions and behaviors. The traumas are confined to the areas that are most open to blows during fights. In the course of combat, rhinos meet head to head and fight using the big front horns (Frame 1972, Grzimek 1973a,b, Hunter 1992). It is quite understandable that in such a position the blows hit most often in the parietal area, or, if the head is turned sideways, on the nasal bones, orbits and maxillary joints.

CONSIDERATIONS ABOUT EXTANT RHINOS

In Figure 8, a photo of the head of an African white rhinoceros (*Ceratotherium simum* BURCHELL) named Barmaley from the zoo of Rostov-upon-Don, one can see traces of fresh wounds inflicted by the horn of a female named Pama. The localization of the wounds precisely coincides with the localization of traumatic damages on the skulls of the woolly rhinos reported here. Rhinos are known to be aggressive at times in the wild. Of extant rhinos only the African two-horned species (the black rhino *Diceros bicornis* LINNAEUS and the white rhino *Ceratotherium simum* BURCHELL) use their front horn in fights. The Indian rhino *Rhinoceros unicornis* LINNAEUS, though having a horn on its nasal bones (this horn sometimes reaches very impressive dimensions), does not use it in fights. This rhino strikes blows with its well-developed incisors, which leave deep

Figure 6 Parietal bone fragment with indentations, same specimen as Figure 5 (ZIN RAN 10.713, the environs of Krasnoyarsk, East Siberia).

Figure 7 Fragment of a parietal bone of *C. antiquitatis* (specimen BKM No. 5, Altai).

lacerations and heavily bleeding wounds. *Rhinoceros unicornis*, defending itself with its teeth, represents an exception. Such a way of fighting can be considered one of the archaic behavioural elements, characteristic o f the ancestral forms of rhinos that either had no horns yet or had very small ones. As for the two-horned rhinos, in both the extant and the Pleistocene extinct forms the front horn is the principal weapon. In adult animals it is two or more times longer than the posterior one. In extant African rhinos both males and females have very long front horns, and cows are record-holders in this respect. The maximum lengths of the front horns reported for female black and white African rhinos are 1345 mm and 1465 mm, respectively. The front horn of woolly rhinoceros often exceeded the skull length (maximum - 850 mm) by 200-250 mm. The black rhino *D. bicornis* is considered the most aggressive of the extant African rhinos (Frame 1972, Grzimek 1973a,b, Hunter 1992). It attacks not only conspecifics, but frequently other animals too (such as elephants and buffaloes). This may be accounted for by the densely vegetated features of its habitats and by its weak sight. If the rhino has not scented an approaching animal of different species before contacting it, the rhino may attack the intruder without hesitation. Conspecific males of white African rhinoceros, especially young animals, often are engaged in fierce fighting with each other. These fights may infrequently lead to serious injuries of rivals (Frame 1972, Grzimek 1973a,b, Hunter 1992).

Of special interest are the changes in behaviour of rhinos kept in zoological gardens. While in their natural conditions males and females treat one another more or less peacefully, but when held in captivity they become very aggressive toward their mates. Usually the cows behave aggressively (Garutt, unpublished data). Under natural conditions they also try to drive away other rhinos that are perceived as being too close, although males may be accepted during the breeding period. In captivity a more aggressive animal will provoke fighting. Sometimes this leads to fierce fighting in which more peaceful or weak animals may become victims and die. The aggressive behaviour of captive rhinos probably can be accounted for by the fact that they are kept in inadequate or crowded enclosures. If the area of an open-air enclosure is too small, the animals begin to compete for living space. In those zoological gardens where rhinos have plenty of room they do not behave aggressively and seem to coexist and mate with minimal aggression (Garutt, unpublished data). On the skulls of extant rhinos traumatic damages are rarely found or reported. It is possible that the Late Pleistocene rhinos were more aggressive when compared with the present ones, which live under climatic conditions characterized

Figure 8 White rhinoceros *Ceratotherium simum* BURCHELL from the Zoo of Rostov-upon-Don, Russia. Traces of the blows struck by a female's horn can be seen on the animal's head.

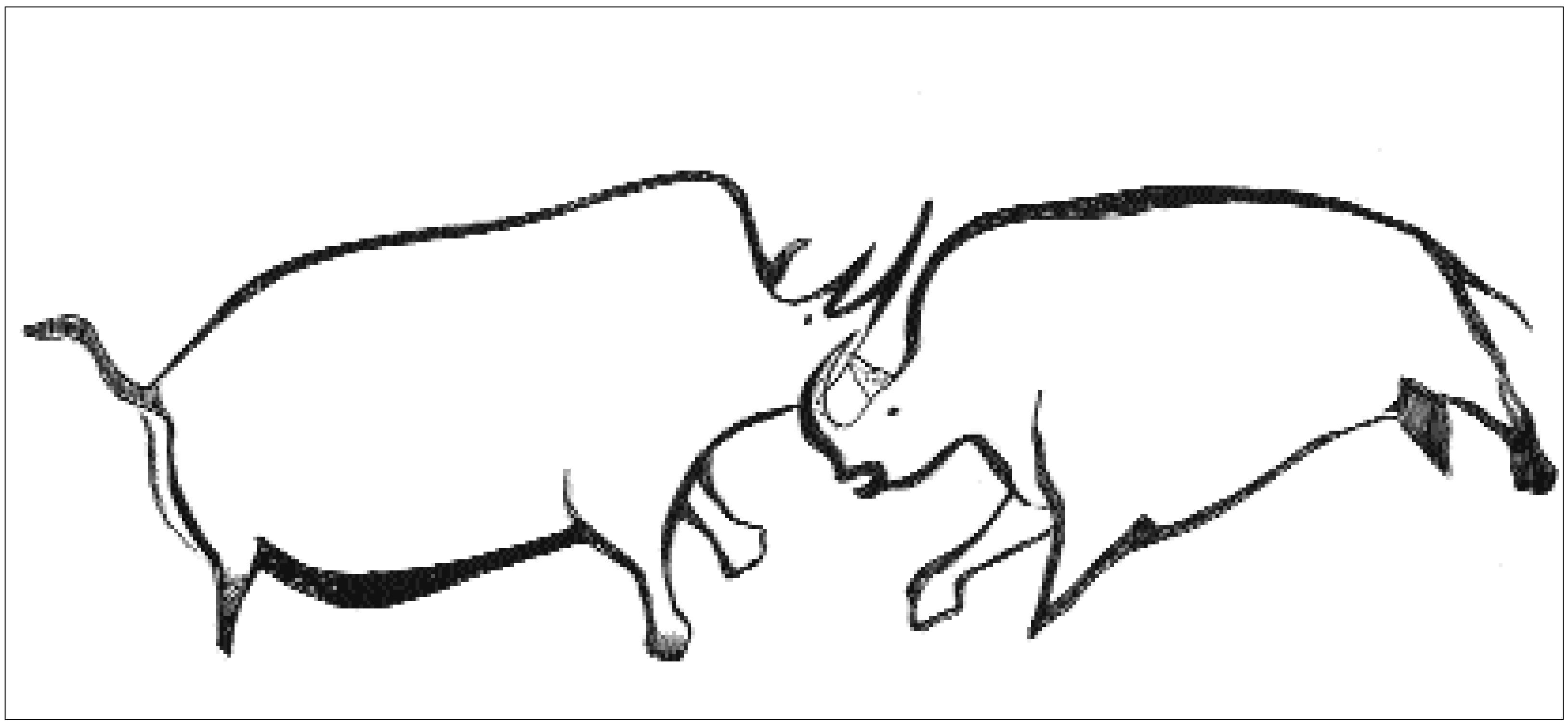

Figure 9 Depiction of two woolly rhinos from Chauvet Cave, France.The animals appear to be in a fighting posture identical to that seen in living species.

by small seasonal fluctuations in temperature. Probably the severe and unstable climatic conditions of the Late Pleistocene increased the degree of inter- and intraspecific competition among rhinos. Support for the similarities in behaviour between the Pleistocene and Recent rhinos is found in Paleolithic art depicting woolly rhinos interacting with conspecifics and other members of the faunal community. The most spectacular example of rhinos in Paleolithic art was found in late 1994, in France, in a cave named after its discoverer, Jean-Marie Chauvet. The rhino images in Chauvet Cave are shown in motion, unlike the images from many other sites, and are numerous, which is also unusual for other cave-painting sites. In one image, two woolly rhinos appear to be fighting in postures identical to those seen with living species (Fig. 9).

The last third of the Late Pleistocene witnessed dynamic climatic changes (Arslanov *et al.* 1981). Numerous rises and falls in temperature occurred within a short period of time. In lower latitudes the borders of the forest-steppe zone continually fluctuated, shifting sometimes to the north, sometimes to the south. The instability of the climate was especially pronounced between latitudes 50 and 60 North, and in the west (West, East and Central Europe) it was stronger than in the east (the Asian part of the continent). In the geochronological scale the climatic microcycles (within the limits of which the alternation of paleoecological stages occurred) may seem very small, but in comparison to a mammal's lifetime they were enormous periods of time, during which many generations changed. The different generations of animals had to adapt themselves to changing environmental conditions. Migratory animals could have sought other pastures. However, rhinos are territorial when living in low densities, and if spatial conditions are limiting due to fragmented habitats, rhinos may not have been able to migrate easily or very far. It has been shown by studies in population genetics that the periods that are very unfavourable for mammals are characterized by a disequilibrium in male/female ratio. Under normal conditions this ratio is 1:1. When unfavourable conditions prevail, males are born in greater numbers than females (V.B. Sapunov & V.V. Savitskii, unpublished data). The increase in numbers of males in a population is a good indicator of unstable and unfavourable environments (Geodakyan 1976, 1987). Taking this into consideration one can suppose that during unfavourable periods of paleoecological change the numbers of male rhinos in some regions could have increased. This would lead to stronger intraspecific competition and aggressiveness. Maybe this was the reason why skirmishes and fierce fights between males of woolly rhinoceros were more frequent than between modern rhino males in the wild. Judging by their dimensions and the development of the orbital processes and zygomatic arches all the skulls with traumatic damages belong to males. Mapping of the finds shows that they all are confined to the areas between latitudes 50 and 60 North, where climatic conditions of the last third of the Late Pleistocene were particularly unstable.

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