Fresh Data on the Food of the Siberian Woolly Rhinoceros

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The ecology of animals of past geological epochs has long engaged the attention of researchers. In this connection the woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach), shown in Fig. 1, evokes great interest. The remains of this wild animal are widely scattered in Eurasia, being embedded in Middle and in particular Upper Pleistocene deposits.

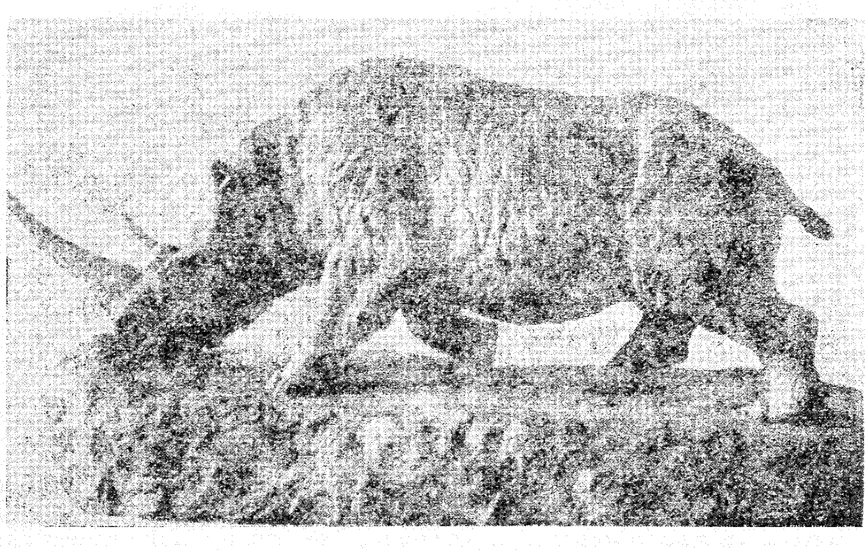

Fig. 1. Woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach). Sculptural reconstruction by V. E. Garutt (1949).

The anatomy and external features of the woolly rhinoceros are well known: investigations have uncovered not only its numerous bone remains but also the carcass with muscle, skin and wool preserved through natural mummification. The first discovery of this rhinoceros, preserved by permafrost, was made in 1771 by Yakutian hunters on the bank of the Vilyui River near Vilyuisk town. The head and two legs (front and hind) of this carcass were brought to Irkutsk and handed over to Academician P. S. Pallas. Under his instructions they were desiccated in an oven; the hairy cover was burned off and even the limbs were charred. The Petersburg Academy of Sciences received this find in this damaged state.

Academician F. F. Brandt [1] and L. I. Schrenk [2] gave descriptions of these relics.

A sad fate also overtook another rhinoceros whose frozen carcass was discovered in 1877 by a Siberian merchant, N. S. Gorokhov, on the bank of the Khalbui River—a tributary of the Bytantai (Balantai) River joining the Yana about 150 km north of Verkhoyansk near 68°30′N. The only part of this excellently preserved rhinoceros that survived was the head which was sent to the Irkutsk Museum (Fig. 2). It was studied by I. D. Cherskii [3-5]. Later, in 1879, the Siberian Department of the Imperial Russian Geographical Society handed the find over to the Zoological Museum of the Russian Academy of Sciences where it was investigated by L. I. Schrenk [2].

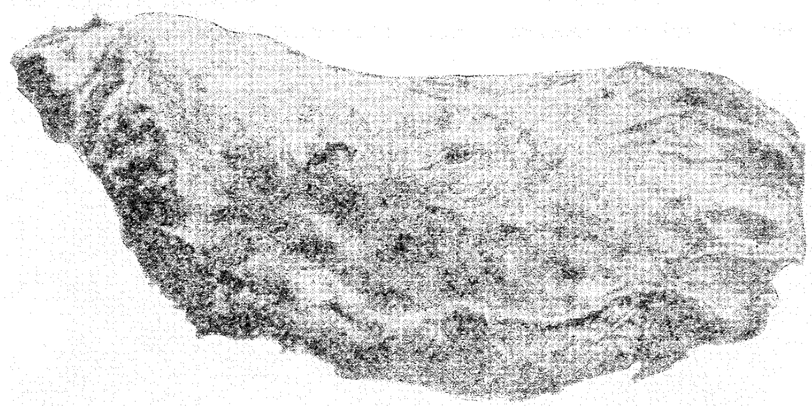

Fig. 2. Head of a woolly rhinoceros discovered in 1877 on the bank of the Khalbui River—a tributary of the Bytantai River (Yana Basin).

Part of the hindquarters of a rhinoceros with soft tissues and skin preserved in the frozen ground was discovered in 1948 in the valley of the Elga River—a lefthand tributary of the Indigirka. The remains of this rhinoceros, studied by Yu. N. Popov [6], were given to the Paleontological Institute of the Academy of Sciences of the USSR (in Moscow).

Two almost complete carcasses of the woolly rhinoceros were discovered (in 1907 and 1929) near Starunia in the Western Ukraine [7-10]. The carcasses of these rhinoceroses were preserved in Quarternary muds steeped in petroleum and salt. One is exhibited in stuffed form in the Lvov Natural Science Museum of the Academy of Sciences of the USSR and the second one in the Cracow Natural Science Museum of the Polish Academy of Sciences.

STUDIES OF FOOD RESIDUES OF THE WOOLLY RHINOCEROS

Investigation of the mummified heads and skulls of the rhinoceros preserved in the frozen ground of Siberia brought to light highly compacted particles of plants—residues of these animals' food—stuffed in deep crevices of the molar enamel.

The study of such plant residues was first undertaken by Academician F. F. Brandt [1] who investigated samples obtained from the teeth of the mummified rhinoceros head from the Vilyui and proved the presence of conifer fruit residues. K. A. Maier found in the plant residues ephedra (*Ephedra*) fruits and K. E. Merklin, willow (*Salix*) twigs.

The food residues from the teeth of the woolly rhinoceros were studied in greater detail in 1876 by I. F. Shmalhausen who received the material of the Irkutsk Museum from I. D. Cherskii and B. I. Dybovskii. Shmalhausen indicated that, judging by the degree of preservation, plant residues extracted from the teeth must have suffered prolonged maceration. In his opinion this justified the inference that they were residues of the animal's food and not just particles of plants that had accumulated accidentally in the dental cavities.

Besides the leaves of monocotyledonous (Gramineae) and dicotyledonous grassy plants Shmalhausen also identified twigs of spruce (*Picea*), larch (*Larix*), willow (*Salix*) and ephedra (*Ephedra*) of the Gnetaceae family. He specifically notes that residues of the stems and leaves of monocotyledonous plants (apparently grasses) predominated.

The inclusion in Shmalhausen's list of identified deciduous plants of spruce, fir and larch, which differ ecologically and are therefore incapable of growing together, may be explained in two ways. First, the food residues could have accumulated in the teeth of this rhinoceros over an extended time span during which the animal moved from one area to another, spending time in different landscapes. Second, the samples received by Shmalhausen from Irkutsk could have been extracted from the teeth not of one but of several skulls belonging to rhinoceroses that lived in different regions of Siberia. Regrettably there are no indications on this score in Shmalhausen's article.

For comparison we will furnish a list of plant residues found in 1929 in the strata enclosing the carcass of the woolly rhinoceros in Starunia (Western Ukraine). According to W. Szafer's data [9] the following forms were identified here: *Betula nana* L., *B. humilis* Schrenk, *Salix reticulata* L., *Dryas octopetala* L., *Polygonum viviparum* L., *P. lapathifolium* L., *Calluna vulgaris* var. *hirsuta* Presl., *Vaccinium uliginosum* L., *Thalictrum alpinum* L., *Thymus sudeticus* Borb., *Armeria* sp., *Phaca* cf. *alpina*, *Taraxacum* sp. and *Carex* spp.

The predominance of residues of dwarf birch, *Salix reticulata*, *Dryas octopetala*, *Polygonum viviparum* and other representatives of the modern tundra flora of Eurasia may provide an indication, according to Szafer, of the arctic climate of the locality at the time the Starunian rhinoceros lived.

In view of the current development of spore-pollen methods in botany, which are more effective than the methods employed earlier, the authors of this article decided to subject the plant remains of the Siberian woolly rhinoceros's food to additional study.

For these investigations it was necessary to obtain material which had been least affected by external factors. It would have been particularly valuable if plant residues from the stomach and kidney of the frozen carcass could have been obtained. Unfortunately these are not yet available.

These authors studied the head of the woolly rhinoceros discovered in 1877 by N. S. Gorokhov. To obtain food residues from the teeth of the rhinoceros V. E. Garutt opened the mouth cavity, which had long remained inaccessible to study. The opening was made from the ventral side of the head where there was no skin cover. The dried residues of muscles and connecting tissues between the rami of the lower jaw were removed by surgical scissors, thereby giving access to the mouth cavity. Plant residue was collected from crevices in the tooth enamel with the help of a dissecting needle and scalpel. The samples were sent in sterilized stoppered test-tubes to the Biogeocenological Laboratory of the Botanical Institute of the Academy of Sciences of the USSR where the material was studied by E. P. Meteltseva under the guidance of Academician V. N. Sukhachev.

The samples were processed by Post's alkali method: the application to sample A of Grichuk's separation method using heavy cadmium-bearing liquid did not materially affect the increase in pollen grains in the sample.

The residues of dried muscle and connecting tissues removed while opening the Rhinoceros's mouth cavity were used to determine the age of this find by radiocarbon dating. The investigations were carried out in Trondheim (Norway) in the Laboratory of Radioactive Dating of the Physical Institute of the Norwegian Higher School under the guidance of Prof. R. Nudahl. The material was sent to Trondheim on the initiative of A. E. Heinz, Director of the Paleontological Museum, Oslo.

Radiocarbon dating revealed that the woolly rhinoceros from the Khalbui River lived and died more than 33,000 years ago.

For comparison we will cite the results of radiocarbon dating of the soft tissues from the leg of the rhinoceros from the Indigirka [6] carried out in the same laboratory. The age of the Indigirka rhinoceros is more than 38,000 years [12, 13].

RESULTS OF SPORE-POLLEN ANALYSIS OF FOOD RESIDUES FROM THE TEETH OF THE KHALBUI RHINOCEROS

A definite count of pollen or spores of the representatives of the following group of plants was detected in samples A and B (Table 1).

What is striking here is the small number of pollens of arboreal forms and abundance of pollens of herbaceous forms. Of the latter the large number of grass and wormwood pollens deserves special mention.

Even granting accidental importation of some pollen grains in recent times, the preponderance of grass pollens (148 grains) and wormwood (37 grains) in the samples indisputably proves that the major part of the pollen entered the rhinoceros's mouth cavity and teeth along with food while it was alive. The pollen analysis is not yet complete: only families and genera are identified.

Table 1

Group	Count of grains, pollen or spores in samples	
	A	B
Arboreal		
Birch (*Betula*)	5	4
Alder (*Alnus*)	1	—
Herbaceous		
Grasses (Gramineae)	90	58
Wormwood (*Artemisia*)	24	13
Crowfoot family (Ranunculaceae)	—	4
Pink family (Caryophyllaceae)	3	3
Thistle family (Compositae)	1	—
Unidentified (pollen defied identification)	5	—
Spore		
Fern	3	—
Club-moss family (*Lycopodium*)	2	—
Spores of unidentified plants	1	—

The two spectra presented are suggestive of a forestless area. The distinct predominance of grasses and wormwood indicates that the plant communities were of the meadow and steppe type.

SOME DATA ON THE MODE OF LIVING OF THE SIBERIAN WOOLLY RHINOCEROS AND THE CAUSES OF ITS EXTINCTION

Our data and the data of other researchers on the composition of the food of the Khalbui rhinoceros allow of the inference that this animal was basically herbivorous and only occasionally may have consumed twigs of shrubs and trees for food.

That the woolly rhinoceros fed on herbaceous plants is also borne out by the following anatomical and morphological features.

1. *Body structure.* Studies of the biology of rhinoceroses living now have revealed the clear dependence of the general structure of the animal's body on the mode of living, more correctly on the type of food. Thus rhinoceroses which feed chiefly on twigs and leaves of shrubs and trees generally have relatively long limbs and short torsos. Forest rhinoceroses such as the Indian unihorned rhinoceros *Rhinoceros unicornis* L., the Zond rhinoceros *R. sondaicus* Dermeret, the Sumatran rhinoceros *Dicerorhinus sumatrensis* (Cuvier) and a denizen of forest steppe, the African black rhinoceros *Diceros bicornis* (L.) exhibit this structure. On the contrary, the limbs of the African white rhinoceros *Ceratotherium simum* (Burchely), which feeds mainly on herbs, are relatively short and the torso therefore appears very elongated.

The woolly rhinoceros we studied also possessed short limbs and a long torso (Fig. 1), i.e. it practically did not differ in structure from the African herbivorous rhinoceros.

2. *Structure of the skull.* The plane of the occiput of rhinoceroses forms an angle with the base line of the skull which varies with the rhinoceros type. The magnitude of this angle is an index of the position of the head relative to the neck and torso which is directly dependent on the mode of living and type of food these animals eat [14, 15]. This angle is smaller for forest and forest-steppe rhinoceroses, such as the Indian and black African, than for the herbivorous white rhinoceros.

The plane of the occiput of the woolly rhinoceros forms an obtuse angle with the base line of the skull.

This indicates that the head is inclined relative to the torso due perhaps to grazing on herbaceous vegetation on the ground.

3. *Structure of the nasal bones and horn.* The skull of the woolly rhinoceros, unlike that of present-day rhinoceroses, had a thick bony nasal septum fused with highly developed nasal and intermaxillare bones.[1]

The woolly rhinoceros had two horns on its head: front and rear. The first bears signs of severe abrasion at the front edge. In our view it is perhaps an indication that the woolly rhinoceros used the front horn, in addition

[1]The nasal septum of young woolly rhinoceroses is not fully ossified.

to its hoofs, to get at food under the snow in winter. This use of the horn would also explain why this animal developed a strong ossified nasal septum

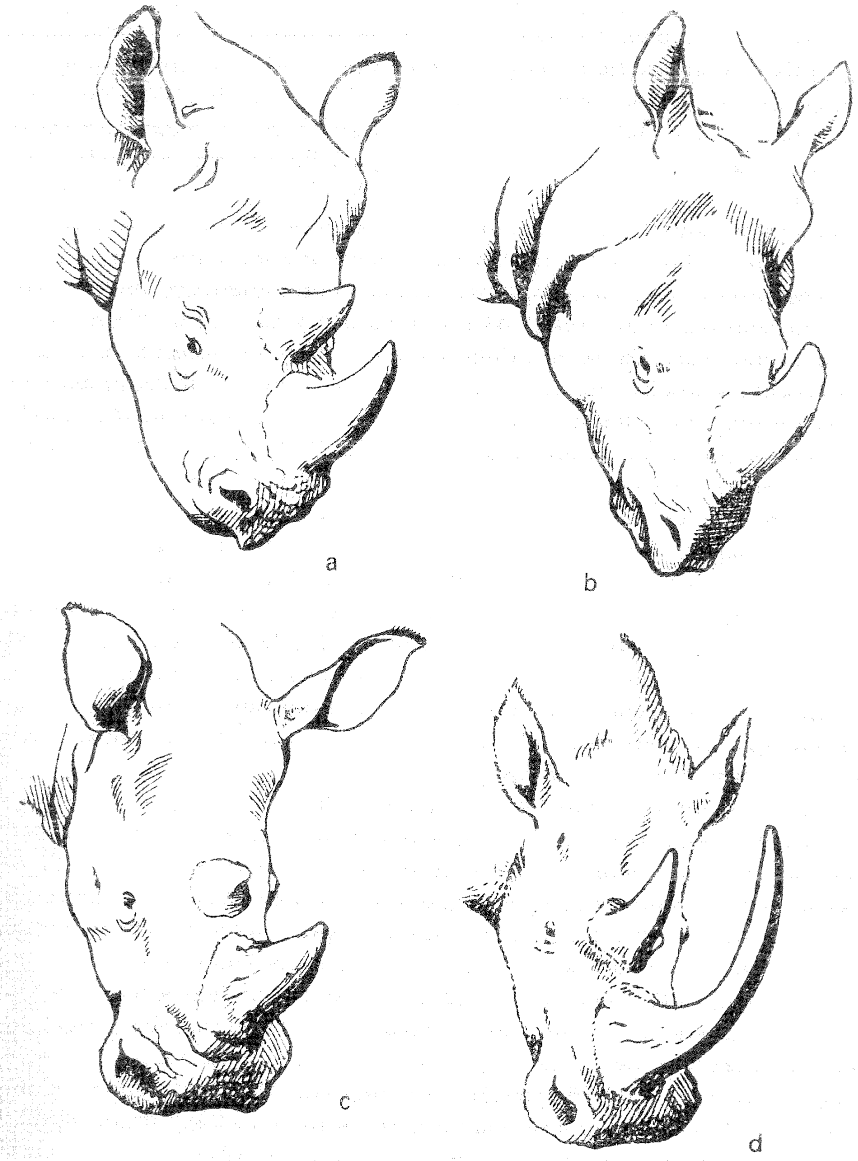

Fig. 3. Structure of the upper lip of rhinoceroses:
a—African black (*Diceros bicornis*); *b*—Indian unihorned (*Rhinoceros unicornis*); *c*—African white (*Ceratotherium simum*); *d*—Woolly rhinoceros (*Coelodonta antiquitatis*).
[Drawing by V. M. Smirin].

—an additional support for the nasal bones carrying the front horn; the nasal septum of other rhinoceroses is formed of cartilage.

4. *Structure of the upper lip.* The upper lip of forest and forest-steppe species of contemporary rhinoceroses feeding primarily on twigs and leaves is highly developed, fairly long, hanging down and very mobile (Fig. 3). Using this lip like an elephant his trunk, these animals clamp on twigs, gnaw the bark off and pluck leaves. The upper lip of the steppe rhinoceros, on the other hand, is short, broad and adapted for grasping herbs (Fig. 3).

Studies of the mummified heads of the Khalbui (Fig. 2) and Starunia rhinoceroses showed that this animal, like the African white rhinoceros, had a broad, short lip, confirming the view that it fed on herbs.[1]

The species *Coelodonta antiquitatis* (Blumenbach) originated and evolved possibly somewhere in Central Asia and North China. Relics of the rhinoceros of the genus *Coelodonta* exhibiting some similarity with the structural features of the woolly rhinoceros[2] were found in Nihowan, China, in deposits corresponding to Villafranchian in Europe. The ancestors of the woolly rhinoceros spread northward and westward to Europe, gradually adapting themselves to the environments of the cold periglacial steppes and tundra.

By the second half of the Pleistocene the woolly rhinoceros was widespread throughout the Eurasian periglacial zone, sometimes right up to the Arctic Ocean coast in the north and Chukchi and Kamchatka in the east.

The largest number of remains of the woolly rhinoceros in the Asian part of its range have been encountered in the Transbaikal region [18] which was a zone of arid steppes and semideserts in the Pleistocene. The number of rhinoceroses discovered decreases northward. A similar phenomenon was also observed in East Europe; no remains of this animal were found in Europe north of 63°N [17, 19].

The decrease in the number of remains of the woolly rhinoceros toward the north proves that this animal occurred more rarely in those places. Apparently living conditions in the north were less favorable in the Pleistocene. The authors of this article agree with the view of E. A. Vangenheim and E. I. Ravskii [20, 21] that the basic ecological factor in the case of the woolly rhinoceros was arid climate rather than low temperature.

According to R. E. Giterman [22] a cold and arid climate with tundra-steppe xerophytic vegetation was a characteristic feature of the periglacial zone of Yakutiya during the Zyryanka and Sartan glaciations. A whole range of evidence of specific periglacial phenomena in the Upper Pleistocene deposits of Siberia (fissured-veined ice, cryoturbation, etc.) bears witness to the cold, sharply continental climate of this period [23].

[1]The upper lip of the head of the Vilyui rhinoceros supplied by P. S. Pallas was not preserved.

[2]H. D. Kahlka [16] characterized this form as a new species, viz. *C. nihowanensis*.

L. V. Golubeva [24] believes that the whole of East Siberia in the first half of the Zyryanka period had periglacial landscapes of the tundra type, where Altai birch flourished, and in some places of the forest-tundra type. Cold steppe-type landscapes dominated by wormwoods, grasses, goosefoots and *Selaginella sibirica* predominated throughout East Siberia in the second half of the Zyryanka period. Periglacial landscapes with a preponderance of steppe elements were also prevalent here during the Sartan period.

According to R. E. Giterman, L. V. Golubeva, E. V. Koreneva and O. V. Matveeva [25] tundra and cold steppe landscapes developed in northern and central West and East Siberia at the close of the Pleistocene. Xerophytic groups were dominant in the vegetation here but tundra elements were also significant. The role of arboreal vegetation at this time was minimal; only in places most favorable for trees do we find birch, larch and some other varieties. Periglacial steppes occupied the southern part of Siberia.

A different view is held by E. M. Shcherbakova [26], who cites the results of the spore-pollen analysis of the alluvial deposits of a 45-meter terrace of the Angara River containing bones of the woolly rhinoceros. A large number of pollens of arboreal plants, viz. birch, cedar, spruce and fir, were found in the enclosing rock, providing evidence, according to this author, that the Angara Basin was highly wooded in the Quaternary period. E. M. Shcherbakova's data, which are visibly at variance with the data of other researchers, perhaps only indicate the existence of forests in the Angara floodplains. Generalizing the results of all the paleobotanic studies, M. P. Grichuk [27] comments that a cold arid climate was generally characteristic of the second half of the glacial ages (xerophytic phase). In his view this generalization is valid for all of the USSR.

We have already referred to remains of the woolly rhinoceros discovered on the Arctic islands. These irrefutably indicate that in certain parts of its range it reached the extremity of the Asian continent which at that time included a large part of the submerged shelf. In this context the question that naturally arises is why the rhinoceros did not enter the American continent across the Bering Strait.

It is well known that in the Pleistocene, when the Bering "bridge" was formed, there were repeated exchanges of faunas between Asia and North America. Many beasts that were contemporaries of the woolly rhinoceros, such as the mammoth *Mammuthus primigenius* (Blum.), the ice-age bison *Bison priscus* Boj., the ox *Ovibos mochatus* Zimm., the saiga *Saiga ricei* Frick, etc., migrated to America. What factors prevented the woolly rhinoceros from migrating there? There are several viewpoints on this score.

C. C. Flerow [28] believes that the rhinoceros could not cross the Bering Land Bridge because of the absence in this region of shrubs whose tender shoots served for food.

V. I. Gromov (oral exchange) is of the view that the woolly rhinoceros lived in the far north of Siberia in the Riss and Riss-Wurm, i.e. at a time when there was no link between Eurasia and America. The first "wave" of immigrants to America occurred some time around the Villafranchian-Pleistocene boundary. There was still no rhinoceros in North Siberia at this time. Apparently it intruded only in the Khazara period, i.e. in the Mindel-Riss, and when the second "wave" of migration to America began (Early Wurm) there was no longer any rhinoceros in North Siberia or only very few.

The woolly rhinoceros became extinct in Eurasia perhaps at the end of the Pleistocene. According to some data it perished somewhat earlier than its contemporaries, such as the mammoth, horse, bison, saiga, etc. Thus V. I. Gromov [29] points to the absence of rhinoceros remains in the Late Paleolithic (Magdalenian) deposits of East Europe and Siberia where remains of the mammoth and other beasts are plentiful.

Some researchers ascribe the extinction of the woolly rhinoceros and of contemporary animals to the exterminating activity of man. It should not be forgotten however that the density of population, particularly in the northern parts of Eurasia, was negligible in the Paleolithic and hence the role of man in the extermination of contemporary animals could by no means have been significant [30, 31].

The reason for the extinction of many Pleistocene mammals, particularly of large ungulates, lies in the change of physiogeographic environment. A general rise in humidity and the attendant increase in ice thickness in winter and in swamp formation in summer recorded at the Pleistocene-Holocene boundary were apparently the causes of the extinction first of the woolly rhinoceros, incapable of adapting to long migration, and then of its associates, viz. mammoth, horse, bison, etc.

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