

Woolly Rhinoceros: Morphology, Systematics and Geological Significance

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INTRODUCTION

Rhinoceros of this type are common in Pleistocene sediments in most of Eurasia, within Russia's borders and across its territory. Numerous woolly rhinoceros remains have been uncovered in a fossil state. Fossils of this group of mammals are not inferior to those of elephants.

Rhinoceros possess massiveness and solidity of the bones of the skull and postcranial skeleton. These aspects contribute to its well-preserved remnants in sedimentary rocks, in contrast to the skulls of elephants, which are poorly preserved in the fossil state.

Relevance of the work: Ever since the first discovery of rhinoceros skulls and mummies brought from Siberia by academician P.S. Pallas, museums in Russia have accumulated considerable osteological material of the woolly rhinoceros. However, to date the genus *Coelodonta* remains poorly understood and its geological significance is lacking in clarity. Also, *Coelodonta* taxonomy is poorly developed due to an insufficiently studied morphology.

Since the beginning of the 20th century and into the present, for the purposes of determining stratigraphy of Pleistocene sediments, scientists used mainly elephant and mammoth teeth or skulls despite sample sizes being small in number.

However, the lack of cranial material of fossil elephant and the use of some of their teeth for the purposes of determining stratigraphy (which are highly susceptible to morphological and functional variability) can lead to errors in the determination of age. On the other hand, rhinoceroses are more promising for age determination and refinement of paleogeographic data: such as climate and landscape.

The purpose of research: The identification of morphological and developmental traits in rhinoceros reflects their adaptation to diverse environmental conditions in the Pleistocene, which could be used to determine their age and more paleogeographic data. To achieve these goals requires the following tasks: a) the study of the totality of osteological material, horns and mummified heads of *Coelodonta* assembled in the territory of northern Eurasia (within the borders of the former USSR), analysis of the distribution and conservation of finds, in accordance with their morphological diversity, b) exploration of the features of ontogenetic development of skull dentition of *Coelodonta* enabling a more precise determination of the age of the remains of animals, c) identification of the ancestral phylogenetic relationships (unknown in the fossil record) between related forms.

Major protected positions: 1. Based on morphological differences highlighted two types of woolly rhinoceros, evolutionary adapted to different environmental conditions: the steppe *Coelodonta lenensis* (Pallas 1772) and the forest *Coelodonta antiquitatis* (Blumenbach 1799), which were previously allocated to the rank of subspecies: *Coelodonta antiquitatis pristinus* Rusanov and *Coelodonta antiquitatis humilis* Rusanov from single specimens from the Pleistocene deposits of Yakutia. This restores the undoubted scientific priority of the Russian researcher P.S. Pallas and his historical first description of the woolly rhinoceros. 2. Historically assumed earlier origins (early Pleistocene) of these two types of woolly rhinoceros which evolved at different geographical locations; Asia (steppe species) and Europe (forest-steppe species). 3. It has been demonstrated that the last *Coelodonta* rhino habitat before extinction at the boundary of the Pleistocene-Holocene was in the Transbaikal territory, Mongolia and northern China.

Scientific novelty: First to examine *Coelodonta* rhinoceros the author sought out all available osteological material in the collections of Russia. Then, the author studied the ontogeny of the dental system of the woolly rhinoceros from the early juvenile stages (milking calves) to very old individuals. At this time the author studied and described the skull of a woolly rhinoceros in its early developmental stages. For this investigation the author studied the large amount of cranial material and specified scheme ontogeny of the woolly rhinoceros skull presented by M. Borsuk-Bialynicka (Borsuk-Bialynicka 1973). Using serial material the author highlighted morpho-adaptive features in the structure of the skull and dentition of *Coelodonta* indicating different habitat conditions in landscaped areas, and thus confirmed the assumptions of F. Zeuner (Zeuner 1934), H. Loose (Loose 1975) and M. Fortelius (Fortelius 1982,1985). In addition the author studied 32 horn samples in detail and *Coelodonta* macromorphology; determined age, sex differences and noted morpho-adaptive signs of the habitat of these animals. Then the author studied intra-vital *Coelodonta* skull injuries, which gave more information about the features and regulation of the intra-specific behavior of woolly rhinoceros. Next, the author completed an audit of the systematics of *Coelodonta* rhinoceros and highlighted two distinct species with characteristics of their habitat, radiocarbon dating, and geological knowledge. Lastly, the author collected generalized materials of woolly rhinoceros residues for radiocarbon dating (34 C14 dates), which are the basis for the conclusions of the distribution and the extinction of *Coelodonta* rhinoceros.

Practical value: The whole set of morphological data allow us to represent the breadth of adaptive responses of *Coelodonta*, as an example this kind of mechanism is presented to illustrate adaptations to different environmental conditions during the Pleistocene by mammals in other global and regional climate equations. The study of different woolly rhinoceros species makes them promising for determining stratigraphic age and useful for determining paleogeographic data.

Factual material: Remains examined during the study include; a collection from the Mining Museum, St. Petersburg Mining Institute (Technical University), collections of the Zoological Institute, and materials from the Geological Institute of the Russian Academy of Sciences in Novosibirsk, the Geological and Mineralogical Museum of the University of Kazan, the Geological Museum in Vernadsky, the Zoological Museum of

Moscow University, and the Anthropological Museum at Anuchina. The author also studied materials in the collections of local museums in 35 cities of Russia and neighboring republics, which she found particularly valuable, as they present a serial of regional material, the value of which is usually not recognized sufficiently.

The study of local museum collections (which are often represented as piles of bones in storage), was preceded by a great work of systematizing, identifying and preserving of samples in decaying adhesive solutions. To further assist, the author conducted trainings with local museum staff on the methods of study, identification of the fossil materials, as well as its preservation, in order to help to preserve these collections.

For preparatory background during the years (1978, 1979, 1982, 1986), the author conducted field research on the excavation of Paleolithic encampments at Kos-Tenko (Voronezh region), Yudinovo (Bryansk region) and Gunners (Ukraine), where woolly rhinoceros was the definition of osteological material.

For comparison, the author studied the collections of Pleistocene rhinoceroses from localities of Ehringsdorf, Untermaasfeld, Sussenborn and others in the collection of the Institute of Quaternary Geology of Weimar (Germany). The author also studied a large collection of skulls of modern rhinos; *Diceros bicornis* Linneaus and *Ceratotherium simum* Burchell (70 samples) in the Natural History Museum of Berlin (Germany).

During 1989, 1990 and 1991 observations were made by the author on living two-horned rhinos; *Diceros bicornis* L. and *Ceratotherium simum* B. at the zoos of Tallinn (Estonia) and Rostov-on-Don (Russia). During observations the author made numerous drawings reflecting different aspects of the behavior of these animals.

Testing work: The main results of the dissertation were presented at the All-Union Conference on the study of Mammoth Fauna (1987, 1988, 1991, St. Petersburg), at the International Symposium for the Study of Mammoth (1995, St. Petersburg), at the International Museum Symposia (1995, St. Petersburg) and at the All-Russian Paleontological sessions (1996, 1997, 1998). Topics of the dissertation are published in 20 papers. Three articles are in print at the time the dissertation was written.

Structure and scope of work: Dissertation is presented in 247 pages, includes 51 drawings, 107 pictures, and 13 tables. The work includes an introduction, 10 chapters, a conclusion and bibliography (with 106 references, including 59 foreign sources).

CONCLUSIONS

These findings do not contradict morphological studies of the author, who attributes this pattern to the steppe adapted woolly rhinoceros *Coelodonta lenensis* Pallas, that inhabited exposed areas of steppe landscapes and ate mostly herbaceous vegetation.

In Nakhodka in 1972 in the village of Curapcha (Yakutia) a complete skeleton of a woolly rhinoceros was found with the remains of soft tissue and frozen monolith intestine. Spore-pollen analysis of its contents revealed the presence of a large number of herbaceous plants of steppe associations: *Artemisia*, sedges, Asteraceae, and Caryophyllaceae. Pollen of the following trees was determined P. 205 larch, birch, spruce and pine (Lazarev 1998).

Recent results on radiocarbon dating showed C14 age of the Churapchinsky rhino at 19,000 years, which corresponds to the Sartan time in Yakutia. Studying leftover food from the stomachs of Pleistocene mammals, researchers are better able to judge the food preferences of the animal in a short time before its death. Almost all corpses of Pleistocene mammals which have had food residue investigated, had died in the late summer or early fall. Accordingly, regarding the balance of the plants that were in the stomachs of animals at the time of their death, it is difficult to judge the floristic composition and percentage of herbaceous and woody plant species in their food in the winter or spring seasons. In addition, regarding migration behavioral features, woolly rhinoceros are not considered to be an active migrating animal species.

Because of insufficient information on the composition of the food of woolly rhinoceros, now we can take into account some of the morphological features of the skull, dentition and postcranial skeleton of a woolly rhinoceros, which show some aspects of adaptation to the adjustment of eating food with high content of woody plant species (mostly shrubs). These morphological features were characteristic of the low elevation woolly rhinoceros *Coelodonta antiquitatis* Blumenbach that lived in areas of the river beds, especially where thickets of willow, birch and aspen were located. Land occupied by sedges and cotton grass also provided good habitat.

According to many researchers (Tikhomirov 1962, Grichuk 1982, Velichko, Gerasimov 1981) the Kazantsevo era (Mikulino) interglacial characterized Europe p. 206 and Russian Asia as dominated by widespread deciduous and coniferous-deciduous forests. Steppes and tundra zones did not exist, whereas in Siberia steppes and tundra landscapes were dominate. To a great extent this opinion agrees, as radiocarbon dating residues of woolly rhinoceros from the area of the northeast Siberia show that during the middle Pleistocene woolly rhinoceros was widely distributed in the area. However, rejecting the presence of even small areas of steppe landscape in the western part of the continent, it is difficult to explain how the woolly rhinoceros could get to western Europe during the middle Pleistocene, and the species probably experienced a period of required adaptation to produce some morphological adaptive properties for the existence in the new environmental surroundings.

So the above point of view could explain why the woolly rhinoceros was less common (and consequently its scarcity of fossil remains) in western Europe during the middle Pleistocene, but it is highly doubtful to assume that in eastern Europe during the middle Pleistocene woolly rhinoceros was not available because of the dominance of forest landscapes. If we accept this assumption, then it would suggest rhino fossil remains and measurements should be significant for the east European plain, as noted in western Europe. However, the fossil remains of *Coelodonta* rhinos are rare on the east European plain.

In the climate caused changes of plant communities according to V.V. Ukraintseva there are two main stages: The late Pleistocene and Holocene. Major trends that characterized the late Pleistocene stage were multiple shifts of warm (interglacial) and cold (glacial) rhythms. Interglacial vegetation was characterized by the dominant forests. The general plan of biozoning was p.207 similar to the modern zonal structure of northeast Siberia (Ukraintseva 1988).

Following (Kazantsevo) the Karginsky interglacial captures the nature of vegetation change in all regions of Siberia (Kind 1974). At this time it was warmer in Siberia than in the European part of the continent (Arslanov 1982, Kind 1974). The dominant type of vegetation in Siberia was forest. Chukotka grew larch woodland with an undergrowth of elfin cedar and some areas were covered by shrub tundra (Yurtsev 1974).

On the Kolyma lowland larch-birch forests grew with shrub birch and alder with widely developed sphagnum bogs present (Giterman 1985). Similar type of forests grew in the mountainous part of the Kolyma River basin (Yurtsev 1974). In the lower reaches of the Indigirki River swamp forests and woodlands of Gmelin larch spread, alternating with areas of different types of tundra (Throat 1982). Farther south in the upper Indigirka larch trees mingled with birch (*Betula platyphylla*, *Betula* sp.), spruce (*Picea ajanensis*, *Picea obovata*), siberian pine (*Pinus sibirica*), and woolly alder (*Alnus hirsuta*). In central Yakutia steppe grass-forb and sagebrush-forb (Tomsk 1981) were widespread. The northern part of the west Siberian lowland was dominated by coniferous forests. As the latitude of Omsk and Novosibirsk moved into forest-steppe the south was dominated by desert.

These paleo-floristic studies by the above authors linked well with the data dissemination of bone remains of woolly rhinoceros. Obviously during the Karginsky interglacial the forest-steppe, small species of woolly rhinoceros *Coelodonta antiquitatis* were widely distributed in northeast Siberia. In these areas the large steppe species *Coelodonta lenensis* were inferior in number p.208 maintaining populations below the southern latitudes 48 ° - 50 ° of Siberia and Baikal, where a number of fossil remains of this species have been discovered.

10.4. Paleo-etiological aspects of woolly rhinoceros behavior: Observations in nature of the specific behavior of modern African rhinoceros *Diceros* (calving) and *Ceratotherium*, which belong to the same subfamily *Dicerorhinae* as *Coelodonta*, suggest

the possibility of some similarities in behavior between modern rhinos and woolly rhinoceros.

Unlike nutritional habits in black and white African rhino is also reflected in the features of their behavior: the group behavior, relations between the sexes, and mating behavior.

Most similar to the ecology of the woolly rhinoceros, the African white rhino live in open steppes and will form in groups of 10 - 15 and even up to 20 individuals (Grzimek, 1973). This group behavior of a steppe species is understandable when you consider that in open spaces with visible predators even a very large solitary animal is unprotected.

African black rhinoceros, which lives in dense, thorny acacia scrub where they find food, are hidden from large predators, and therefore do not form large groups. Most often, they browse and scatter singly into a territory, rarely forming groups of up to 5 individuals (Grzimek, 1973). When two animals come together, it is usually a female with a calf or two males. Only during watering for a short time of the day, do black rhinos form small groups.

Rhinos develop a nervous type and difference in the speed of defensive reactions relative to features of their group behavior. The African white rhino inhabits steppe environs and is generally calmer and will tarry. P 209 As in other animals within group behaviors the individual rhino feels well protected in the group.

Forest black rhinos have an unstable nervous type, can be easily irritated and aggressive, and often do not attack the enemy who is in front of them (Grzimek 1973). In thickets, not seeing the enemy and only depending on hearing and smell the black rhino is always ready to repel an attack.

(Fig. 10.3) Herd of woolly rhinoceroses. Wall mural of Paleolithic age from the cave at Chauvet, France

In extant species of rhinos all of the above behaviors were probably inherent to a certain extent and the woolly rhinoceros is no exception. On the Paleolithic cave murals of the Franco-Cantabrian region there are images of rhinos. However, these ancient frescos in time corresponding to 30,000 - 40,000 years ago depict solitary figures of animals, despite the fact that the drawings are very detailed. However, also in the cave at Chauvet, France, the age and cultural layers of frescos which date to 20,000 years ago, a unique fresco depicting a herd of woolly rhinoceros was discovered (Fig.10.3).

How can we explain these different facts? Especially if earlier hunters had not developed the ability to track and plot the image, or the fact that while the woolly rhinoceros may not be so numerous in western Europe, and did not congregate in large groups?

Paleolithic images of rhinos (Fig.7.9) show some differences in exterior features. There are figures with a long body, short limbs and an elongated head, extended at the end of the muzzle. Other figures are almost square, with short and broad heads with only a few having pointed muzzles. Perhaps ancient man portrayed woolly rhinoceros belonging to different species: the steppe and forest?

Visible differences in the morphology of two species of woolly rhinoceros allow the author to suggest that only the steppe species of woolly rhinoceros *Coelodonta lenensis* Pallas formed in relatively large groups of several dozen individuals which could be called herds.

The other type of woolly rhinoceros *Coelodonta antiquitatis* Blumenbach, which lived in forested landscapes, according to the author, congregated in small groups, but probably not as small in number, as in contemporary African black rhino.

Comparing modern rhinos, which live in a tropical climate, with no significant difference in the variation of seasonal temperatures, it is necessary to take into account the fact that the woolly rhinoceros, as well as other representatives of the mammoth fauna lived during a temperate Pleistocene and in northern latitudes during a period of global cooling. The difference in the amplitude of seasonal temperature was very high.

Therefore, despite some similarities in their ecology and behavior peculiarities with living rhinos, woolly rhinoceros had significant differences.

Harsh climatic conditions during the Pleistocene strengthened the competitive relationship between individuals in the population. This was particularly important for the survival of females, ensuring stability of the existence of the species as a whole. Despite good adaptation to the Pleistocene mammalian cold climate conditions, the adverse effects of natural selection in temperate and northern latitudes was stronger than in the warm tropics.

In modern rhino species both *D. bicornis* and *C. simum* exhibit particularly marked territorial behaviors. Females with calves will exhibit aggressive behaviors by driving away adult males. Also males of white and black rhinos fight among themselves, during which animals rarely hurt each other. Although there have been cases when these contests ended in the death of one of the animals (Grzimek 1973). Probably, fierce fighting took place in unfavorable periods of drought, when with a shortage of food and water competitive relationships are enhanced in animals.

Also, in late Paleolithic cave murals are images of woolly rhinos fighting with mammoths (Fig.10.4a-b). In 1994, in the Chauvet cave, a woolly rhinoceros image (Fig. 10.4g) depicting conflict between individual rhinos was discovered.

These images are eloquent testimony that among these large Pleistocene mammals intra-specific competitive relations was pronounced, and was aimed towards the survival of the population in extreme climatic conditions.

(Fig.10.4) Paleolithic prints and murals depicting mammoths and woolly rhinoceroses in a combat poses; a - mammoth in cave La Madeleine b - mammoth in cave Laugerie-Haut, v - mammoth in cave Rouffignac, g - woolly rhinoceros in Chauvet cave.

Besides the above evidence of competitive behavior in the woolly rhinoceros the author offers more conclusive facts.

In the study of a large series of woolly rhinoceros craniological material the author has identified intra-vital skull damage to the bones. Currently the author has located 15 such samples.

(Fig.10.5) The skull of a woolly rhinoceros NIN sample № 170-5, Middle Volga, a - top view, b - fragment of the parietal bones with injury.

Skull damage is localized in the parietal bone where there are deep dents (from 5 to 18 mm) in the outer layer of the parietal bone despite having a very strong and thick compaction. The outer edge dents are biased towards the direction of impact of bone tissue. (Fig.10.5a-b,6a-b,7a-b). Due to the strength and massiveness of the parietal bones and the minimum thickness of muscle and skin layer in this area, inflicted wounds of this type were not fatal to the animals and healed quickly without disease complications.

(Fig.10.8) The skull of a woolly rhinoceros, GMKGU sample number 742, Kazan Province, Middle Volga, a - top view, b - fragment of damaged bones.

This is another example of a lifetime skull injury with skull damage localized in the region of the nasal bones, eye sockets, and jaw joint. However on the bones exposed to injury painful changes developed. The initial mechanical trauma became complicated by post-traumatic diseases; osteomyelitis or arthrosis. (Fig.10.8a-b,9a-g).

Tissues below the scalp are vital. Here are important groups of muscles, ligaments, nerves and blood vessels. Injuries to these tissues can lead to soft tissue destruction and strong trophic disorders in the body. Recuperation often requires p. 216 more time, so individuals are exposed to infection and complications from other diseases. Injuries of this magnitude usually lead to a more rapid death of the animal, as evidenced by the absence of compensatory changes in the skulls (Fig.10.9g).

(Fig. 10.9) The skull of a woolly rhinoceros, the sample GMGPP 7/357. Perm region, Urals, a- view from the teeth, b - lower jaw, top view, g - fragments of zygomatic process of the temporal bone of the skull and the articular head of the mandible damaged by arthrosis.

Localization of traumatic injuries is dependent on posture and techniques used by animals when fighting. Traumatic injuries are distributed to those areas that are the most open and accessible to attacks by opponents. During fights woolly rhinos converge head to head and attack with the large frontal horn. Naturally, in this

position horn strikes often reach the parietal region, and at the lateral surfaces of the head where blows fall in the region of the nasal bones, eye socket and jaw joint.

(Fig.10.10) African white rhino (*Ceratotherium simum*) at the zoo of Rostov-on-Don. At the head of the animal, in the crown, peri-oral area around the jaw joint and the orbit visible injuries from female horn blows.

In 1990, the author was able to watch the fight between the female and male African white rhinoceros in the zoo at Rostov-on-Don. A female white rhino constantly behaved aggressively towards the male, attacked him, and began to hit the male in the head using her frontal horn. After some time, the zookeepers removed the angry female rhino to a winter room. Author photographed the male rhino head with traces of fresh wounds. Their localization on the head of the animal exactly coincides with the localization of traumatic injuries to the woolly rhinoceros skull bones (Fig.10.10).

(Fig.10.11) The skull of a woolly rhinoceros, GMKGU sample number 747, Kazan Province, Middle Volga, a - side view, b - dorsal view.

In a series of traumatic injuries of the woolly rhinoceros skulls with osteoma belong to a special group. This feature tends to be localized in the occipital-parietal ridge (Fig.10.11a-b,12a-b). Osteoma is a benign tumor that forms in cartilage damage. At the site of trauma cartilage cells begin to divide rapidly, forming a tumor, which eventually ossifies. Osteoma is formed only during the early stage (pediatric age) of an organism (Revell 1993).

Localization of lesions in the occipital-parietal region of the skull of a woolly rhinoceros and knowledge of their nature entitles the author to assume that any osteoma at that wound site, occurred early in life.

(Fig. 10.12) The skull of a woolly rhinoceros, CHKM sample number 6997. Neighborhood of Cheboksary, Middle Volga, a - top view, b - a fragment of the occipital-parietal region of the skull with osteoma.

Injury probably caused by a large predator, which could have been a cave lion. Only felines attack while keeping one paw on the nape of the victim and bite at the skull base. This assumption is confirmed by the author who infrequently finds bones of cave lion remains associated with woolly rhinoceros skulls that have this osteoma. In the biocenosis food chain of the Pleistocene, big cats were closely associated with pachyderms: mammoth and rhinoceros. These large predators quickly died out almost simultaneously with these other species despite the fact that other large ungulates: bison, native reindeer, and musk ox, continued to exist.

(Fig.10.13) Skulls with intra-vital injuries

One of the woolly rhinoceros skulls with localization of damage in occipital-parietal region, which is stored in the Paleontological Museum of Tomsk University, has no development of osteoma. But clearly visible in this skull are deep furrows from the clutches of a cave lion. The fact that in this case osteoma is not formed indicates

that an older animal was injured, as the injury occurred after cartilage synostosis between the parietal and occipital bones had ossified.

All occurrences of woolly rhinoceros skulls with intra-vital lesions are located in areas of the greatest distribution of its fossil remains between 50 ° and 60 ° latitude (Fig.10.13). On this basis, we can assume that in this latitude belt, woolly rhinoceros population density, as well as types of mammoths, was highest in the late Pleistocene.

10.5. Path of evolution and distribution: Currently very little is known about the earliest ancestral forms of Coelodonta. The oldest finds of Coelodonta come from the top series of Sivalik middle Pliocene sediments of India. Present in this strata also are found the remains of Dicerorhinus. In the pebble and gravel horizons (Tatrot and Pindzor) of the early Pleistocene diverse fauna including large mammals and many species were discovered of which can be regarded as ancestral forms of: Canis, Crocuta, Lutra, Mellivora, Panthera, Felis, Archidiskodon, Equus, Bubalus, Bos, Bison, Dicerorhinus, and Coelodonta whose descendants were widely distributed in the middle and late Pleistocene in Eurasia, and some of which survived to exist today.

Mammal migration from India to the regions of Eurasia was probably associated with the general cooling of the climate at the boundary of the Pliocene and Pleistocene, during which extensive mountain glaciers in the Himalayas were created. Krishnan notes (Krishnan 1954) at this time that glaciers descended from the mountains to very low elevations.

The most proximal region where Coelodonta ancestors could penetrate was in the areas of China, Mongolia and Transbaikal. Remains of woolly rhinoceros were found in the Sanmen strata of Eopleistocene age and in the Nihevan horizons of the river basins in Shanxi Province. Early forms of Coelodonta have also been found in Transbaikal in the Pleistocene sediments from Tologoi. In the village of Zhoukoudia the fossil remains of a woolly rhinoceros was found in conjunction with other species belonging to the genera: Ursus, Hyaena, Felis, Archidiskodon, Hipparion, Equus, Cervus, and Bison. These species also occur in the cultural layers of cave settlements of the paleoanthropines in China (Kahlke 1963).

Among the mammalian fauna from Choukoutien sediments at early Pleistocene levels (Li Ssu-Kuang 1964) warm adapted forms mixed with cold adapted forms. Woolly rhinoceros and other fauna that would become in the future, typically Holarctic, are present with the remaining species retaining warm adaptations: rhinoceros, buffalo, and monkeys (genus macaque). In the early stages of evolution ancestral forms of woolly rhinoceros lived in conditions with a relatively warm and humid climate. And, warm adapted fauna existed in cold climates for some time, before there was a "rectification" to a cold adapted species (which included Coelodonta rhinoceroses). This hypothesis put forward by the author may p. 223 confirm the findings of researchers (Barbour 1930, Teilhard de Chardin 1930, 1933, Young 1934) that during the Pleistocene in north China climate repeatedly changed from warm and humid to cold and arid. Terrain features and the textures of sedimentary rocks in the mountainous

regions of China indicate the presence of local mountain and valley glaciation processes. Wide valleys and bowls deepening on mountaintops (traces of ancient glacial cirques), the completion of these elements of the relief boulder clay presence faceted boulders with dashed-raising indicate glaciation. In the highlands of China, where there are glaciers today are very low ancient glacier boundaries, up to only 1000 meters.

Due to moisture absorption by glaciers growing in northern part of India, Tibet and China, the surrounding lowland areas of central Asia during the Eopleistocene became arid with a cold climate. Snowfall at low temperatures of winter in the open landscape led to compaction of the upper layers of snow cover. Only under such environmental conditions that were formed early and gained a foothold in the genes of *Coelodonta* was the morphological feature of the vivo ossification of the nasal septum an evolving selective advantage. Constant rubbing and irritation of the epidermis on the muzzle end in the snow, when the animal was in the winter forage, created the conditions for the mutation.

In cold climates in open terrain in the early Pleistocene of central Asia quickly formed rhino populations that differed in large size, long and massive skull with developed occipital crest, with massive and shortened long bones. Prismatic, hypsodont tooth crowns with flat chewing surfaces and p. 224 sturdy, rough, and thick enamel was well adapted to the chafing of dry herbaceous forage. Probably this ancestral form led to the emergence in the early Pleistocene steppe species of woolly rhinoceros *Coelodonta lenensis*, which quickly distributed into northern latitudes and spread into the Transbaikal region and Yakutia (Fig.10.14a).

The original ancestral form of the steppe species *Coelodonta antiquitatis* was less large and easier on the structure of the body, according to the author, is also likely to occur during the Eopleistocene of northern China. Given the multiple variations in climate at the time at which the separation of the primary warm adapted fauna and cold adapted species occurred, we can assume the development of polymorphism in populations of *Coelodonta* rhinos. The original ancestral form was a less specialized *Coelodonta* rhino that could coexist for a while poorly specialized, as a thermophilic population with a more specialized cryophilic population. Probably a lesser degree of evolutionary advancement is evidenced by remains of woolly rhinoceros from the Nihevan horizon as compared to a rhinoceros of the Choukoutien (which was long a polemic in the literature (Kahlke 1961, Movius 1944, Kurten 1959, Oakley 1962)) however these authors did not specify different ages for the material and the existence of two types during the early Pleistocene.

Other heat loving species such as rhinos of early forms of *Dicerorhinus*, adapted with a browsing dental system for twig- type deciduous food also migrated during a cold period of the Eopleistocene to a narrow strip of forest and forest-steppes of central Asia in its southern latitude, and later on into western Europe. Unlike *Dicerorhinus* rhinos *Coelodonta* rhinos penetrated into western Europe very slowly, as livable vast steppe and forest landscapes assimilated them.

The first reliable finds of woolly rhinoceros in western Europe from the middle Pleistocene deposits are at the locations of Frankenhausen (Kahlke 1963) and in the Harz Bornhausen (Sickenberg 1962). O. Sickenberg notes rhinoceros molars with less pronounced features of specialization. Tooth crowns are more rounded, have enamel slightly rough, unlike angular, prismatic dental crowns and rough thick enamel characteristic of late Pleistocene steppe species. Sickenberg assigned this weakly specialized form from middle Pleistocene deposits in Germany as a subspecies.

Ancestors of *C. antiquitatis* penetrated during the late early Pleistocene into western Europe. However, *C. antiquitatis* arrived there with numerous other rhino species (Fig.10.14a). Bone remains of *Dicerorhinus* rhinos dominated the middle Pleistocene sediments in western Europe over the remains of minority *Coelodonta antiquitatis* populations. In the competition for living space with *Dicerorhinus* rhinos, *C. antiquitatis* became smaller and acquired a number of adaptations for life in forested landscapes. Only during the upper Pleistocene at the turn of the Wurm glaciation, did a modified form of small *C. antiquitatis* begin to dominate in the number of rhino remains/measurements, which by that time gradually became extinct due to the reduction of suitable landscapes for their survival.

During the cold glacial phase of middle and late Pleistocene, the maximum development of open landscapes in Eurasia p. 227 occurred (theory of the east European plain) (Fig. 10.14b). Probably at the beginning of the late Pleistocene this small form of *Coelodonta* species penetrated in small numbers into western Europe, but there this species is not widespread. (Fig.10.14.v). Also, local populations of steppe woolly rhinoceros prevented resettlement of migrants from north Asia.

In turn, the forest-steppe species *C. antiquitatis* during warm interglacial phases of the late Pleistocene of western Europe began to penetrate into the eastern part of Europe (the territory of the east European Plain), and later in Siberia (Fig.10.14v). Probably at that time there is a union of the two species and they coexist in a large area of distribution. (Fig.10.14g). Any inter-specific competitive relationship was weakened by the existence of these species in different ecological zones. When cohabitation occurred in eastern Europe in latitudes 50 °-60 ° south, west and east Siberia and Baikal, range in size was dominated by steppe species in western Europe and northeastern Siberia. In southern latitudes, east European and Asian portions of Eurasia, local (for specific environmental conditions) habitats were occupied in the middle and late Pleistocene by rhino populations of *Dicerorhinus* and *Elasmotherium*.

At the end of the Wurm glaciation the number of *Coelodonta* rhinos decreases sharply in western Europe, which further led to their complete extinction, probably due to the influence of increased anthropogenic factors (Fig. 10.14d).

In eastern Europe, at this time, the area of distribution of both species is significantly narrowed (Fig.10. 14d). Obviously this is due to the development in the late Pleistocene of the subarctic zone p. 228 in eastern Europe and western Siberia and the meager resources of coarse tundra. It is possible that the reduction in the total number of two types of woolly rhinoceros within their generalized distribution

area was reduced to small local habitats and populations separated by large geographical space. (Fig.10.14d). By this time representatives of *Dicerorhinus* and *Elasmotherium* were completely extinct.

Recent representatives of *Coelodonta* rhinos, based on the dating of the youngest C14 (10,000 - 15,000 thousand years) bones from the cultural layer Paleolithic sites of Mal'ta and Buret (Priangare) probably lived in the territory of central Asia. At the turn of the late Pleistocene and Holocene woolly rhinoceros gradually narrowed their distribution and survived in their ancestral home, living in the territory of Mongolia and northern China up until species extinction (Fig.10.14e).

Noteworthy is the extreme paucity of finds of remnants of woolly rhinoceros in the territory of Chukotka and their absence in the territory of the Amur region. Isolated finds of bones and woolly rhinoceros horns were found in Kamchatka and on Wrangel Island. Reliable findings of *Coelodonta* from the territory of Alaska (North America) are still not known. From this it follows that the woolly rhinoceros did not penetrate Berengia and follow mammoth and other species into North America.

Migration activity of representatives of the *Rhinocerotidae* is smallest compared with other mammal families. Apparently this can be explained by the rapid pace of their extinction. From a wide variety of genera of this family in the Neogene p. 229 by the end of the Pleistocene the number of genera were very few. So far, only four genera survived each represented by a single species: *Diceros*, *Ceratotherium*, *Didermoceros* and *Rhinoceros*. Probably, this is the main reason, and that explains why representatives of *Coelodonta* did not penetrate North America.

The main cause of the extinction of *Coelodonta* is its high state of adaption to the harsh climatic conditions of the Pleistocene. Then, climate change in Eurasia at the turn of the late Pleistocene and Holocene led to the reduction of suitable livable habitats (which forced a decrease in the size of populations). Finally, general population downsizing coupled with the increasing negative impact of anthropogenic factors led to forced extinction.

In archaic beliefs and practices of the peoples are often stored information about the relation of man to a certain type of animal, and its use in economic activities and religious cults. Well-known archaeologists acknowledge the cult of the cave bear practiced by Neanderthals and Cro-Magnons. It is known that in the Paleolithic monuments of Mal'ta and Buret were found not only the numerous bones of the woolly rhinoceros, but also horns. Perhaps this may indicate an interest by Cro-Magnon to hunt woolly rhinoceros for ritual purposes. Maybe this is the origin of persistent beliefs in the minds of the eastern nations about the miraculous power of rhino horn in strengthening reproductive functions. The sharp decline in the number and the possible extinction of modern rhino species is directly related to this "archaic" conviction, and the continuation of hunting rhinos, so far, for the sake of his horns.

CONCLUSIONS: The main provisions developed in this dissertation:

1. History of the study and description of the woolly rhinoceros shows that first priority description (of concrete samples, which are stored in a collection of type specimens of the Zoological Institute) belongs to the Russian researcher, academician P.S. Pallas, and not the German researcher J.F. Blumenbach whose species name *C. antiquitatis* currently enshrine with the woolly rhinoceros.
2. Significant morphological differences in the structure of the cranial skeleton of woolly rhinoceros provide sufficient grounds for distinguishing two distinct species; *Coelodonta lenensis* Pallas and *Coelodonta antiquitatis* Blumenbach, which represent two ecological groups: the steppe and forest-steppe, which existed during the Pleistocene at all times (Fig. 7.3 Reconstructions a-steppe rhinoceros, b- forest-steppe rhinoceros).
3. Giving these two original names by Pallas and Blumenbach, the priority of the first description is recognized in the Russian scientist who retains the right of authorship (oldest description first).
4. Morphological differences of the steppe and forest-steppe species of woolly rhinoceros show a spectrum of adaptive responses aimed at adaptation to different environmental conditions in the unstable climate of the late Pleistocene. Features of the structure of the skull in the steppe species *C. lenensis* appear in general as elongated proportions of facial and brain, lengthening and strengthening of dentition with hypsodont teeth determine its adaptation to the open steppe landscape and grassy vegetation.
5. In contrast to the *C. lenensis* steppe species, the forest-steppe species *C. antiquitatis* acquired in its evolution some morphological traits, indicating this species was a forest-steppe inhabitant p. 232 of woodlands with not only a grassy diet, but also feed on twigs.
6. Shortening of the facial part of the skull, increasing its total height (by increasing the height of the maxillary bone and skull base) raising of the cranium over facial bones, strong protrusion of the occipital bone and articular condyles provided this kind of great mobility of the head in the dorsal-ventral direction and strengthening contraction movements of the jaws for grinding woody food components.
7. Considering these two kinds of morpho-adaptations the morphological evolution of the woolly rhinoceros *Coelodonta* is well represented within the rising main evolutionary directions of the Pleistocene rhinoceros including *Dicerorhinus* and *Elasmotherium*.
8. Global cooling of the climate during the Pleistocene caused seasonal temperature difference to increase and led to the formation of snow cover in winter, which affected the morphological evolution of the skull in all Pleistocene rhinoceroses to form similar morpho-adaptations.

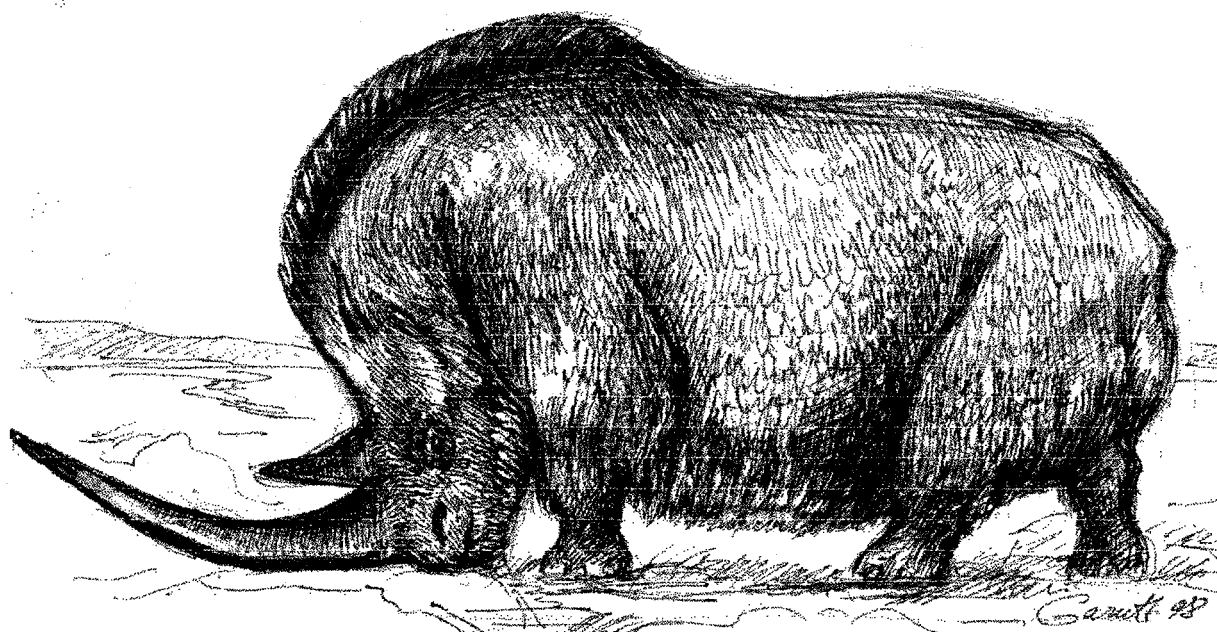
9. Elongation of the facial part of the skull of the Pleistocene rhinoceroses is associated with an increased length of the airways to warm inhaled cold air in the winter.
10. Bone elongation of the facial part of the skull also led to an increase in the size of the oral cavity, as it was important to warm the food mass mixed with snow.
11. Elongation of the nasal bones and increase of their area due to the increase in the load from the front horn, which was used extensively by animals foraging under the snow.
12. Enhancing the impact of friction from snow on the epidermis of the facial end of the animals, and an increase in load on the nasal bone p. 233 from pressure on the horn base ultimately led to the development of bone septum.
13. Bony septum formed in the phylogeny of the representatives of all the genera of Pleistocene rhinoceroses: completely in the *Coelodonta* and *Elasmotherium*, but incomplete in *Dicerorhinus*.
14. The presence of bone in the nasal septum of Pleistocene rhinos can prove the existence of snow cover in the winter habitats of these species.
15. Bony septum of *Dicerorhinus* rhinos did not reach the stage of complete phylogeny ossification may indicate that milder climatic conditions were present during the Pleistocene in western Europe.
16. A late stage of ossification of the nasal septum in woolly rhinoceros from areas in Europe, compared with woolly rhinoceros that lived in north Asia, also points to a less severe climate in the European part, in comparison with the climate in the Asian mainland.
18. Studies of the microstructure of the woolly rhinoceros horns showed their identity in the structure of their main elements viz., filaments which are similar to those present in modern rhinoceros horns.
19. Differences in the structure of the horns of *Coelodonta* with modern rhinos are determined by a greater area of lateral surfaces of the anterior horn, and a greater area of compacted filaments in the middle part of the horn, which created its characteristic flattened shape.
20. Transverse bands on the *Coelodonta* horns reflect uneven seasonal growth of its filaments, and indicate a significant difference between summer and winter temperatures of the Pleistocene climate.
21. The degree of preservation of bone remains of *Coelodonta* and radiocarbon dating showed that the greatest number of woolly rhinos came from the Late Pleistocene deposits of Eurasia, making *Coelodonta* rhinos particularly promising for paleogeographic data throughout the continent.

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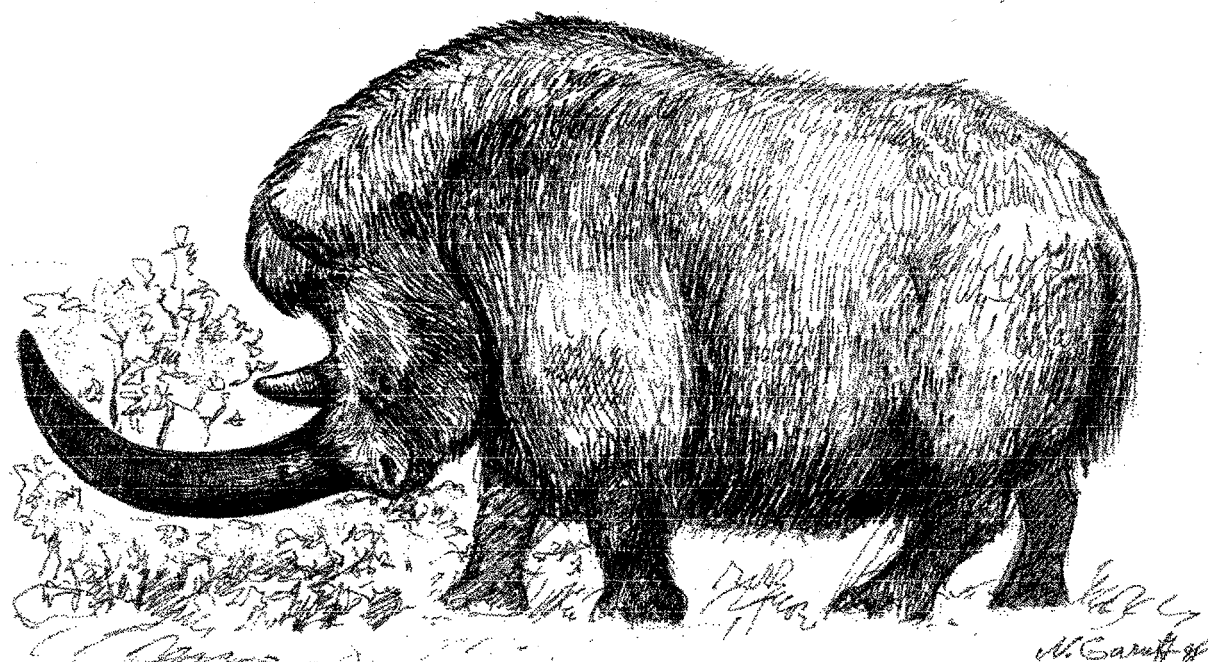
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а



б

**Рис. 3.7; Реконструкция внешнего облика
двух видов шерстистых носорогов.
а - степных ландшафтов; б - лесостепных ландшафтов.**

Эволюционно исходная форма шерстистого носорога, которая сформировалась в условиях открытых ландшафтов, имела крупную, массивную, удлинённых пропорций голову, низко опущенную к земле. На длинных носовых костях крепился больших размеров передний рог, который по длине превышал размеры головы живот-

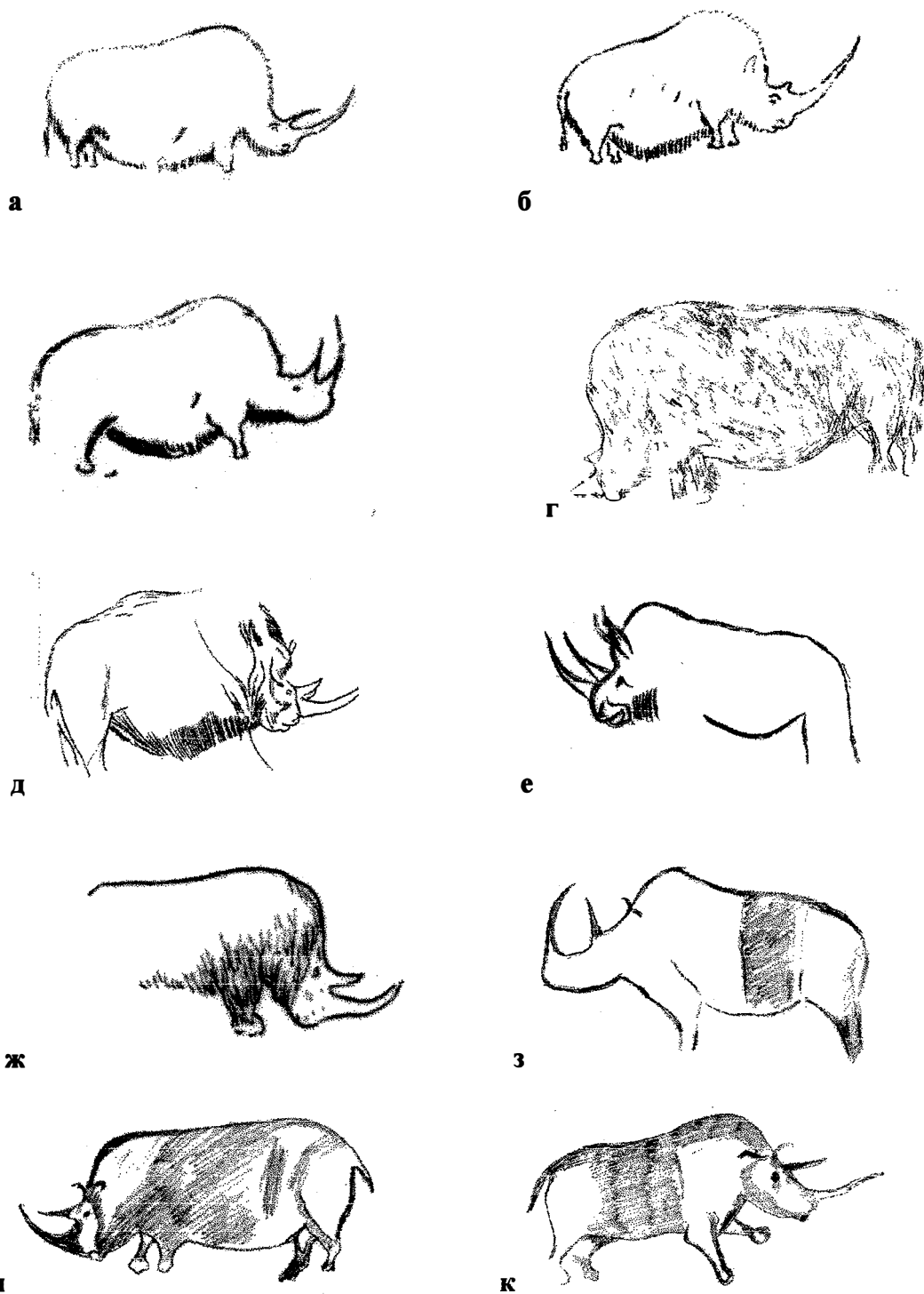


Рис. 9.7. Палеолитические изображения *C. antiquitatis* из пещерных поселений человека древне-каменного века.

а-в. Руфиньяк (Rouffignac) Франция.

г. Гоннерсдорф (Gonnernsdorf) Германия.

д-е. Комбарель (Combarelles) Франция.

ж. Коломбьер (Colombiere) Франция.

з-к. Шаве (Франция).

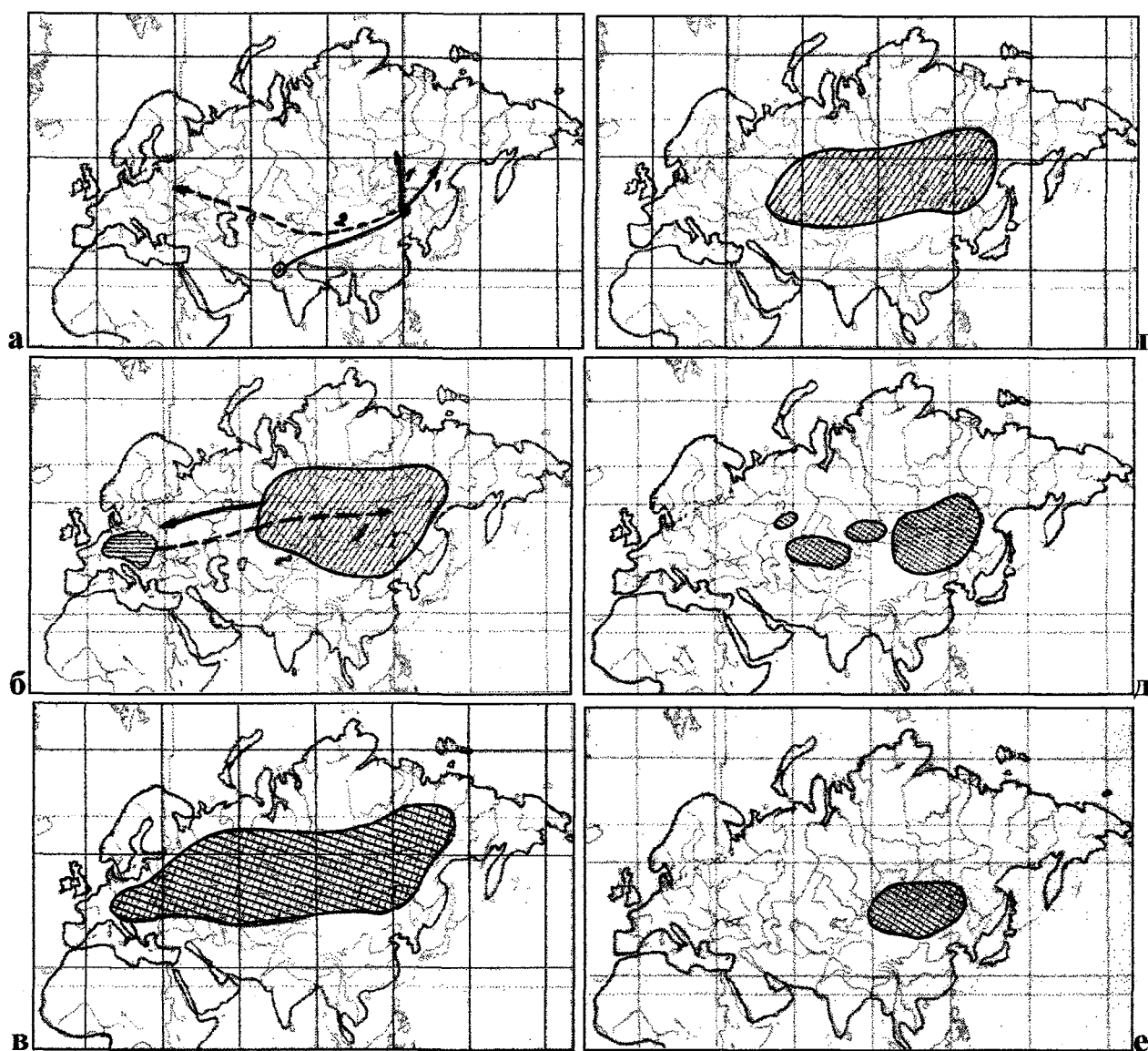


Рис. 14.10. Происхождение и распространение носорогов рода *Coelodonta* в плиоцен - плейстоцене.

а. Проникновение предковой формы носорогов рода *Coelodonta* из Индии в Центральную Азию и распределение на два вида в раннем плейстоцене. *Coelodonta lenensis* Pallas; *Coelodonta antiquitatis* Blumenbach.

б. Распространение европейского *C. antiquitatis* и азиатского *C. lenensis* видов в пределах своих ареалов в среднем плейстоцене и взаимопроникновение (обмен) в ареалы обитания на границе среднего и позднего плейстоцена.

в. Совмещение ареалов обитания в первой трети позднего плейстоцена.

г. Сужение ареала обитания в конце позднего плейстоцена.

д. Распадение общего ареала на локальные небольшие ареалы.

е. Последний ареал обитания носорогов рода *Coelodonta* перед вымиранием в голоцене.