On the fossil rhinoceros *Elasmotherium* (including the collections of the Russian Academy of Sciences)

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Summary

This article summarizes the results of nearly 200 years of study of the fossil rhinoceros *Elasmotherium*, first described by Gotthelf Fischer in 1808. Problems of its geographical and chronological distribution are discussed, and morphological and ecological reconstructions of the species by various researchers are demonstrated and discussed. The article also gives information about the original type material of G. Fischer, which originally was preserved in the Natural History Museum of the Imperial Moscow University, and is presently stored in the Vernadsky State Geological Museum of the Russian Academy of Sciences. Especially the extensive work of assistant professor V.A. Teryaev of the Moscow Institute of Geological Exploration on *Elasmotherium* are highlighted.

Samenvatting

Dit artikel vat de resultaten samen van bijna twee eeuwen van studie van de fossiele neushoorn *Elasmotherium*, oorspronkelijk beschreven door Gotthelf Fischer in 1808. Problemen betreffende de geografische en chronologische verspreiding van dit genus worden besproken, en morphologische en ecologische reconstructies door diverse onderzoekers worden gepresenteerd en besproken. Het artikel geeft daarnaast informatie over het originele type materiaal van G. Fischer, dat oorspronkelijk bewaard werd in het Museum voor Natuurhistorie van de Keizerlijke Universiteit van Moskou, en die momenteel opgeslagen ligt in het Vernadsky Staatsmuseum voor Geologie van de Russische Akademie van Wetenschappen. Het uitgebreide werk van assistent professor V.A. Teryaev van het Moskou Instituut voor Geologisch Onderzoek over *Elasmotherium* krijgt bijzondere aandacht.

Introduction

During the second half of the Pleistocene (presently viewed as Neopleistocene), during the Holocene and during historic times, many large sized mammals got extinct. Humans often played a direct or indirect role in the extinction of species or even genera. This article will focus upon the nature of the many-sided relations between animals and humans. It is presumed that the extinction of the megafauna was to a greater extent connected with human hunting activities than previously acknowledged. It may even be considered to be not just a result, but also one of the causes of the Late Pleistocene landscape revolution (Zhegallo *et al.*, 2001). In order to review previous morphological and autecological reconstructions and for the purpose of an extensive analysis of the nature of the interrelations between humans and animals, we use as much data as possible, obtained by archaeological and prehistorical art studies, in addition to the traditional palaeontological information. As far as animals which got extinct in historical times are concerned, we also use photographs, drawings, descriptions by contemporaries etc. The role of these animals in modern and past cultures will also be mentioned.

One of these large-sized mammals that got extinct is *Elasmotherium*. Its extinction is usually placed in the Middle Pleistocene. Claimed evidences of the animal's interactions with humans are extremely rare and questionable. However, it is believed that *Elasmotherium* has been well-known to prehistoric humans as a potential hunting object, and is even regarded by some as a prototype of the mythical unicorn. One of the aims of this article is to present the facts underlying such ideas. Another aim is to review the scientific studies on *Elasmotherium* itself.

The original idea for this article was developed by V. Zhegallo and N. Kalandadze, the main text was prepared by N. Kalandadze, A. Shapovalov and E. Tesakova, the sections on *Elasmotherium* remains from the collections of the SGM RAS (Vernadsky State Geological Museum of the Russian Academy of Sciences, hereafter referred to as SGM RAS) were written by Z. Bessudnova and N. Noskova, and the section "On the history of Elasmotheriinae" was written by V. Zhegallo.

Fig 1 Discoverer of the *Elasmotherium*, Johann Gotthelf Fischer von Waldheim (1771-1853). After Shchurovsky (1871)

De ontdekker van *Elasmotherium*, Johann Gotthelf Fischer von Waldheim (1771-1853). Naar Shchurovsky (1871)

On the genus *Elasmotherium* Fischer, 1808

The genus *Elasmotherium* Fischer, 1808 is placed within the Order Perissodactyla OWEN, 1848, family Rhinocerotidae GRAY, 1821. Later, in 1877 J.F. Brandt moved this genus into a separate subfamily: the Elasmotheriinae. Recently, McKenna & Bell (1997) considered the species *Elasmotherium* to be closer to the modern and the wooly rhinoceroses, and placed them all in one subtribe, the Rhinocerotina.

The type species of the genus, *Elasmotherium sibiricum* Fischer, 1809 was described by Gotthelf Fischer, professor at the Moscow University and director of the University's Natural History Museum at that time (fig. 1). The species was based on the left hemimandible with four molars and an alveolus for the third premolar. In a note, Fischer (1808) suggested as genus name for the fossil animal *Elasmotherium* and as species name *sibiricum*; these names were published a year after (Fischer, 1809). The specimen originated from the "Cabinet of Natural History and Other Rarities" that was gifted to the Moscow University by the former President of the Russian Academy of Sciences, princess Ekaterina Dashkova in 1807. During the Patriotic war of 1812 the major part of the collection was lost and the remaining mandible of *Elasmotherium* was only protected and saved due to its evacuation to the city of Nizhny Novgorod. Much later, in the middle of the 20th century, it was transferred to the Palaeontological Institute of the Academy of Sciences of the USSR in Moscow. The exact age of the mandible and place of its origin are unknown. The specimen is kept in the collection of the Institute among other remains of Quaternary fossil vertebrates, of which the exact data of location of the findings are all lost.

The genus name *Elasmotherium* is derived from the Greek words *elasmos* - lamina - and *therion* - mammal -, and relates to the laminated folding of the tooth enamel, which is a characteristic of this genus. The species name *sibiricum* was usually explained by the fact that the major part of princess Dashkova's collection originated from field trips to Siberia. However, it should be noted that the border of "Siberia" at that time was considered to run along the left bank of the river Volga, thus placing areas leftward of the Volga and the Ural region into "Siberia".

It is also interesting to note that between the year 1808, when the specimen was described by Dr Fischer, and 1864, when Dr Johann Friedrich Brandt figured this animal in his paper, the type specimen apparently lost its second molar. Most likely it was the tooth that Fischer on purpose extracted from the mandible and depicted in a plate in his paper. The subsequent fate of the specimen is unknown.

Junior synonyms of the genus *Elasmotherium* are *Stereoceros* Duvernoy, 1855 and *Enigmatherium* Pavlova, 1916. The genus *Stereoceros*, derived from the Greek *stereos* - bodily, solid, volumetric - and *ceros* - horn -, was defined on the basis of the occipital part of the animal's skull. These remains were difficult to compare with the type material of Fischer. Nevertheless, the Darmstadt researcher Johann Kaup suggested the remains to belong to the genus *Elasmotherium* (Kaup, 1840). Even though he only used the published drawings of the skull from the Rhine and the mandible from Moscow, he had a most brilliant argumentation for his view, and J.F. Brandt could not but agree with his conclusions (Brandt, 1864; see also Anonymous, 1865).

The specimen originated from the collection of the Austrian naturalist F.J. Gall. The location of those remains is thought to be the sediments of the Rhine valley. Later, the remains were

acquired by the Natural History Museum in Paris, where the skull was examined by Duvernoy, who published the results of his studies in 1855 and suggested the scientific name of *Stereoceros galli* for the new "would-be pachyderm". In subsequent years the number of findings of *Elasmotherium* remains increased significantly. After the study of an almost complete skull of *Elasmotherium* found in the Lower Volga river region by Alexander Knoblokh, Brandt (J.F. Brandt, 1878) was able to confirm the assumptions suggested earlier by Kaup.

The other junior synonym, *Enigmatherium*, is derived from the Greek *enigma* - riddle -, and *therion* - *mammal*. It arose out of a misunderstanding. The "Enigmatic Mammal" was described by Pavlova (1916) on the basis of a single tooth from Pleistocene sediments of the Northern Caucasus. While being described, the tooth was positioned in a wrong perspective that resulted in a wrong position of the genus-specific elements of the tooth crown. Later this mistake was discovered and corrected, and the species *Enigmatherium stavropolitanum* Pavlova, 1916 was declared synonym of the species *Elasmotherium fischeri* Desmarest, 1820 (Teryaev, 1929).

The transliterated genus name *elasmoteriy* is usually used in the Russian literature for this rhinoceros, besides some other names. In his list of materials of the collection of the Moscow University, G.E. Shchurovsky (Anonymous, 1841) used the name *listozub* - leaf-tooth animal - for the type specimen found by Fischer. Some scholars call *Elasmotherium* a "unicorn" (Teryaev, 1929; Flerov, 1953; Shvyreva, 1995). Teryaev (1948) suggested to call *Elasmotherium* "dome-forehead rhinoceros" or just "dome-forehead" due to its peculiar swelling on the frontal bones.

Elasmotheriums are known from the Palearctic, mostly from Russia, Ukraine, Moldova and China. Findings from Germany, Hungary and Italy were also noted but their reliability is currently questioned. The earliest finds of the elasmotheriums are known from the Late Pliocene of Moldova and the Azov Sea region (the Khaprov faunistic complex), and the latest palaeontological findings possibly originate from the basin of the river Volga and are dated as early as the Mikulin interglacial (Khromov, 1999).

Nowadays three species are identified within the genus: *E. sibiricum* FISCHER, 1809 (= *E. fischeri* Desmarest, 1820; the Siberian *Elasmotherium*), *E. caucasicum* Borissiak, 1914 (the Caucasian *Elasmotherium*) and *E. peii* Chow, 1958 (Pei's *Elasmotherium*). Abundant findings of teeth and bones of the cranial and post-cranial skeleton originate from the Early and Middle Pleistocene sediments of the European part of Russia, Ukraine, the Urals, Western Siberia, Transbaikalia (the eastern part of Lake Baikal region), Kazakhstan and Central Asian states, and the Late Pleistocene of the European part of Russia. *E. caucasicum* from the Late Eopleistocene of Ukraine and Northern Caucasus is known predominantly by its teeth. *E. peii* of the Late Pliocene of Ukraine (Shvyreva,

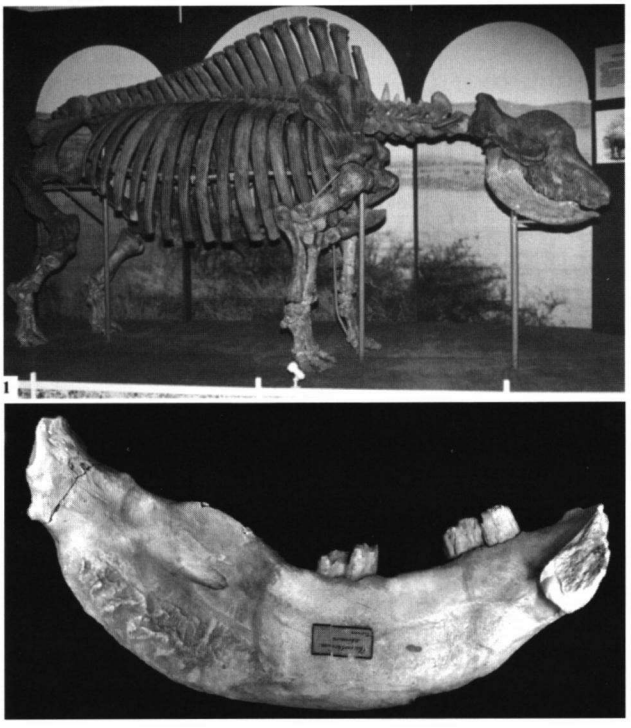

Fig 2 *Elasmotherium sibiricum* Fischer, 1809. 1) The skeleton of the Sibirian *Elasmotherium* restored in the exposition of the Stavropol regional museum, based on an almost complete skeleton found in 1964 near the village Gaevskaya (Stavropol region). Courtesy Stavropol Museum named after G.N. Prozritelev and G.K. Prave. 2) The cast of Fischer's type material, which he used for the description of the genus and species of *Elasmothrium sibiricum* [Fischer, 1808; 1809]; at present at the SGM exposition (PV-156). The length of the label is 6,5 cm

Elasmotherium sibiricum Fischer, 1809. 1) Het skelet van de Siberische *Elasmotherium* opgesteld in the tentoonstelling van het Stavropol regionale museum, gebaseerd op een vrijwel compleet skelet, gevonden in 1964 bij het plaatsje Gaevskaya (Stavropol regio). Met dank aan Stavropol Museum (G.N. Prozritelev en G.K. Prave). 2) Afgietsel van Fischer's type materiaal, gebruikt voor zijn beschrijving van het geslacht en de soort *Elasmotherium sibiricum* [Fisher, 1808; 1809]; momenteel in de SGM expositie (PV-156). De lengte van het etiket is 6,5 cm

1995) and the Early Pleistocene of North-East China was described on the basis of several teeth from the upper jaw of one individual. For the latter material, Shvyreva (1995) suggested the species name *E. inexpectatum* Chow, 1958, which has been described on the basis of one upper molar.

E. sp. from the Late Pliocene of the Northern Caucasus and the Southern part of Moldova is probably a stand-alone new species. It was many times noted (Gromov, 1948; Baigusheva, 1971; Alexeyeva, 1977; Shvyreva, 1995), that the species demonstrates differences with both the Caucasian and the Siberian elasmotheriums. Notwithstanding the fact that the origin of the genus was undoubtedly located in Central Asia, the *E.* sp. is currently the oldest of any *Elasmotherium* found (Shvyreva, 1995).

Numerous remains of the Siberian and Caucasian elasmotheriums are kept in the collections of the Palaeontological Institute and of the Geological Institute of the RAS (Vernadsky State Geological Museum, Moscow), Zoological Institute of the RAS (Saint-Petersburg), National Museum of the Bashkortostan Republic (Ufa city, Russian Federation), Geological and Mineralogical Museum of the Kazan University, regional museums of Vol'sk, Rostov-na-Dony, Samara, Saratov, Stavropol, Khvalynsk and other cities. An almost complete skeleton of the Siberian elasmotherium, discovered near Gaevskaya village, was mounted under the guidance of V.E. Garutt in the Stavropol regional museum, named after G.N. Prozritelev and G.K. Prave (fig 2: no. 1). In Yu. A. Orlov's Palaeontological Museum in Moscow there is an incomplete skeleton composed of the remains of different individuals, mounted under direction of E.I. Belyaeva (Palaeontological Institute of the RAS).

The body length of the known specimens of the Siberian *Elasmotherium* reaches 4,5 m, and the shoulder height is over 2 m. When we take into account the fact that the size of isolated molars of the Caucasian *Elasmotherium* in the collection of the Palaeontological Institute of the RAS significantly exceeds those known from the upper and lower jaws of the Siberian *Elasmotherium*, it is reasonable to assume that the length of the Caucasian *Elasmotherium* reached at least 5,0-5,2 m. The body weight of the animal is estimated to have been around 4-5 tons.

A large skull with dome-shaped swelling of the frontal bones formed by spongy bone tissue is characteristic for the Siberian elasmotherium. The external side of the dome is covered by numerous grooves for blood vessels. Height of the dome is 15 cm and diameter is about 30 cm. Nasal bones are long, straight, significantly thickened and narrowing toward the front end, which bears some rugosity. Osteal nasal septum is full. Front sides of the eye-sockets are rimmed with large strong outgrowths. Occipital part is low, wide and not bent backward. Incisors and canines are absent, whereas milk incisors are presumed to have been present, considering the alveolar sockets in the mandible. Premolars and molars have remarkably high crowns that are much more hypsodont than those of other perissodactyls. The teeth are prismatic with highly developed dental cement and plicated enamel. The dental formula is

$I_0\ C_0\ P_2\ M_3\ /\ i_0\ c_0\ p_2\ m_3$

All cervical vertebras are very robust. The atlas bears transverse processes up to 30 cm long. the spinal processes of the thoracic vertebra are also highly developed with a length up to 53 cm. The front limbs bear three functional toes (II-IV), and a relatively small side-toe (I). The middle toe (III) exceeds the size of the other two main toes. The rear limbs are three-toed (II-IV).

During the study of the skulls of the Siberian *Elasmotherium* E.I. Belyaeva (pers. comm. to N. Kalandadze, 2002) noted a sexual dimorphism expressed in differences in skull size between males and females as well as in shape and size of the frontal dome. Females, with their smaller and more gracile skulls, are marked with a less developed frontal dome and their frontal bones are jointed to the nasal bones without an obvious bend in the frontal part of the swelling (fig 3: 6).

Remains of *Elasmotherium* at the Vernadsky State Geological Museum

As noted above, the holotype of the species *Elasmotherium sibiricum* Fischer, 1809, being also a name-bearing type for the genus *Elasmotherium* FISCHER, 1808, was originally kept at the Natural History Museum in Moscow and came from the collection of princess Ekaterina Dashkova. The "Moscow mandible" was described and pictured in three perspectives (Fischer, 1808), the size of the pictures was a quarter of the real size of the fossil (fig. 4). A sepa-

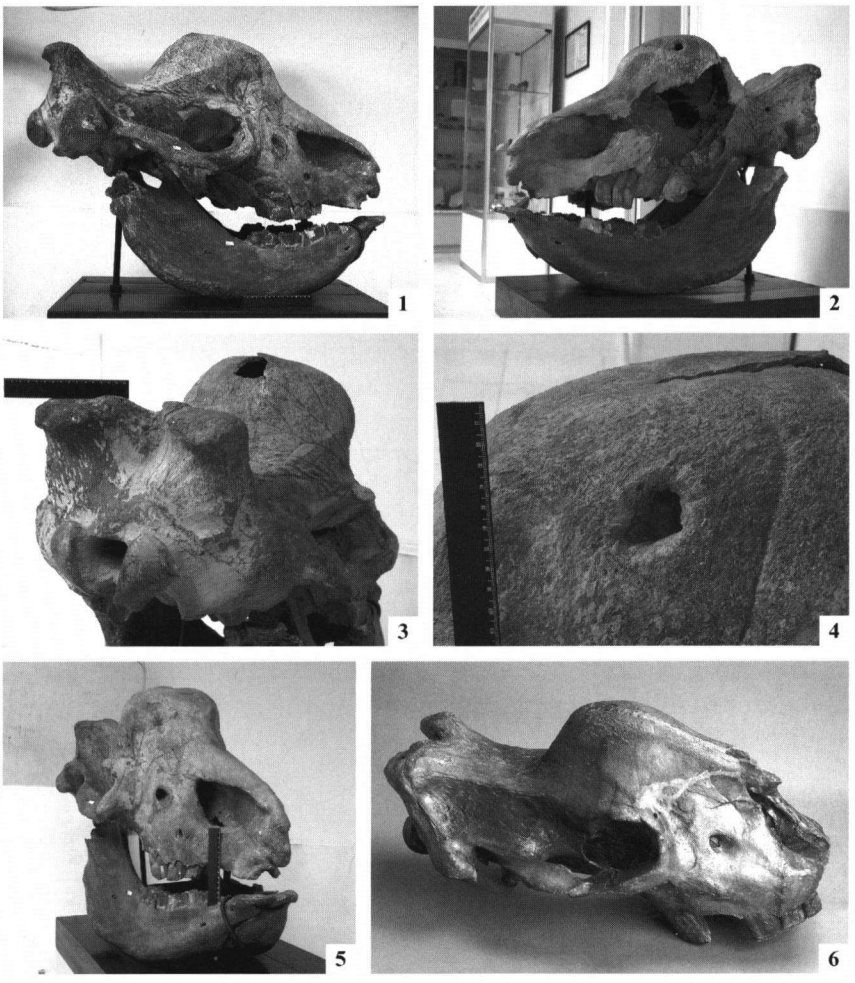

Fig 3 *Elasmotherium sibiricum* Fischer, 1809. Nos 1 - 5. The skull (no. PV-167) of a bull from the SGM exposition, brought from the cis-Caspian Sea region by V.A. Teryaev in 1928. Location is Guriev city. The skull is assembled with the mandible of another individual (PV-168). The length of the ruler is 15 cm. Photo by S. Bogdanov. 1 - seen from the right side; the imprints of the larger blood vessels in the frontal swelling can be distinguished; the cancellous osseous tissue, typical for growth zones of horn structures, is seen; 2 - seen from the left side; parts of left maxillary, frontal and jugal bones are destroyed; in the frontal swelling the premortem damage is seen; 3 - occipital part of the skull; the occipital structures (tubera superooccipitalia, condyli occipitales, foramen magnum) can be observed; the damage at the posterior part of the frontal swelling is a result of bad skull conservation; 4 - the damage of the frontal swelling with evidence of healing; the relation between aperture and blood vessel imprints is seen; 5 - frontal view of the male skull; the relation between the spoon-like symphysis of the mandible and the sphenoidal rostrum of the upper jaw; together they function as a food-grasping organ; 6 - The skull of a female individual from the collection of Yu.A. Orlov's Palaeontological Museum in Moscow. The rostrate area of the skull is destroyed.

Elasmotherium sibiricum Fischer, 1809. Nummers 1-5. De schedel (no. PV-167) van een stier uit de SGM tentoonstelling, afkomstig van de cis-Kaspische Zee regio en gebracht door V.A. Teryaev in 1928. Vindplaats is de stad Guriev. De schedel is gecombineerd met een onderkaak van een ander individu (PV-168). De lengte van de meetlat is 15 cm. Foto door S. Bogdanov. 1 - rechterzijde; de afdrukken van de grotere bloedvaten op de voorhoofdszwelling zijn zichtbaar; het sponzig bot, typisch voor groeizones van hoornstructuren, is te zien; 2 - linkerzijde; gedeeltes van de linker bovenkaak, voorhoofds- en jukbeenderen zijn vernield; op de zwelling op het voorhoofd is de beschadiging te zien die tijdens het leven is toegebracht; 3 - achterhoofdsgedeelte van de schedel; de achterhoofdsonderdelen (tubera superoccipitalia, achterhoofdsknobbels, achterhoofdsgat) kunnen onderscheiden worden; de beschadiging aan het achterste deel van de voorhoofdszwelling is een gevolg van slechte schedelconservatie; 4 - de beschadiging aan de voorhoofdszwelling met tekenen van genezing; de relatie tussen de opening en afdrukken van bloedvaten is te zien; 5 - vooraanzicht van de mannelijke schedel; de relatie tussen de lepelvormige symphysis van de onderkaak en de ronde einding van de bovenkaak; tesamen functioneren ze als een orgaan om voedseldelen te pakken; 6 - De schedel van een vrouwelijk individu uit de collectie van het Yu. A. Orlov's Paleontologisch Museum te Moskou. Het snuitgedeelte van de schedel is vernield.

rate plate presented three perspectives of the second molar, half the real size (M2). We believe the depicted tooth was the one that had been still present in the mandible pictured in Fischer's work, but was already absent in the picture shown by Brandt (J.F. Brandt, 1864; Anonymous, 1865). The ramus of the mandible and the tooth were drawn by A. Frolov, an artist who was specially appointed to assist Prof. Fischer in depicting specimens from the collection of the museum and to prepare lithographic models for printing. George Cuvier united the two plates from the Fischer's article (Fischer, 1808) and reprinted the picture of the "Moscow mandible" in his atlas (Cuvier, 1836).

After its evacuation to the city of Nizhny Novgorod, the specimen was returned to Moscow. The assumption that the mandible was kept in the Museum collection since then, was proven by the catalogue of the collections (Fischer, 1822) and also by G.E. Shchurovsky mentioning the "listozub" in his report as one of the most precious specimen of the museum collection (Anonymous, 1841). In the course of preparation of the rooms of the Natural History Museum, the remains of the vertebrates were sent to the Zoological Cabinet in which, *inter alia*, the "Moscow mandible" was kept. In 1859, on request of J.F. Brandt, the Moscow University considered an issue of transferring the elasmotherium mandible to the Academy of Sciences in Saint-Petersburg to conduct researches. There is a special file on that transfer in the archive of the Moscow University. In the results of the research by J.F. Brandt, summarized in the popular scientific magazine "Naturalist", there was also a reference to the fact that "the member of the Academy, Prof. Brandt expressed a wish to study the said mandible anew and requested the Moscow University to send it to the Academy, which was duly fulfilled" (Anonymous, 1865: 1). The study resulted in a fundamental work in which all the by then available materials of elasmotherium were analyzed and in which the animal was undoubtedly affiliated to the Rhinocerotidae (Brandt, 1864). After this temporarily transfer to Saint-Petersburg the type specimen was returned to the Zoological Cabinet. Afterwards the Zoological Cabinet was re-established as the Zoological Museum of the Moscow University holding all the collections of its progenitor.

The above-cited magazine "Naturalist", also noted that Brandt used replicas of the "Moscow mandible" for comparison purposes in the course of working with elasmotherium remains in other museums: "Thanks to obligingness of Mr d'Archiac, Brandt closely studied a part of the animal's cranium kept in the Paris museum and compared it to the gypsum replica of the "Moscow mandible" (Anonymous, 1865: 5). According to N.V. Garutt (pers. comm. with S.V. Kruskop), four such replicas were produced. One of them is still kept in the collection of the Zoological Museum of the Moscow University (No. 945 EEM-1006). Another one (fig 2: 2) was given to the Geological Cabinet (Museum) of the Moscow University in 1886 by order of the museum director, the famous zoologist and anthropologist Anatholy P. Bogdanov (1834 - 1896) (Anonymous, 1887). Nowadays that replica is kept in the exhibition of the State Geological Museum (PV-156).

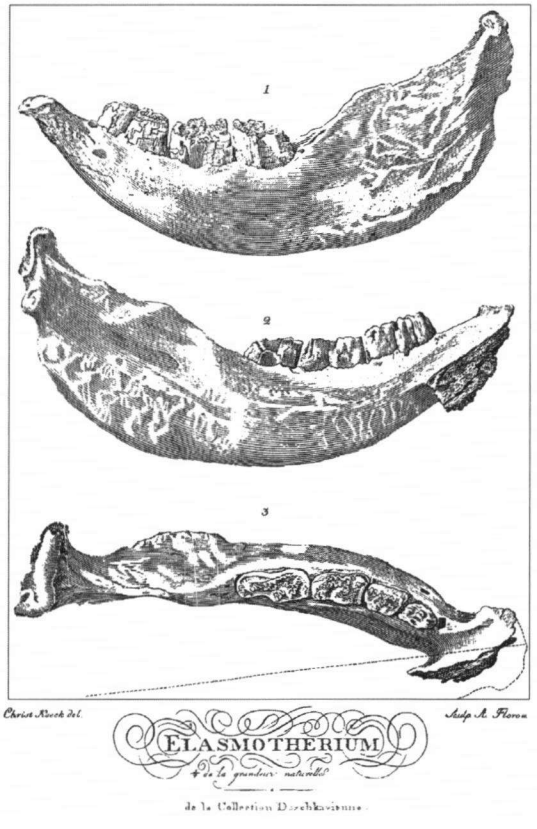

Fig 4 The plate with a drawing of the left ramus of the mandible from the princess Dashkova's collection, created by the artist A. Frolov. From the work by J. Gotthelf Fischer (1808)

De originele plaat met tekening van de linker tak van de onderkaak uit de verzameling van prinses Dashkova, getekend door de tekenaar A. Frolov. Uit het werk van J. Gotthelf Fischer (1808)

Fig 5 Valentin A. Teryaev (1891-1966) in the Geological Museum during preparation of an exposition for the XVII International Geological Congress in Moscow, 1937. Photo by Mr Zatsky. From the photographic collection of the Vernadsky State Geological Museum, Moscow

Valentijn A. Teryaev (1891-1966) in het Geologische Museum tijdens voorbereidingen voor een tentoonstelling voor het 17de Internationale Geologische Congres in Moskou, 1937. Foto door dhr Zatsky; uit de fotografische verzameling van het Vernadsky Staatsmuseum voor Geologie, Moskou

Fig 6 Sibirian *Elasmotherium* in Z. Burian's reconstruction. After Spinar (1974)

Siberische *Elasmotherium* in Z. Burian's reconstructie. Naar Spinar (1974)

Currently, the "Moscow mandible" is kept in the Palaeontological Institute of the RAS. According to entry no. 404 in he Collection Register of the Mammal Laboratory of the Palaeontological Institute, collection no. 170 was transferred to the Palaeontological Institute from the Zoological museum of the Moscow University in 1937 as part of the transfer of so-called "non-relevant" collections. According to the entry, it combined the materials "collected by various individuals in various locations in various times". The collection included remains of the "Quaternary Elephas, Rhinoceros etc. replicas", in total 537 specimens. Typically, exact locations of the findings of the remains are not known. With regard to specimen no. 170/460 in the List Book for the collection (no. 170 in 1938) there was an entry as follows: "*Elasmotherium sibiricum* Fischer, left part of a mandible from Siberia presented by the princess E. Dashkova. Listozub. Original. For the work by Fischer". Furthermore, the title of the work and a date-line were given.

In 1881 Vladimir O. Kovalevsky (1842 - 1883) was appointed for a short time as the Head of the Geological Cabinet (Museum). In January of the same year he was installed as assistant professor of Geology and Palaeontology at the Moscow University. Upon his request, molds were produced in Saint-Petersburg for the purpose of making replicas of the elasmotherium remains kept in the museum of the Saint-Petersburg Mining Institute. Modeler Repin copied the shapes of the animal's skull and twelve non-described bones (Anonymous, 1883) and made two replicas of each item. As agreed with the modeler the molds remained in the possession of the Geological Cabinet (Museum) and could be used for making copies for international museum exchange. Now the templates are kept in the studio of Repin in Saint-Petersburg. Most likely, only a small number of copies were actually produced. For instance, V.A. Teryaev notes the presence at various organizations of gypsum replicas of limb bones of the elasmotherium kept in the Mining Institute's Museum in Leningrad;

he also notes that a description of the discovered bones and their images were made by A. Gaudry and M. Boule on the basis of those replicas as long ago as 1888 (Teryaev, 1930). Perhaps, besides the templates and replicas of the skull and limb bones, replicas of the animal's teeth were also produced at the same time or soon after. This is not mentioned in the report by V. O. Kovalevsky but all those specimens (series of 8 teeth, limb bones, skull, mandible and a rib fragment) are numbered in a sequence from no. 1399 to no. 1419 in the catalogue of collections of SGM (Pavlova, 1910). According to the labels on the replicas, all of them were made on the basis of the specimens from the Mining Institute. Currently, the replicas are kept in the State Geological Museum in the collection of the vertebrates (nos. PV-121 - PV-130; PV-157 - PV-166; PV-172; PV-177 - PV-179.

A small series of replicas (nos. PV-151, PV-152) also kept in the Vernadsky State Geological Museum represents copies of teeth from the type series of *Elasmotherium caucasicum* Borissiak, 1914, collected by I.M. Gubkin in the Taman Peninsula in 1912 and depicted soon after (Borissyak, 1914).

Maria V. Pavlova worked in the Museum (1854 - 1938) for a long time from 1885 till her death in 1938. She described *Elasmotherium* teeth that are

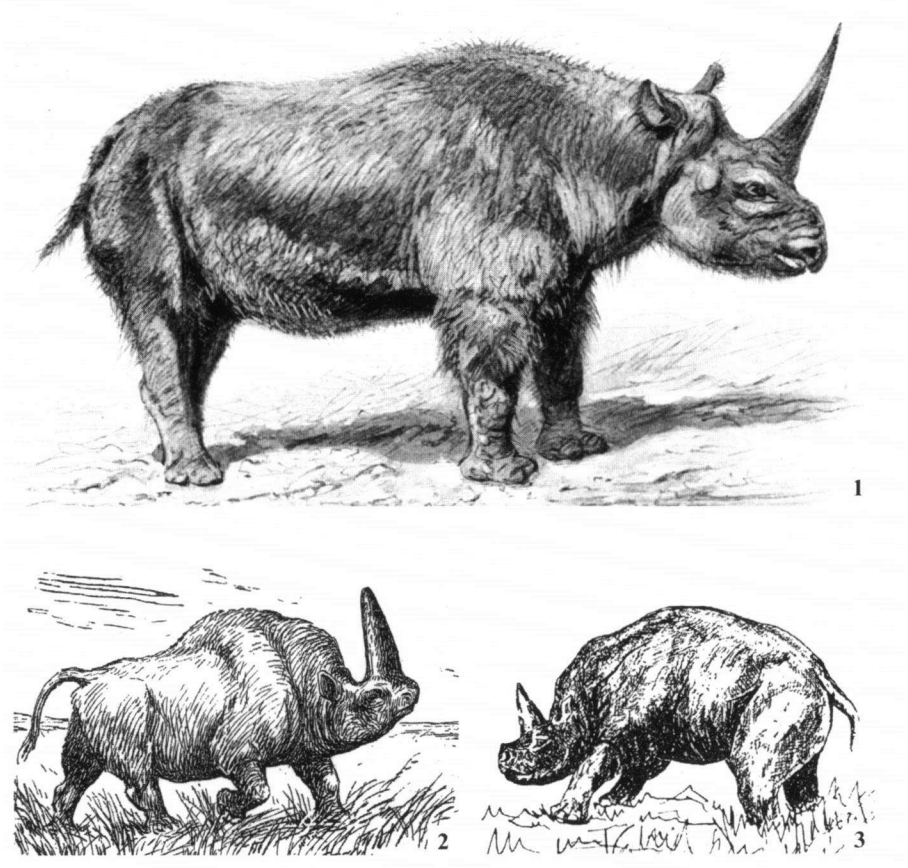

Fig 7 Reconstructions of the Siberian *Elasmotherium*. 1 - W. Kobelt's reconstruction. At the beginning of the 20th century *Elasmotherium* was considered as a representative of the mammoth fauna complex. Just as the mammoth and the woolly rhinoceros, *Elasmotherium* was pictured with thick hair-covering (Kobelt, 1903). 2 - Reconstruction of M. Polesskikh, E. Gavrilov and V. Sitnikov (Polesskikh, 1951). 3 - Reconstruction of Yu. Sofiev and V.S. Bazhanov (Bazhanov & Kostenko, 1962)

Reconstructies van de Siberische *Elasmotherium*. 1 - W. Kobelt's reconstructie. Aan het begin van de 20ste eeuw werd *Elasmotherium* beschouwd als een vertegenwoordiger van het mammoet-fauna-complex. Net als de mammoet en de wolharige neushoorn werd *Elasmotherium* afgebeeld met een dikke haarvacht (Kobelt, 1903). 2 - Reconstructie van M. Polesskikh, E. Gavrilov en V. Sitnikov (Polesskikh, 1951). 3 - Reconstructie van Yu. Sofiev en V.S. Bazhanov (Bazhanov & Kostenko, 1962)

now kept in the collections of the Museum (Pavlova, 1916). Among the teeth was the type material of the genus *Enigmatherium* and the species *Enigmatherium stavropolitanum;* the latter was included into the list of synonyms of *Elasmotherium* by V.A. Teryaev (PV-150).

In 1928 Valentin A. Teryaev (1891 - 1966) joined the staff of the Geological Museum of the Moscow University on leaving the Chair of Palaeontology that was under the direction of M.V. Pavlova. Teryaev was probably one of the most prominent researchers of the elasmotheriums (fig. 5). After the field season of 1928 the *Elasmotherium* collections in the Geological Museum of the Moscow University was significantly enlarged thanks to new specimens brought by Teryaev from the cis-Caspian region, the shore of the Caspian Sea, the mouths of the rivers Volga and Ural, and from other locations (Teryaev, 1929). Heads of the local museums gave a part of the findings to him. Teryaev brought, *inter alia,* an almost complete elasmotherium skull (the so-called "Guriev skull" - fig 3: 1-5) in a good condition - only some parts of the left maxillary, frontal and zygomatic bones were destroyed (PV-167; now this specimen is in the exposition of the Hall of "Historical collections of the Vernadsky State Geological Museum of XVIII - early XX centuries"). A remarkable feature of this specimen is a damage of the frontal swelling that occurred during the animal's life-time due to a sharp-pointed object, which made a perforating trapeziform wound several centimeters in size (fig 3: 2, 4). The wound is usually interpreted as a result of male fights during the mating period or, more often, as a result of human predation. The stab was likely done from above with a sharp object penetrating deeply into the spongy bone tissue of the frontal bones with the object being probably removed afterwards. There are signs of healing along the perimeter of the bone damage, which prove that the stabbing itself was not the reason for the animal's death.

After the reorganizing in 1930 of the departments of the Geological Faculty of the Moscow State University into a Moscow Institute of Geological Exploration (MIGE), the Museum was transferred to the MIGE. Prior to the establishment of the Vernadsky State Geological Museum, the *Elasmotherium* cranium (the "Guriev skull") was kept in the Geological Museum of the MIGE named after A.P. Pavlov and M.V. Pavlova. Also other specimens studied by V.A. Teryaev and depicted in one of his works (Teryaev, 1929; PV-145, PV-147, PV-150) are kept in the Museum.

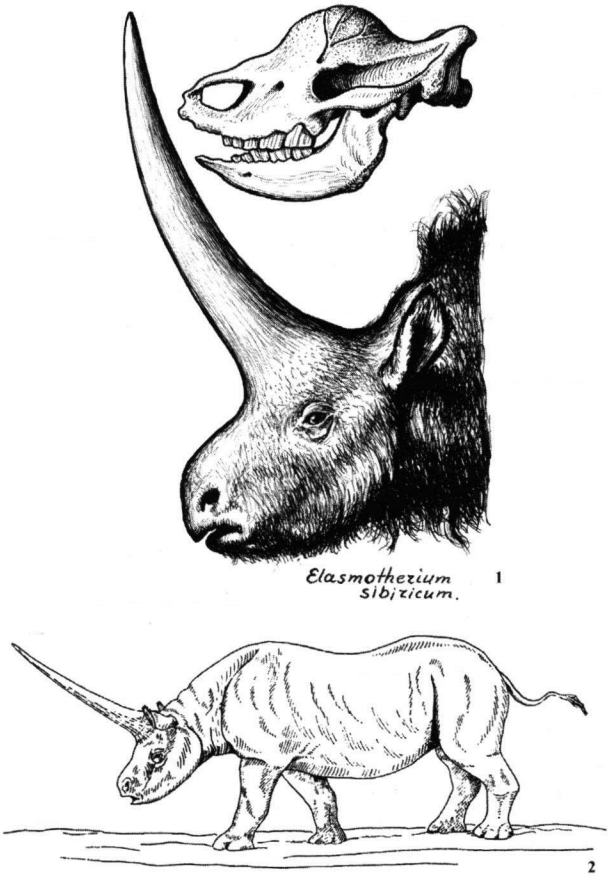

Fig 8 Reconstructions of the Siberian *Elasmotherium.* 1 - Reconstruction of A.P. Bystrov (from the archives of the Palaeonthological Institute) with the skull above it. The gigantic single horn crowns the frontal swelling of its skull. The horn of the woolly rhinoceros was used as a model for the reconstruction of the horn of *Elasmotherium.* The size of the reconstructed horn was determined by proportional increase of the size of the model size. 2 - B. Kurtèn's reconstruction (Kurtèn, 1972). The African black rhinoceros (*Diceros bicornis* Linnaeus, 1758) was used as actual model for this reconstruction

Reconstructies van de Siberische *Elasmotherium.* 1 - Reconstructie van A.P. Bystrov (uit de archieven van het Palaeontologisch Instituut, Moskou) met de schedel erboven. De gigantische enkele hoorn bedekt de voorhoofdszwelling van de schedel. De hoorn van de wolharige neushoorn stond model voor de reconstructie van de hoorn van *Elasmotherium.* De maat van de gereconstrueerde hoorn werd bepaald door verschaling van de grootte van het model. 2 - B. Kurtèn's reconstructie (Kurtèn, 1972). De Afrikaanse zwarte neushoorn (*Diceros bicornis* Linnaeus, 1758) diende als model voor deze reconstructie

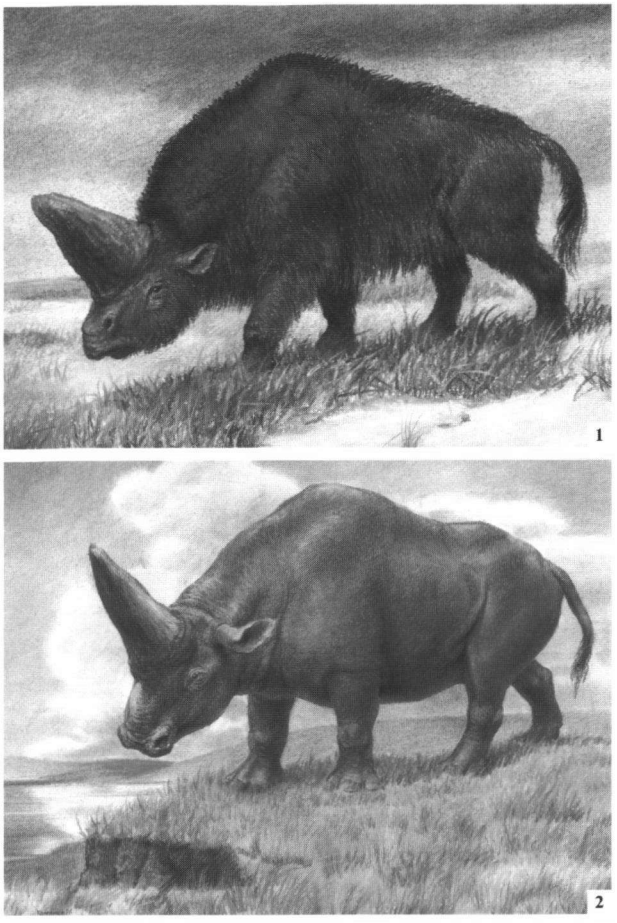

Fig 9 Reconstructions of *Elasmotherium*. by Vladimir D. Kolganov under guidance of Irina A. Dubrovo. From the exposition of Yu.A. Orlov's Palaeontological Museum in Moscow; 1 - *E. sibiricum* Fischer, 1809, created in 1987; 2 - *E. caucasicum* Borissiak, 1914, created a year earlier, in 1986

Reconstructies van *Elasmotherium* van Vladimir D. Kolganov en Irina A. Dubrovo, nu in de expositie van Yu. A. Orlov's Palaeontologisch Museum in Moskou; 1 - *E. sibiricum* Fischer, 1809, gemaakt in 1987; 2 - *E. caucasicum* Borissiak, 1914, gemaakt in 1986, een jaar eerder

Reconstruction of the appearance and ecology of the species

Attempts to reconstruct the external appearance of *Elasmotherium* were quite numerous. Among them are those by Z. Burian (Špinar, 1974; fig 6), V.S. Bazhanov and Yu. Sofiev (Bazhanov & Kostenko, 1962; fig 7: 3), E.W. Berry (1929), A.F. Brandt and Mr Rashevsky (Brandt, 1878), A.P. Bystrov (Gromov & Mirchink, 1937; Shvyreva, 1995; fig 8: 1), N.K. Vereshchagin and A.Z. Sylova (in the exposition of the Zoological Museum of the RAS), A. Woodward (1928), V.E. Garutt (Schaurte, 1964; Shvyreva, 1995), I.A. Dubrovo and V.D. Kolganov (in the exposition of the Palaeontological Museum, Moscow; fig 9), A.M. Kazansky (Teryaev, 1948), J. Kaup (1840), B. Kurtèn (1972; fig 8: 2), W. Matthew (1931), W. Kobelt (1903; Obermaier, 1913; fig 7: 1), M. Polesskikh, E. Gavrilov and V. Sitnikov (Polesskikh, 1951; Khromov *et al.*, 2000; fig 7: 2), P.V. Serebrovsky and M. Pashkevich (Serebrovsky, 1935), V.A. Teryaev and V.A. Vatagin (Menzbir, 1934; Teryaev, 1948), K.K. Flerov (1953). Most of the reconstructions depict *Elasmotherium* as a steppe-dwelling woolly animal with a huge horn on its forehead. Typically it was depicted as a one-horned rhinoceros though there are some exceptions. The *Elasmotherium* was pictured to be double-horned on one of the first reconstructions created by the etcher Rashevsky on the basis of a drawing by Alexander F. Brandt (1878) after studying the animal's skull given to the Zoological Museum of RAS by A. Knoblokh (fig. 10). According to Brandt, the main horn corresponded to the frontal bone swelling and was "very impressive" in size "possibly exceeding the length of the whole cranium". Brandt proves a very large size of that horn based on the size of the blood-vessels that encircled the dome and left their imprints on its surface. In addition, the formation of a special frontal bone structure, which acted as an osteal basis for the horn and which is lacking on the skulls of other rhinoceros species, made him assume an exceptionally large horn size. Taking into account a small rugosity at the front end of the nasal bones, A.F. Brandt presumed that there was a second horn located at the tip of the animal's muzzle, which was shaped as a low, horn-like plate. However, no fossil *Elasmotherium* horn has been discovered so far.

A.F. Brandt not only pictured the head of the animal but reconstructed the complete animal - in line with the remains available to him. Other reconstructions of the late 19th - first half of 20th century depicting the whole animal were essentially close to Brandt's ideas. Yet it is worth noting that being prior to yet to prove findings of the post-cranial skeleton, all these reconstructions remained highly speculative. Typological models for the reconstructions were usually the, by that time already existing, reconstructions of the woolly rhinoceros, which species was already known to the scientific community not only by its complete skeletons but also by sub-fossilized remains from the permafrost soils of Eastern Siberia and natural tar pits of Galicia (Spain). The reconstructions of *Elasmotherium* and woolly

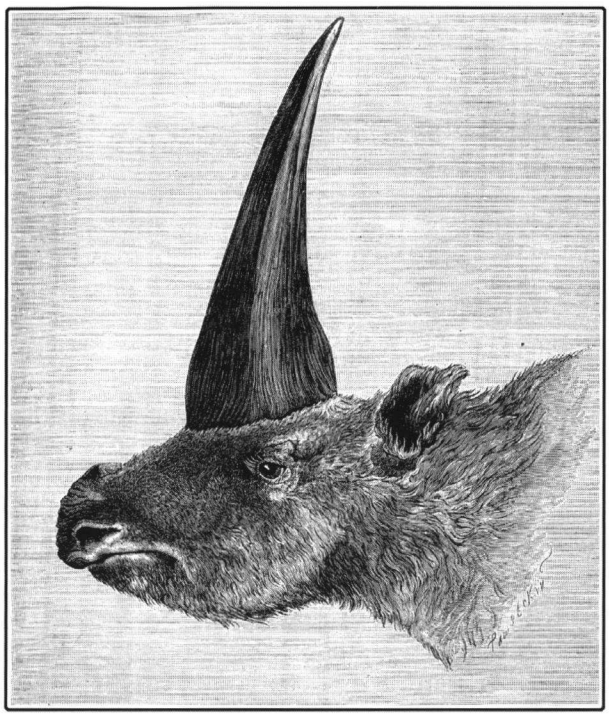

Fig 10 The first published reconstruction of the Siberian *Elasmotherium* has been made by the etcher Rashevsky under the guidance of A.F. Brandt. After Brandt (1878)

De eerste gepubliceerde reconstructie van de Siberische *Elasmotherium* is een ets gemaakt door Rashevsky onder begeleiding van A.F. Brandt. Naar Brandt (1878)

rhinoceros made by the artist M. Pashkevich (Serebrovsky, 1935) illustrate this point since they only differ from each other in details (fig. 11).

In 1934 Zeuner (1934, 1936) measured the angle between the plane of the occiput and that of the skull base of modern and fossil rhinoceros species. He noted that this angle indicates the position of the animal's head relative to its neck and body and thus may indicate which layer of vegetation served as the main food source for a rhinoceros. For example, modern great Indian rhinoceros and African black rhinoceros browsing primarily on leaves and sprouts of bushes have a sharp occipital angle while the grazing white rhinoceros has an obtuse occipital angle. The head of the white rhinoceros unlike those of the black and great Indian ones is bent downward. The occipital angle of *Elasmotherium* turned out to be the most obtuse of all measured species. This fact allowed him to assume that the elasmotherium head was bent downward in relation to the body to a higher degree than in the living rhinoceros species with the field layer being certainly the basic food source for the animal. Unfortunately he did not present his reconstruction of the animal's external appearance.

The reconstructions by Konstantin K. Flerov (1953), V.A. Teryaev and V.A. Vatagin (Teryaev, 1948) are to be noted among the most interesting attempts in approaching the appearance of *Elasmotherium*. Flerov based his reconstruction on the

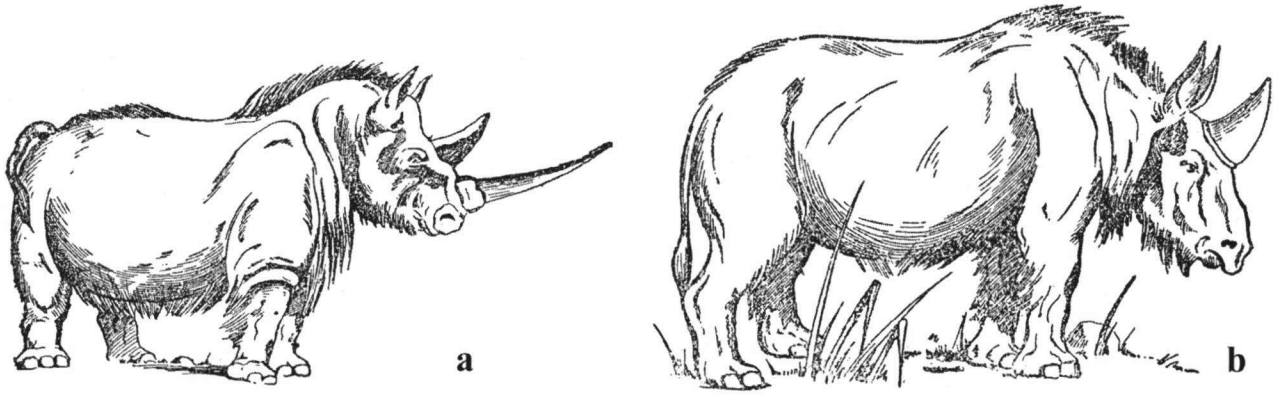

Fig 11 Reconstructions of the woolly rhinoceros (a) and *Elasmotherium* (b) created by M. Pashkevich under guidance of P.V. Serebrovsky. *Elasmotherium* was depicted with the woolly rhinoceros as model. The two reconstructions only differ in details. After Serebrovsky (1935)

Reconstructies van de wolharige neushoorn (a) en *Elasmotherium* (b) getekend door M. Pashkevich onder leiding van P.V. Serebrovsky. *Elasmotherium* is afgebeeld naar het model van de wolharige neushoorn. De twee reconstructies verschillen slechts in details. Naar Serebrovsky (1935)

Fig 12 *Elasmotherium* as steppe-dweller in the reconstruction of K.K. Flerov (from Detskaya Entsyklopedia, 1959)

Elasmotherium als bewoner van de steppe in de reconstructie van K.K. Flerov (uit de Detskaya Encyclopedie, 1959)

skeleton assembled in the early 50's of the 20th century in the Palaeontological Institute of the Academy of Sciences of the USSR. In this reconstruction, *Elasmotherium* was a massive, bare-skinned rhinoceros with high withers, sloping back and relatively small low-bent head (fig. 12). A single low horn was located on the animal's forehead and covered the dome-like swelling of the frontal bones in a cap-like manner. In this concept *Elasmotherium* represents a steppe-dwelling animal feeding, at least partially, on the underground parts of plants that the animal sought by ploughing the soil with its muzzle. This feeding behavior was the reason for the formation of the reinforced narrowed nasal bones and the possible keratinizing of the snout (the part of the animal's muzzle bearing the smaller horn according to Brandt), an adherent nasal septum, frontal apophysis of the eye-sockets protecting the eyes, excessive hypsodonty of the teeth in order to cope with the intensive abrasion while feeding on the plant material mixed with soil. Flerov connected the animal's feeding habit with the dome-like swelling of the frontal bones. He believed that the purpose of the formation was primarily to intensify the smelling abilities rather than to support the massive horn. The inner cavities of the dome-like swelling were in fact hypertrophied frontal sinuses connected with the nasal cavities. According to Flerov, they provided additional space to the region which maintains olfactory sinuses for increased smell detection ability in many mammalian species. Such sinuses are essentially necessary for an animal feeding on underground parts of plants and the size of the sinuses have a significant meaning. The cap-like horn covering the swelling probably only protected the frontal apophysis and did not play any other role.

According to the view of Teryaev (1948) *Elasmotherium* had completely different habits. The zoologist Vasily A. Vatagin who made the illustrations for his article, depicted an animal, which resembles more a hippopotamus rather than a rhinoceros both in appearance and in life style (fig 13: 1, 2). Teryaev assumed an amphibious mode of life for *Elasmotherium* even earlier, in 1930, mainly based on his study of the middle metacarpal bones of the rhinoceros and a reconstruction of the animal's lower front limb. In his concept, the front extremities of *Elasmotherium* were four-toed, like those of modern-day tapirs, rather than three-toed ones typical of the rhinoceroses. Tapirs mostly inhabit wetlands and marshy areas. Teryaev studied the locations for the attachment of the fifth metacarpal bone to the fourth one and found them large enough to allow the supposition of the existence of a developed fourth digit, remains of which were absent in the collections. Recently, his views did not prove to be true (Shvyreva, 1995): the fifth metacarpal bone is rudimentary and *Elasmotherium* had only three functional digits. The animal's wide-spread digits were enough to prevent sinking of the animal's feet into boggy soils. In the view of Teryaev, the elasmotheriums were typical dwellers of reed-beds and probably good swimmers that fed on the green parts and rhizomes of water plants, "torn out by the animals from the swamp tussock at the bottoms of water bodies" (Teryaev, 1948). Another evidence which proved Teryaev's assumptions of a semi-aquatic life-style of *Elasmotherium* came from taphonomic observations of the burial of an *Elasmotherium* skeleton discovered in 1938 in the buried humus layer where the rivers Karaman and Nakoi join, not far from the city Saratov. The skeleton was found in the pose of being bogged down: the animal's limbs were sunken down vertically and trapped in the clay underlying the humus layer. The bone fragments above the humus layer were gnawed by some predator. The skeleton was overlain with fluvio-lacustrian sediments of the third (above flood-plain) terrace of the river Volga. In 1964 and 1966 two almost complete skeletons of

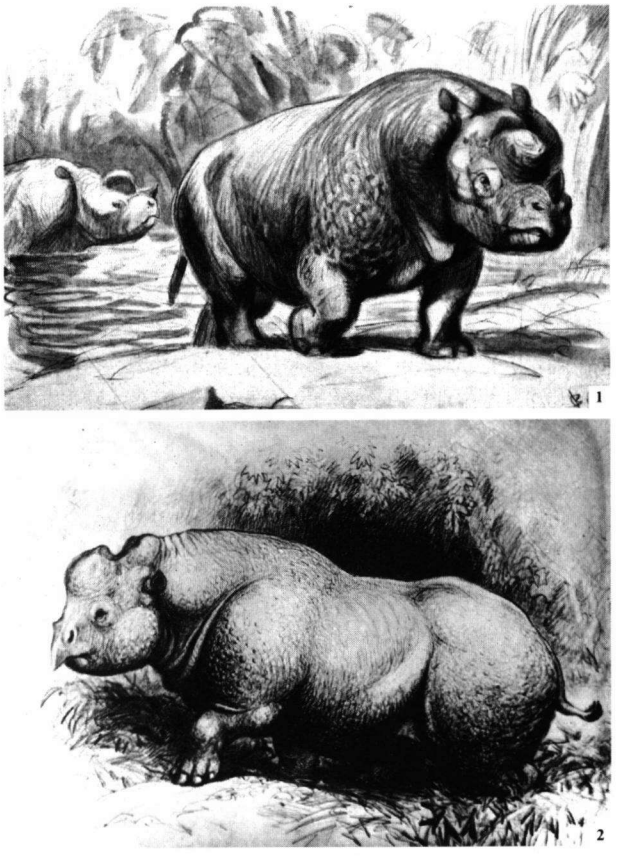

Fig 13 Reconstructions of the Siberian *Elasmotherium* by V.A. Teryaev and V.A. Vatagin; 1 - their first published reconstruction (Menzbir, 1934); 2 - a similar reconstruction (from the archives of V. Zhegallo)

Reconstructies van de Siberische *Elasmotherium* door V.A. Teryaev en V.A. Vatagin; 1 - hun eerste gepubliceerde reconstructie (Menzbir, 1934); 2 - een vergelijkbare reconstructie (uit de archieven van V. Zhegallo)

Elasmotherium were discovered in the Stavropol region. Judged by their position, these animals drowned in the swamp as well.

Another particular feature of Teryaev's reconstruction of *Elasmotherium* is the absence of a horn on the frontal dome-like swelling. He believed the thin-walled frontal swelling to be among the most vulnerable spots in the skull; it is at this spot that the skull can be easily broken into halves. Thus, he reconstructed the area without a horn at all, only placing the latter in the form of a small spike on the tip of the muzzle.

The fate of these reconstructions differed in the Russian palaeontology. The reconstruction by Flerov was reprinted many times including in encyclopedias that were published in huge circulations (Anonymous, 1957; Anonymous, 1978; Detskaya Entsyklopedia, 1959; also Flerov, 1970 etc.), and thus this reconstruction became almost a "textbook picture". But the image of Teryaev's *Elasmotherium* was only published a couple of times. Although there were painted, graphical and sculptural images of the animal thanks to cooperation between V.A. Teryaev and the artist V.A. Vatagin, only part of them (often in altered form) became known to a larger audience (Menzbir, 1934, fig 13: 1; Druzhinin, 1947; Teryaev, 1948). Currently, two of the less-known works created in the course of their cooperation are exhibited in the State Geological Museum. Those are a small gypsum sculpture (fig 14: 2) and a reconstruction of the animal in its environment (fig 15), a part of which was published in one of the Teryaev's (1948) articles as an "Ecological panorama with flora and fauna of the "Dome-forehead's epoch" (1948). Unfortunately,

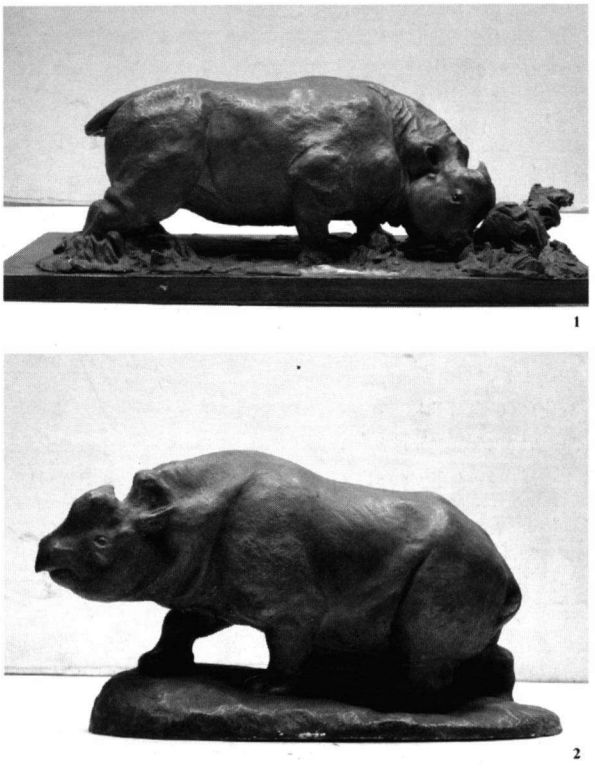

Fig 14 Sculptural reconstructions by V.A. Vatagin of the Siberian *Elasmotherium* acccording to the view of V.A. Teryaev; 1 - «Male»; plaster with gouache, 44,5 x 18 x 16 cm; from the SGM stock; 2 - «Female»; plaster with gouache, 35 x 15 x 18 cm; from the SGM exposition. Photos by S. Bogdanov

Plastiek reconstructies door V.A. Vatagin van de Siberische *Elasmotherium* volgens de inzichten van V.A. Teryaev; 1 - «Mannetje»; gips met gouache, 44,5 x 18 x 16 cm; uit het SGM depot; 2 - «Vrouwtje»; gips met gouache, 35 x 15 x 18 cm; uit de SGM expositie. Fotos van S. Bogdanov

due to limited polygraphic abilities of the journal "Sovetskaya geologia" ("Soviet Geology") at that time the fragment was reprinted in black-and-white. Another sculptural reconstruction by Vatagin is kept in the museum stock (fig 14: 1). The authors supposed that a small forehead horn existed, seen this reconstruction, despite the above-stated views of V.A. Teryaev, and that this horn was placed at the backside of the forehead dome and directed backwards. According to Zhegallo *et al.* (2002), the first figurine represents a female and the second one a male *Elasmotherium*. Few people know that the picture of *Elasmotherium* with a tremendous horn at the ceiling of the Hall of Evolutionary Morphology of the Zoological Museum of the Moscow State University is a modified reconstruction by V.A. Teryaev and V.A. Vatagin that was painted by the latter as part of a series of paintings for the Museum.

Most of the above-mentioned reconstructions were made in the course of preparation of the monograph by V.A. Teryaev "Elasmotherium from the USSR and a reconstruction of this animal" that was completed in 1932 (Menner, 1967) but has never been published, notwithstanding the positive opinions about his work and his scientific researches in general, as is evident from his personal file stored in the Department of the History of Geology of the Vernadsky State Geolo-

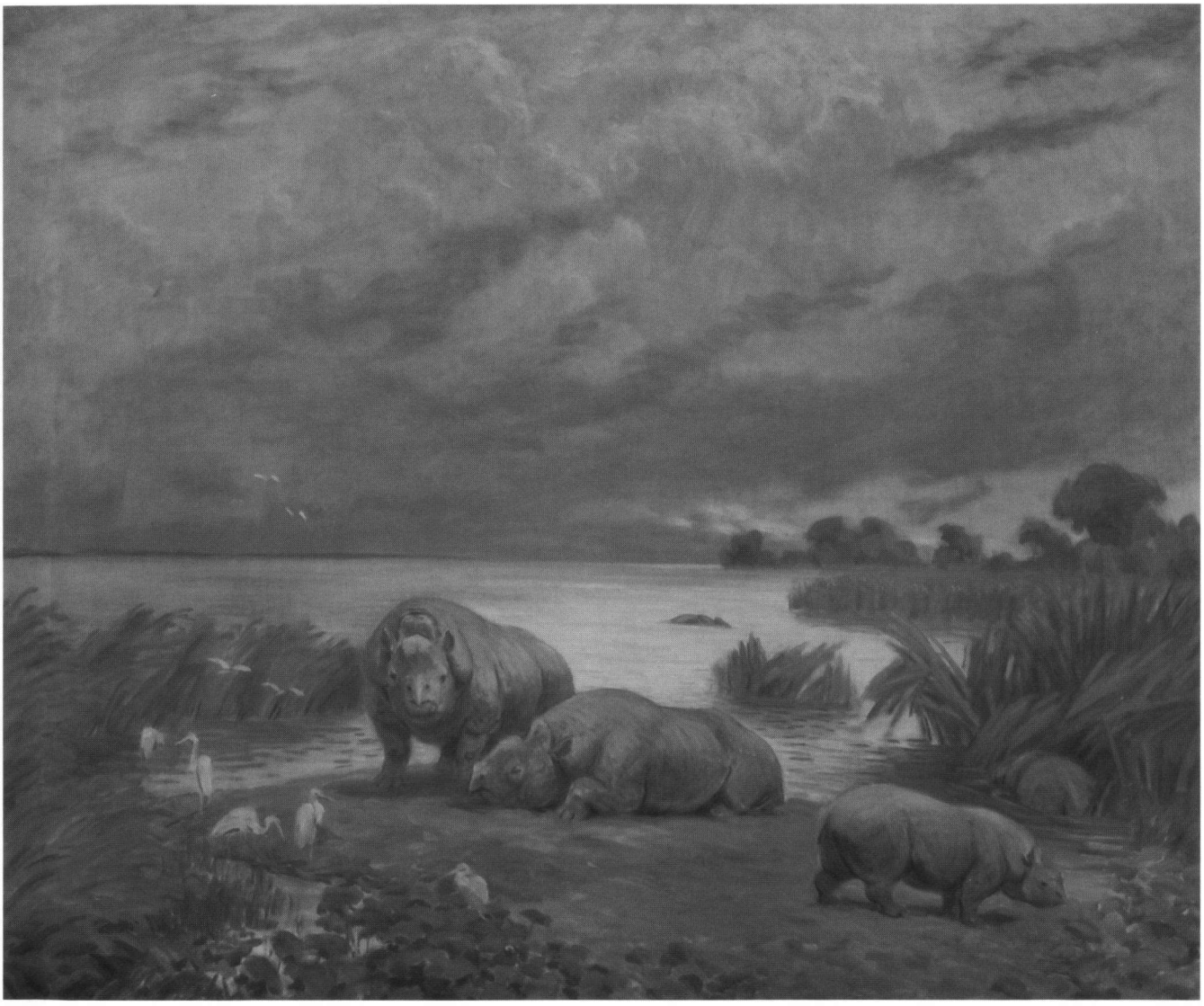

Fig 15 «Ecological panorama with flora and fauna of the "Dome-forehead's epoch"» by V.A. Vatagin. The landscape reconstruction was made according to V.A. Teryaev's view. Oil on canvas, 145 x 120 cm, SGM.

Ecologisch panorama met flora en fauna van het "Koepel-voorhoofd's tijdperk" van V.A. Vatagin (de term "koepel-voorhoofd" werd gebruikt voor *Elasmotherium* vanwege de voorhoofdszwelling). Deze landschapsreconstructie is gemaakt naar het standpunt van V.A. Teryaev. Olie op canvas, 145x120 cm, SGM

gical Museum. V.A. Teryaev was granted with a PhD in Geology and Mineralogy without the need to defend his thesis on the basis of the aggregate of all his works. A significant part of them was devoted to *Elasmotherium*. One of the attempts to publish his monograph is known for certain to have been undertaken in 1940. There is a document containing the opinion of G.F. Mirchink, who was a professor of the MIGE at that time, and dated 20 April 1940 that reads as follows: "I find the work absolutely worthy publishing". Yet this attempt again failed. Somewhat earlier in 1938 V.A. Teryaev had to leave the MIGE "due to ceasing of researches on vertebrate palaeontology in the Institute" (Menner, 1967). During later years his work was hardly related to palaeontology at all. In the second half of the 40's he lived in the Autonomous Republic of Komi (Russian Federation) and in the Arkhangelsk region. From 1939 to 1948 he did not publish a single article. In 1948 a summary of his monograph (Teryaev, 1948) was released but after that he did not appear in any published material for the next twelve years. It was only in the last six years of his life when Teryaev had already retired (1960 - 1966) that he prepared and submitted five articles on vertebrate palaeontology.

It should be noted that the morphological reconstruction of *Elasmotherium* suggested by V.A. Teryaev did not find any significant support from the next generation of palaeontologists. The results of his comparative anatomical and morpho-functional analyses of the animal's skeleton, however, make us realize that Teryaev was not that far from reality in his characterisation of the *Elasmotherium* habitat.

Recently, some arguments have been presented in favor of the above mentioned statements (Zhegallo & Noskova, 2001). Firstly, *Elasmotherium* is one of the largest known species of rhinoceros, modern and fossil, and it belonged to the realm of the largest land animals of the Pleistocene. *Elasmotherium* approached mammoths and present-day elephants in size. A forage reserve for such an animal could not be provided for by low productivity biotopes with xerophilous plant-life and had to be supplied either by high-grass steppes or by near-water biotopes. Secondly, the formation of the highly hypsondont molars of *Elasmotherium* was induced by abrasive mineral particles in the feeding material rather than rigidity of the food itself. The content of such particles in the diet increases while feeding on the underground parts of plants and it increases even more pronounced while feeding on the underground parts of plants growing in the wet substrate of the near-water habitats. Thirdly, such features of *Elasmotherium* as the keratinized wedge-shaped rostrum that blocked the use of the lips and the orbicular muscle of the mouth for grasping food, the absence of incisors that prevented cutting a plant off and the presence of a long diastema with a keratinized edge, as well as hypertrophy of the transverse processes of the atlas allow for the affirmation that *Elasmotherium* predominantly used a sideward way of picking food materials and also tore them off also by a sideward jerk of its head. A frontal grasp was possible as well due to interactions of the massive tongue and spoon-like keratinized symphysis of the mandible.

It is likely that the structure of the food-grasping organs itself, which combined a spoon-like symphysis of the mandible and a wedge-like rostrum of the upper jaw, can be explained in terms of feeding on the underground parts of water and bog plants. The spoon-like mandible easily penetrates into the semi-liquid underwater soils and takes the underground plant material as well. The wedge-like upper jaw presses the plant material during occlusion and keeps it fixed until the plants are torn from the substrate with a sideward jerk of the animal's head. This mechanism seems primarily designed for picking up plants that reproduce with rhizomes and are firmly anchored to the substrate with their numerous additional roots: many monocotyledonous species such as sedge, cattail and naiad, and some dicotyledonous such as water-lilies. Such plants are relatively indifferent to the type of substrate and many of them readily grow on highly abrasive sand soils. This provides an additional argument to explain the "absolute" hypsodonty of *Elasmotherium* molars.

Nevertheless, there is no point in identifying the elasmotheriums as strictly semi-aquatic animals as Teryaev suggested. The structure of the food-grasping organs favors his hypothesis, but the skeletal proportions and features of the animal's locomotory apparatus demonstrate adaptations to open landscapes. This allows adding meadow and steppe biotopes to the animal's habitat. These probably were used as zones of migratory routes between preferred forage areas. Here we may reasonably go back to Flerov's ideas of *Elasmotherium* being a "plough-beast". The animal got its underground food-supply by ploughing soil with its pointed rostrum and picked up rhizomes and other underground part of the plants.

Summarizing the above, a combination of elements of both reconstructions suggested by Teryaev and Flerov allows us to identify the habitat of *Elasmotherium* as a steppe landscape which included riparian plant associations being the preferred feeding grounds (Zhegallo & Noskova, 2001). In the northern part of its range, in the forested zone, *Elasmotherium* was a valley-dwelling animal. Its habitats, in addition to the river flood-plains, could also include a lacustrian biotope with the supralittoral zones being typically areas of a particularly intense growth of the rhizomatous plants.

Evolution of the Elasmotheriinae

Among the numerous (no less than seven) subfamilies of the Rhinocerotidae, the closest relation to the Elasmotheriinae is found in the Paleogene representatives of the Caenopinae-like large, long-legged rhinoceros of the genus *Ronzotherium*, which is noted for its long and sphenoidal skull, and which occurred in the Oligocene of Eurasia. A trend of grouping the Elasmotheriinae and *Aceratherium*, that existed until recently, was caused by a lack of information on the existing diversity within the subfamily and absence of information on the most primitive representatives of the latter. After the first description of the remains of the genus *Begertherium* (Belyaeva, 1971) it became clear that it is impossible to judge the morphological identity of the subfamily on the basis of three previously known genera only (*Elasmotherium, Sinotherium, Hispanotherium*) and that the subfamily should include the formerly defined subfamily of the Iranotheriinae (with the genera *Gobitherium* and *Iranotherium*). Moreover, modern ideas of the morphological diversity of the Elasmotheriinae make it reasonable to believe that there is enough basis for including the woolly rhinoceros *Coelodonta* into this subfamily, even though formerly it was traditionally included into the Dicerorhinae, which view is no less supported than that for the similar inclusion of *Iranotherium* (Garutt & Boeskorov, 2001).

Currently the following evolutionary scenario for the Elasmotheriinae is considered to be probable. The history of the subfamily is proven in terms of palaeontology beginning only from the Early Miocene. However, since the Elasmotheriinae had already appeared as a radiated group by this time, the ancestral group should be sought in the Oligocene when the Rhinocerotidae families finally delimited the spheres of habitation and resource usage. The swamp-dwelling rhinoceroses Aminodontidae took hold of the lower part of the range in the near-water habitats; the giant Indricotheriidae utilized the food resources of the arboreal level and the highly specialized (in comparison to the previous two groups) Hyracodontidae and Rhinocerotidae were limited to resources of the lower layer of the plant associations. Ancestors of the Elasmotheriinae probably lived in habitats of the upper part of the range that were so distant from the taphonomic traps of the local erosion bases that their chances to get included into the palaeontological records were next to zero.

These conditions continued into the Early Miocene only for the unknown preceders of *Coelodonta*. The habitat boundaries of the radiated Elasmotheriinae went down along the range. The probability of their inclusion into the fossil record increased significantly and four genera of the Elasmotheriinae got included into the records: *Gobitherium* and *Begertherium* of the Eastern Palaearctic and Beljaevina and *Hispanotherium* from the Western Palaearctic (though there is one occurrence of the latter in the Northern China).

It is possible to presume on the basis of the scanty taphonomic data available for ecological interpretations that *Hobitherium*, which occurs very rarely in the fossil records, represents habitats close to the watersheds. Alternatively, *Begertherium*, the remains of which are found in almost all early-Middle Miocene fossiliferous sites of Central Asia, inhabited areas near the zones of the flood-plain sedimentation. Yet, both species lived in dry habitats.

Judging by the geochronology and comparative morphology of the early Elasmotheriinae and by the palaeogeographical situation in general, the area of the subfamily's origination and evolution was Central Asia. Uniformity of the landscape of the semiarid zone during periods of aridization in the Early Miocene allowed the Elasmotheriinae to spread westward to the Western parts of the Palaearctic probably including Northern Africa.

In the Late Miocene when the diversity of the perissodactyls decreased everywhere due to the rapid expansion of the ruminants, the diversity of the Elasmotheriinae only decreased insignificantly and the subfamily was represented by the genera *Iranotherium, Sinotherium* (both in the Eastern Palaearctic) as well as by the relic genus of the *Hispanotherium* in Northern Africa.

The rhinoceroses of the genus *Sinotherium*, which are quite reasonably considered to be the ancestors of *Elasmotherium*, achieved an evolutionary success by utilizing the food resources of wetter habitats than the earlier Elasmotheriinae and at the same time retained and developed further their adaptation to highly abrasive forages as well as their specific locomotory features of open landscape dwellers. By the end of the Miocene this genus had spread all over Central Asia from North-East China to the Zaisan Depression and their range was within that of the amphibious rhinoceroses of the genus *Chilotherium* of the subfamily Teleoceratinae. The two genera partially shared habitats.

At the end of the Miocene the descendants of *Sinotherium*, unlike the other Central Asian rhinoceroses, survived the crisis of continental ecosystem integrity without any serious morphological transformation, as far as can be judged by the example of the Early Pliocene *Parelasmotherium* from China. After the crisis that lead to extinction of more than half the genera of the Miocene mammals everywhere, and up to three quarter of the genera in Central Asia, and to an uncompensated drop in biodiversity, the Elasmotheriinae almost entirely vanished from the palaeontological record for 3,5 million years. And then, in the form of a single genus *Elasmotherium*, they started a rapid spread into a vast area between the Carpathian Mountains and the Huanghe river predominantly in steppe and wooded steppe zones. The animals reached as far north as latitude 60 along the broad river valleys and as far south as latitude 38 (North) via wet habitats.

Around 2.5 million years ago *Elasmotherium* was an important element of the Khaprov mammalian fauna of Eastern Europe; 1.8 million years ago the species *E. peii* occurred all over the area from Central Asia to the region near the Black Sea; 1 million years ago the largest of all the elasmotheriums ever, *E. caucasicum*, inhabited the region around the northern part of the Azov Sea, and in turn gave rise to *E. sibiricum* in approximately 200 thousand years. The latter expanded its range into the territory of the South Caucasian states, Central Asia and Southern Siberia and then reached Transbaikalia (eastern part of the area around Lake Baikal). In this case, unlike the earlier Central Asian scenarios, the centre of the evolution of the taxon was probably located in Eastern Europe. At any rate, it was the western part of the animal's range that hosted the highest density of *E. sibiricum* population and the period of its existence was longer here than in the East.

The Elasmotheriinae achieved probably the greatest evolutionary success among all the rhinoceroses of the Late Cenozoic. The reason could very well be the very successful elimination of genetic limitations for increase of hypsodonty, which correlated with intensifying of the enamel folding. That enabled the animals to take advantage of the opportunity to expand the forage resource base progressively due to continuous taking on more and more abrasive food. The next successful step was the transformation of the food-grasping organs that led to the complete loss of incisors and keratinizing of the rostrate area. Such a system proved to be more versatile than that of other rhinoceroses even though in terms of morphology, it appears to have been quite specialized. Retaining an archaic (non-specialized) locomotory structure was also important for their evolutionary success since it did not impose any significant limitation on the choice of habitat.

The hypertrophy of some evolutionary trends characteristic of rhinoceroses in combination with archaic features in the elasmotheriums gives the impression of some disharmony in these animals. This "disharmonic" evolutionary strategy, however, turned out to be very effective and only succumbed to the landscape-climate stress of the ecosystem caused by the Riss Glaciation. It is quite possible, however, that the last straw that broke *Elasmotherium*'s back was put by man.

Range of elasmotheriums during the Late Pleistocene and its possible co-existence with man

Remains of *E. sibiricum*, which species is characteristic of the Pleistocene, are known from the European part of Russia, the Urals, Western Siberia, Transbaikalia, Ukraine, Kazakhstan, and Central Asia. Currently there is no proven information about *Elasmotherium* remains beyond the borders of the former USSR. Two of the three Central and Western European findings that are usually mentioned in scientific sources (namely Hungarian and Sicilian ones) are supported with no images, descriptions nor materials that could be a basis for their identification. The location of the third finding, the occipital part of a skull that is currently kept in the Museum of Natural History in Paris, was long considered to originate from the Quaternary sediments of the valley of the

river Rhine. Nevertheless, the original owner of the collection, the Austrian physician and naturalist Franz Joseph Gall, better known for his foundation of phrenology, could not provide any reliable information on the origin of the specimen (Milne-Edwards, 1868, translation in Teryaev, 1948). Afterwards, Milne-Edwards noted a shell of the bivalve mollusk *Dreissena fluviatilis* stuck in a crack of the skull while conducting studies of the longitudinal section of the specimen. The mollusk is characteristic for the basin of the river Volga, and this fact allowed him to conclude that the specimen originated from Russia.

The Siberian *Elasmotherium* is traditionally considered member of the Middle Pleistocene Khazar faunistic complex of the East European Plain (Gromov, 1935; Lazukov, 1965; Vereshchagin, 1977). Some scientists even restrict the time-range of the species to the more ancient Tiraspol faunistic complex (Shvyreva, 1995). Currently, new information appeared that indicate that *Elasmotherium* was also a member of the Late Paleolithic faunistic complex, and it is noted that Elasmotherium, however rare, still occurred in the Middle River Volga region within the mammoth fauna complex (so called Shkurlat faunistic subcomplex) during the Mikulin interglacial period (Khromov, 1999). Khromov (1999) dates a molar of *Elasmotherium* aff. *sibiricum* to the Late Pleistocene. The finding is kept in the collection of the Volsk regional museum (OFOG No. 2522/11). The molar originates from the site at the river island Khoroshevsky, which got submerged in the Volga waters after the creation of the Saratov reservoir (Khromov, 2001; Khromov *et al*, 2000). Radio-carbon datings of *Elasmotherium* remains are not known.

Works of surviving Paleolithic art may provide us with an indirect evidence of the existence of *Elasmotherium* during the Late Pleistocene. A monochrome outline image of a one-horned rhinoceros was found among the rock paintings discovered in 1956 in the Rouffignac Cave on the right bank of the river Vézère, Dordogne, France (Nougier & Roberts, 1959). These paintings have not been radio-carbon dated, however, their Late Paleolithic age is considered quite reasonable. The depicted rhinoceros had unusually high withers and a bent-down head (fig 16: 1). The single huge horn was located on the animal's forehead rather than at the tip of its snout. Researchers of Paleolithic art typically treated all rhinoceroses images in rock paintings as the woolly rhinoceros, *Coelodonta antiquitatis*. But the above-

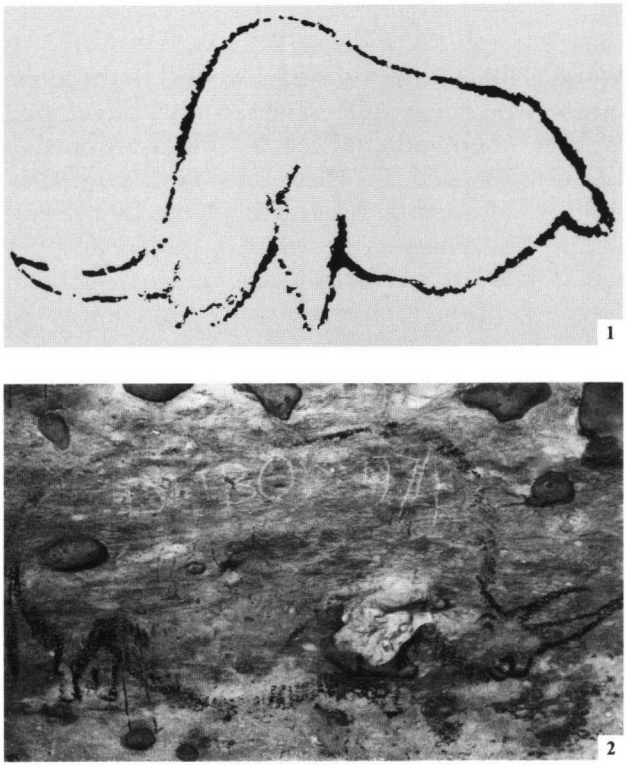

Fig 16 Paleolithic art; 1 - drawing of a rhinoceros from Rouffignac Cave, which was interpreted as *Elasmotherium* by W. Schaurte (1964); the outlines are restored based on the photograph published by Schaurte; 2 - drawing of a wooly rhinoceros from the same Rauffignac Cave (after Prideaux, 1973)

Kunst uit de Oude Steentijd; 1 - tekening van een neushoorn in de grot Rouffignac, die gezien werd als *Elasmotherium* door W. Schaurte (1964); de herstelde omtrek is gebaseerd op een foto, gepuliceerd door Schaurte; 2 - tekening van een wolharige neushoorn uit dezelfde grot Rouffignac (naar Prideaux, 1973)

mentioned features of the animal are characteristic of *Elasmotherium* rather than of the woolly rhinoceros (fig 16: 2). An image of the latter is also known from the same Rouffignac Cave (Prideaux, 1973). Just like the former, the image depicts high withers but the head is positioned more horizontally and the bigger of the two horns is located at the snout rather than forehead. The assumption that the monochrome image from Rouffignac Cave depicts *Elasmotherium* was first suggested by Schaurte (Schaurte, 1964), and later supported by Shvyreva (1995), but was also independently suggested by N. Spassov (pers. comm. to N.N. Kalandadze, 2001). Comparison of the images of the two rhinoceroses, in our view,

allows for additional reasoning. We, however, understand that it is only the number of horns that unambiguously indicates differences between the two rhinoceroses since the rate of pronouncement of the withers, head incline and location of the horns could vary depending on the pose of the animals pictured or be within the unknown limits characteristic of the generic outline.

If the assumption of an *Elasmotherium* being the prototype of a rhinoceros image in Rouffignac Cave is correct, then this fact significantly modifies our ideas about the animal's chronological and geographical range. It means that *Elasmotherium* is no longer an almost entirely Asiatic animal with no proven remains to the West of the Carpathian Mountains. It also means that the Western European finds could be those of *Elasmotherium* indeed.

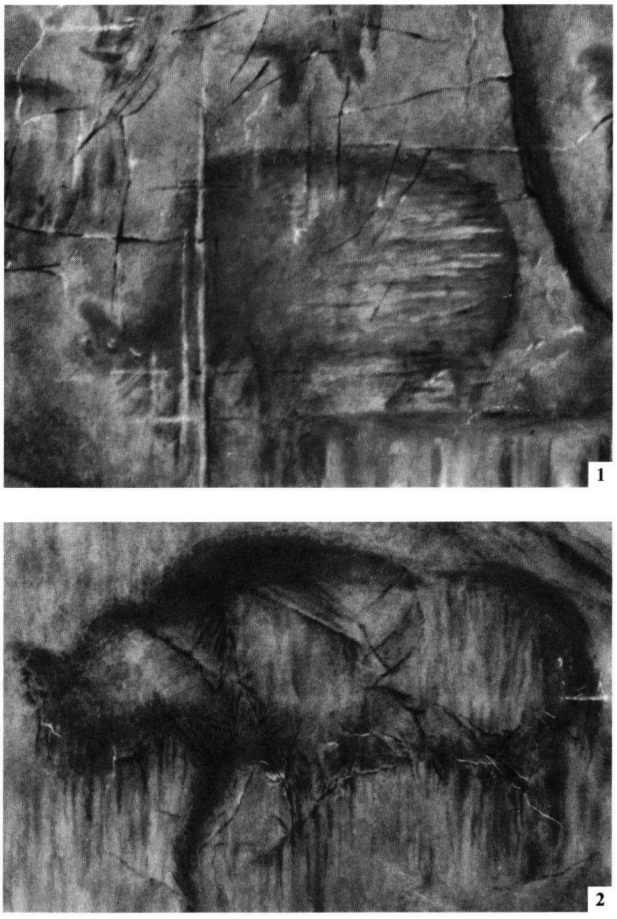

Fig 17 Paleolithic art (after Bader, 1965); 1 - the rhinoceros with head down from Shulgan-Tash (Kapovaya Cave); according to V.I. Gromov the painted animal could be an *Elasmotherium*; 2 - the other type of rhinoceros from the same Shulgan-Tash (Kapovaya Cave)

Kunst uit de Oude Steentijd (naar Bader, 1965); 1 - de neushoorn met laag gedragen kop in Shulgan-Tash (Kapovaya Grot); volgens V.I. Gromov kan dit geschilderde dier een *Elasmotherium* zijn; 2 - het andere type neushoorn in dezelfde grot Shulgan-Tash (Kapovaya Grot)

Another image of a rhinoceros (fig 17: 1), which is usually considered to be related to *Elasmotherium*, was made with red ochre at the wall of Kapovaya Cave (original name Shulgan-Tash) in the Southern Urals. V.I. Gromov was the first who was of the opinion that the image proportions more resemble those of Elasmotherium rather than those of the woolly rhinoceros (Bader, 1965). In addition, the image in Kapovaya Cave is very similar to the *Elasmotherium* image from Rouffignac Cave in its general form even though the outline drawing of the rhinoceros with red ochre does not represent detailed features of the animal. Bader (1963), who supervised the first expedition to study this cave's rock paintings points out that the head of the image was in a poor condition and that other details of the drawing, in particular the shortened body length, of this rhinoceros could be the result of lack of space for drawing between the horse image and the vertical groove in the wall.

Just like Rouffignac Cave, the Kapovaya Cave contains an image of another rhinoceros that was depicted in a completely different manner (fig 17: 2). Its withers are less pronounced and the position of the head position is almost horizontal. However, the drawings by the Paleolithic artists in Kapovaya Cave are much less accurate than the monochrome images of the Rouffignac Cave. Animals of Kapovaya Cave can be guessed at and recognized from their images rather than exactly seen. The Kapovaya Cave artists seem to have decorated its walls rather than kept documentary records of objects. Their attention concentrated on the artistic picture and not on details. According to A. Leroi-Gourhan, the caves were painted according to a strict pattern that implied nonrandom locations of images in particular places, which is a characteristic of a mature stage of cave art aiming at a complex artistic (or mystic) solution rather than at representing a single image. So some of the animals' parts are not drawn in details or even omitted entirely (for example, the extremities of some mammoths and horses). Considering these features and the limited possibilities of the exact rendering of an object with ochre at a cave wall, we are not inclined to regard the Kapovaya Cave images as proven evidence for the co-existence of *Elasmotherium* and Paleolithic man in the south-western

cis-Urals. Nevertheless, this possibility can not be eliminated entirely.

Datings of the images at Kapovaya Cave based upon the artistic style classification as given by A. Leroi-Gourhan are not before the period Late Solutreen - Middle Madeleine (Bader, 1965). This corresponds with the end of the Würm Glaciation in Western Europe. In addition to the realistic images, the dating was based on the geometrical drawings at Kapovaya Cave. The age of the cultural layer with bones of a cave bear, hare, and lemming and artifacts made of the South Ural jasper was identified to be 14.680 ± 150 years BP on the basis of radio-carbon evidence (Shchelinsky, 1986; Shchelinsky *et al.*, 1985). The layer contained, amongst others, particles of ochre, fragments of limestone with traces of a colorful image, and fragments of a mammoth tusk; all these allow us to consider the age of the cultural layer to be synchronous to the age of the rock paintings in the cave.

Findings of *Elasmotherium* bones at archaeological sites of paleolithic humans are not known. The only possible documentary evidence of the "predator-prey" type of relationship between man and *Elasmotherium* could be the damage to the frontal bones of the skull of the Siberian *Elasmotherium* from Guriev (the "Guriev skull") that occurred during the animal's life. But in our opinion, such an assertion must be confirmed by additional palaeontological or archaeological studies.

Summarizing the above, currently two variants of views on the geographic and chronological range of *Elasmotherium* exist. The first one is based on proven findings of the animal's remains. These restrict the geographical range of *Elasmotherium* within the borders of CIS and China and set the upper limit of its chronological range above the Khazar faunistic complex. The findings are all hard evidence and repeatedly proven. The second view is based on indirect palaeontological evidences (the Paleolithic art) and on the finding of *Elasmotherium* aff. *sibiricum* at a vanished site. These data may allow to suggest the co-existence of *Elasmotherium* and man in the same eco-systems both in Eastern and Western Europe at least during the Late Pleistocene.

Elasmotherium as possible prototype of mythological animals

Assuming a possible co-existence of *Elasmotherium* and paleolithic man, it seems logic to presume that knowing about such a huge, massive and obviously unusual animal must have led to some traces in the folk epos, myths and legends in much the same way as it happened to, say, the mammoth; even though tales of a huge creature dwelling underground are evidences, above all, of the palaeontological findings rather than of the real existence of the animal. Many authors noted that fact repeatedly; examples follow here.

Brandt (A.F. Brandt, 1878) noted, based on an essay about the folk literature of the Turkish-language speaking tribes of Eastern Siberia and Dzungaria by the Russian orientalist and traveler Radloff (1866), a Yakut legend about killing a huge black bull with a spear, the bull bearing a single horn, the size of which was so tremendous that it was impossible to be carried in their hands and needed to be put in sledges for transportation. Brandt suggests that it was the single-horned *Elasmotherium* that was camouflaged under the name of the single-horned bull. Much in the same line is Shimkevich (1904), who wrote that, judged by some Yakut legends, *Elasmotherium* could have lived in Siberia during the same age as man.

Obermaier (1913) writes about *Elasmotherium* that, according to the sources from the Siberian ethnical minorities, a giant who came from the underground and expelled our ancestors from the Biblical paradise rode this monstrous creature.

According to Zhegallo, an idea of *Elasmotherium* transformed in the folklore could have been the prototype for an image of a fabulous monster on the southern wall of the Kyafar tomb of the 11th century from the Upper River Kuban area (Northern Caucasus). The creature was pictured massive, three-toed with disproportionately large tail and, most important, with a snout horn and three enigmatic forehead domes. There are warriors who raise their arms in despair as it is obviously hopeless to fight the huge and ferocious beast (Okhonko, 1994).

Yet, attempts to link the once really existing *Elasmotherium* with the mythical unicorn are the most interesting. The earliest supposed images of the unicorn are known from the cultural remains of

the third millennium BC of Ancient India. The creature was depicted in the form of a single-horned bull on seals of the ancient cities of the valley of the river Indus valley, Mohenjo-Daro and Harappa, and is explained as one of the most sacred images (Ivanov, 1998). The unicorn was also pictured in the form of a bull in the bas-reliefs of the Ashtart gates at ancient Babylon (6th century BC). The gates are currently reconstructed within the Pergamon Museum at Berlin. Typically it is the later Indian tradition that is linked to the appearance of the unicorn in the Near-Eastern mythology and afterwards in the mythology of antique Europe. Texts by Ktesius in the versions by Aelian (Jacoby, 1969), Aristotle (1977) and Plinius the Elder (edition 1996) are usually considered to be evidences for that. These texts linked the origin or range of the unicorn ("single-horned donkey", "Indian donkey") with India. The animal was considered to exist in reality.

However, the most ancient image of the unicorn as discovered at Mohenjo-Daro proves that the depicted animals on seals can only be called "Unicorn" conditionally. First, their images are neither mythological nor aggregative, but correspond to a really existing animal. Second, the bulls on the stamps were pictured strictly from the side-view and thus they only seem to be one-horned. It seems probable that the name "unicorn" used by the art historians for identifying those animals was chosen on a conventional basis. Using such a name apparently served for stressing the diversity of images on the seals since, apart form the "unicorns", there are typical bulls and other Bovidae images found at Mohenjo-Daro, amongst others the zebu *Bos taurus indicus* and the Indian bison *Bos gaurus*. The animals on these seals were pictured from different points of view and so sometimes both horns are distinctly seen. In addition, it should be noted that the realistic steatite bull figurines of the Indus valley have nothing to do with the enigmatic line of unicorn images.

The conception of the unicorn was already influenced by rhinoceros features in the classical European sources. Information about rhinoceroses living in India probably reached Ancient Greece and Rome. Such a mixture of ideas and images of animals was impossible in ancient India itself as the one-horned Indian rhinoceros (*Rhinoceros unicornis*) was a common, wide-spread and thus a well-known animal of the North Indian fauna. Yet the appearance of the Indian rhinoceros has little in common with the image of the single-horned bull on the Ancient Indian seals. In the later tradition, the unicorn was pictured in another way. Different authors wrote about it as being an animal with a body of a goat, a horse, a donkey, a fox, a cat-like carnivore (summary by Thenius & Vávra, 1996; Belova, 2001; Ivanov, 1998; Yurchenko, 2001). In the second half of the past millennium the unicorn was generally pictured as a horse with a long, straight or spiralled horn, likely after identification of the narwhal's tusk with a unicorn's horn (Plavilschikov, 1941; Simonov, 1985; Thenius & Vávra, 1996). The unicorn image was greatly influenced by Christian symbolism in later tradition, which treated the unicorn as a symbol of Christ and the legend of taming the unicorn as the legend of the Virgin Birth (see details in Yurchenko, 2001).

Elasmotherium could only have been a prototype for the unicorn if we assume that the first legends about the unicorn arose in relation to the ethnic groups who inhabited areas within the range of *Elasmotherium*. In this case the Indian sources can never be original as *Elasmotherium* did not inhabit India, and they must have been borrowed from the cultures of the Northern Eurasian peoples. The survival of the image of the huge black, single-horned bull in the legends of the Turkish-language speaking ethnic groups that correspond to the earlier tradition of picturing the unicorn may possibly give additional weight to this hypothesis.

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