

THE MORPHOLOGY AND PALEOBIOLOGICAL SIGNIFICANCE OF THE HORNS OF *COELODONTA ANTIQUITATIS* (MAMMALIA: RHINOCEROTIDAE)

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ABSTRACT—All known nasal horns of the Pleistocene Palearctic woolly rhinoceros, *Coelodonta antiquitatis* (Blumb.), are laterally flattened and transversely banded. A nasal horn discovered in the Museum of Paleontology, University of Helsinki, Finland, is described and figured. The old literature on woolly rhino horns is reviewed and the relevant plates from Brandt (1849) are reproduced. The differences between nasal and frontal horns are discussed and the shape of the nasal horn is interpreted as primary. The old contention that the woolly rhino used its nasal horn to shovel snow is supported, and the dynamics and significance of this behaviour are discussed. The transverse bands are interpreted as annuli and suggest a stronger sexual dimorphism in horn size in *Coelodonta antiquitatis* than in living rhinos. Such dimorphism in a probably migratory rhinoceros of a strongly seasonal environment would be in accordance with the general relationships proposed by Geist (1974) and Jarman (1974).

HISTORICAL REVIEW

In 1769 the naturalist and explorer Peter Simon Pallas published a paper entitled *De ossibus Sibiriae fossilibus craniis praesertim rhinocerotum atque buffalorum, observationes*. Apparently, this was the first time that fossil rhinoceros horns from Siberia were described and figured in the scientific literature, although it is possible that such horns circulated in Europe during medieval times (Nordenskiöld, 1880:392). The historical connotations of the Siberian rhino horns are complex, and I am far from competent to discuss them properly. But for the benefit of equally ignorant fellow paleontologists I would still like to relate a few things which I have come across during the preparation of this paper.

Fischer (1836) ties the horns historically to the legend of the gold-guarding gryphons of the ancients, to which they are connected, if not in a material sense, at least etymologically. We tend to think of gryphons as half-lion, half-eagle mythical creatures, but this has not always been their nature. According to Fischer (1836:5), the earliest known reference to gryphons is by Herodotos, who is obviously talking about people, not fabulous beasts. The Gryphons, Herodotos says, are one of the three peoples of the North, and they live “where gold is found,” between the Arimaspes (=Scythians according to Fischer) and the Hyperbo-reans of the icy northern coast. Fischer (1836:6) places them somewhere in the Ural-Berezow area, adding that “Il est à présumer que les Grypes connaissaient déjà les sables aurifères de ces contrées; l’art des mineurs s’étant établi plus tard chez les Romains.”

Still following Fischer (1836:7), the more familiar “composite” gryphon was introduced by the Elder Pliny

and Pomponius Mela, who altered the details of Herodotos’ account, and it was this later gryphon which inspired “les naturalistes allemands” to name the gigantic Siberian raptor with claws more than a meter long *Gryphus Antiquitatis*. The chief purpose of Fischer’s paper, as a matter of fact, was to establish the identity of these “claws” as fossil rhinoceros horns and to dispel the myth of a giant bird, which was still included in various faunal lists at the time.

Birds, and particularly raptors, are an essential element in Siberian shamanism. Parts of birds and bird figures frequently form part of the shaman’s dress, and during the trance the shaman travels through the various worlds and spheres in the shape of a bird (Bo Lönnqvist, pers. comm. 1982). The association of the fossil rhino horns with giant birds, which appears to be of native Siberian origin, is probably best explained in this light. Thus, although birds of supernatural size appear to be common in folklore in many parts of the world, Siberian versions are of interest in this context. Donner (1915:134ff) gives a brief account of a prose epic which he heard in the winter of 1912–13 among the Samoyeds of the Ket River (a tributary of the Ob River). This epic contains a fight between the bird Pyne (which was so big that it devoured large boulders and whole trees), a sea monster, and a giant fish with a curved horn. During the fight the claws of the bird are torn loose and remain stuck in the back of the fish, which returns to its home beyond the seas. After this unfortunate accident, the bird becomes very weak and wretched, and eventually turns to the hero Itje for help. Itje is happy to oblige. He builds a musical instrument somewhat in the line of a Finnish “kantele,” and, like Orpheus, gathers all the beasts of the earth, air, and water together by his playing. Last of all the unicorn fish

arrives, and Itje, still playing, is able to remove the claws from the sores which have begun to fester and trouble the fish greatly. Itje returns the claws to the bird, which regains its strength and becomes his loyal helpmate.

That the claws could be detached, and so might in principle occur on their own, is suggestive in that most, if not all, known rhino horns from Siberia are isolated finds. That the bird's strength resided in the claws is also interesting and consistent with Nordenskiöld's (1880:391) opinion that the "claws" were thought to have powerful magical properties. Incidentally, of the giant birds of the Finnish epic "*Kalevala*," unfortunately of very mixed and partly late origins, at least the *Vaakalintu* appears to have Siberian connections (Turunen, 1949:315f). It is perhaps unlikely that there is any connection to the Siberian horns, but I find the remote possibility fascinating.

In the nineteenth century Siberian rhino horns were discussed by several authors (Eichwald, 1835; Fischer, 1836; Brandt, 1849; Nordenskiöld, 1880; and others), but subsequently interest seems to have abated. I suspect that this is at least in part due to the authoritative word of Brandt, who stated very definitely that most of the horns which had reached European museums (meaning, of course, mainly Moscow and St. Petersburg) were not preserved in their original form, but had been damaged by native Siberians, particularly the Yukagirs (Brandt, 1849:203). This suggestion had been put forward already by Pallas (1769:458), but seems to have been doubted both by Eichwald (1835:752) and Fischer (1836:14). By reverting to Pallas' viewpoint, Brandt reduced the potentially interesting occurrence of two distinctly different types of horns to a pure artefact, and apparently his word prevailed. Re-examination of the matter indicates that Brandt was almost certainly mistaken, and that the two types represent nasal and frontal horns in more or less unaltered condition. The peculiarly flattened nasal horn, which Pallas and Brandt thought to have been damaged, has particularly interesting paleobiological implications, and it is the purpose of this paper to revive the rather prematurely terminated discussion as well as to present data that for all practical purposes have been lost to western paleontology.

I received the first impulse to write this paper when in 1978 I found in the collections of the University of Helsinki Museum of Paleontology (UHMP) an odd unregistered object which, according to oral tradition, was "the horn of a woolly rhino." Investigation proved this to be correct. The specimen, now UHMP 43, is extremely similar to the nasal, or "damaged," horns figured by Brandt (1849, pls. IX, X), here reproduced as Figures 2 and 3. Exasperatingly, there is no information whatsoever associated with this horn, but it is probable that it comes from northeastern Siberia as do the horns discussed by the authors referred to above. It is further probable that it was brought to Helsinki during the nineteenth century, or at least prior to 1917, when Finland was an autonomous Grand Duchy under Imperial Russian rule and Finnish explorers travelled

extensively in Siberia. By far the most likely person to have brought the horn to Helsinki is Alexander v. Nordmann, who held a professorship at the University of Helsinki from 1849 to 1866. Not only did he bring with him a large collection of fossils from Odessa, where he had been a professor at the Lycée de Richelieu prior to returning to his native Finland, but he was also personally acquainted with most European paleontologists of the time. It is particularly intriguing that one of the authors on fossil rhino horns, Edouard v. Eichwald, was also v. Nordmann's close friend and biographer (Eichwald, 1870). As a matter of fact, the Helsinki specimen is so similar to the horn figured by Eichwald (1835, pl. LXII), that without the rather marked difference in size (see Table 1) one might well regard them as identical.

Obscure origin seems to be a malady affecting all woolly rhino horns described in the literature. All appear to be isolated finds, and it is remarkable that of the four woolly rhino carcasses recorded in the literature, none was recovered with the horns. The Vilyuy River (1771) and Yana River (1877) carcasses were apparently found with the horns missing (Pallas, 1773; Schrenck, 1880), as was the first *Starunia* carcass (1907), while in the exasperating case of the second *Starunia* carcass (1929) "The two horns . . . fell off and have successfully resisted all attempts to find them in the surrounding silts up to the present" (Nowak et al., 1930:31). It might be worth pointing out that the horns of the mounted *Starunia* specimen in Cracow, which have served as a base for many reconstructions, are simply plaster fantasies (Stach, 1948:18).

Pallas, Eichwald, Fischer, Brandt, and Nordenskiöld all state that native Siberians know of the fossil horns and use them for various purposes. Both Fischer (1836:12ff) and Nordenskiöld (1880:392) quote Hedenström's (1830:124ff) account of how the Yukagirs use the best preserved (sic!) of the horns for raw material to increase the elasticity of their bows, rhino horn apparently being excellent for the purpose ("Mais l'arc de *Youkahires*, fait avec des griffes, surpasse tous les autres en élasticité, et une fleche qui en est lancée en l'air disparaît entièrement à la vue."; translated and quoted by Fischer, 1836:13). Thus Hedenström, although aware that naturalists in St. Petersburg considered the objects in question to be *rhinoceros* horns, preferred to follow local tradition in regarding them as claws (griffes) of gigantic birds, mainly because of their flat shape.

Such accounts strongly suggest that fossil rhino horns were indeed known to, and used by, the native inhabitants of northeastern Siberia, or at least by some of them. This definitely indicates that the horns could not have been excessively rare, and one might wonder why so few ever reached Europe. Perhaps this is only because northeastern Siberia was a very remote area, or perhaps the horns were efficiently collected by the locals, who had better uses for them than giving them away to strangers?

Whatever the reason, it seems that no more than 16 such horns have ever been figured (some of them twice).

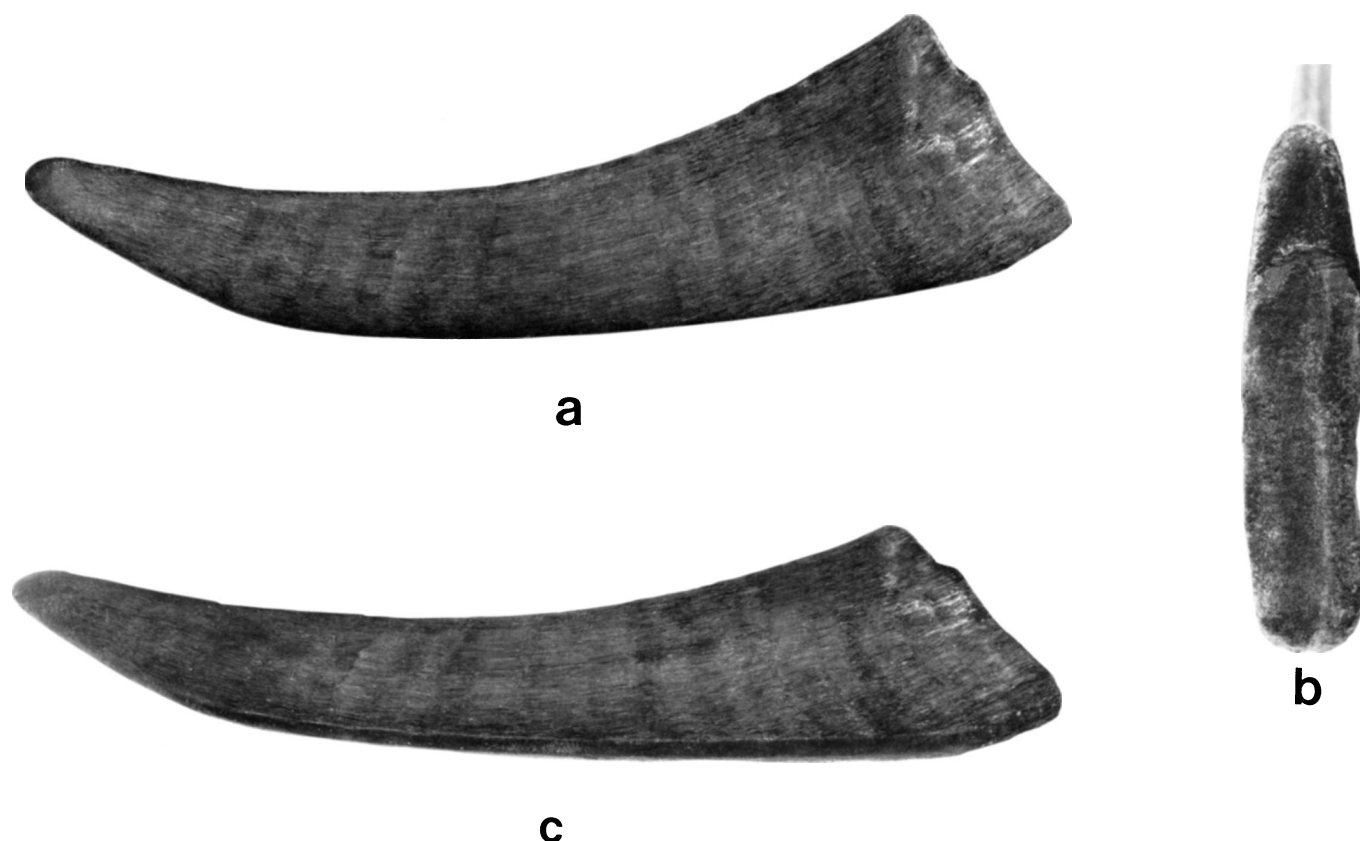


FIGURE 1. Nasal horn of *Coelodonta antiquitatis*, UHMP 43: **a**, lateral view, note banding and facet intercepting anterior curvature; **b**, base, note medial groove; **c**, anterolateral view to show wear facet. Dimensions in Table 1.

Pallas (1769, pl. X) figured two horns of five known to him from St. Petersburg; these and eight others were figured by Brandt (1849, pls. VII–X; here reproduced as Figs. 2–4). Fischer (1836, pl. I) figured five horns from Moscow, and Eichwald (1835, pl. XII) figured one, the location of which he did not state. According to Brandt (1849:204), this figure was reproduced by Blainville (1846, pl. IX). Finally, Nordenskiöld (1880:392) figured one of the big nasal horns previously figured by Brandt. In addition to the figured horns and the one in Helsinki, one nasal and one frontal horn are in the British Museum (Natural History), London (nasal horn Dept. Palaeont. M36780, frontal horn Dept. Palaeont. 14600). Other horns may well exist in museums, but are unknown to me.

DESCRIPTION OF THE HELSINKI SPECIMEN

The *Coelodonta antiquitatis* nasal horn UHMP 43 is long, gently curved, and strongly flattened laterally (Fig. 1, measurements in Table 1). It is of a dark brown colour, with the keratin fibers individually visible on the surface. The alternately tighter and looser adhesion of the fibers gives the horn a characteristic transverse banding. Eighteen such bands are present in all. Of

these, the distal ones are the broadest and the proximal ones the narrowest. The tip is rounded in lateral view and polished; at some time it has been pierced with a fine drill. Along the anterior (ventral) margin a wear facet approximately 63 cm long intersects the curvature, reaching from about the 4th to the 16th band. This facet is also slightly curved in lateral view, but much less so than the horn itself (i.e. the fibers and the opposite margin). Longitudinally it is divided into a left and a right subfacet, which reflect light at different angles. The posterior (dorsal) margin of the horn is unworn and the edge is thinner than anteriorly, almost sharp. A slight lateral ridge is present along the midline on both sides, lying parallel to the direction of the fibers. The base of the horn has a groove about 1.5 cm wide, extending from the anterior margin up to about 5 cm from the posterior one, where there is a shelf-like structure. The keratin fibers are about 0.5 mm in diameter and not unlike stiff bristles. At the base they appear hollow, giving the basal surface a porous texture. There are no cutmarks or other obvious signs of reworking on the horn.

THE QUESTION OF “DAMAGED” HORNS

As mentioned in the Introduction, Pallas (1769) discussed five and figured two Siberian rhino horns. Of

TABLE 1. Dimensions (in cm) of nasal horns of *Coelodonta antiquitatis*. H. UHMP 43, B1–B6 = Brandt's (1849:215ff) "cornua mutilata" one to six, E. Eichwald (1835:751). Values for B1–B6 & E converted as follows: 1 pes = 12 pollici = 120 linija = 30.4794 cm (Pushkarev, 1970). ^a, "Length" unspecified; ^b, Misprint in original 1". 5'"., here read as 1'. 5". (Brandt, 1849:219); ^c, except for UHMP 43 counted from figures, not absolutely reliable; ^d, 19 according to Eichwald (1835:752), but 20 in his figure.

Dimension	H	B1	B2	B3	B4	B5	B6	E
1. Linear length from midpoint of base to tip	78	—	—	—	—	—	—	67 ^a
2. Length of anterior curvature	89	123	122	108	82	88	75	—
3. Length of posterior curvature	73	104	104	88	64	71	58	—
4. Anteroposterior diameter at base	21	23	21	22	23	18	20	—
5. Transverse diameter at base	5	7	—	—	—	—	—	—
6. Anteroposterior diameter at midpoint	13	—	13	13	—	10	8	—
7. Transverse diameter at midpoint	4	9	—	—	—	—	—	—
8. Transverse diameter between midpoint and tip	4	7	10	9	9	7	5	—
9. Circumference at base	48	51	47	49	53	38	43 ^b	—
10. Circumference at midpoint	29	22	29	28	30	23	20	—
11. Number of transverse bands ^c	18	24	22	21?	23	21	23?	20 ^d

these, two were more or less similar to "normal" rhinoceros horns, roughly circular in cross section, gently curved, and tapering to a point. Three, however, were flattened laterally and showed the banding described above for the Helsinki specimen. Knowing that Siberian natives used rhino horns and had handled his specimens, he reached the conclusion that the flat horns, too, had originally been rounded but had been altered by cutting away material from both sides ("... ab ignaro et rudi populo securi, ut videtur, ablatam fuisse ab utroque latere substantiam; ...") (Pallas, 1769:458). Eichwald (1835:751f), however, discussing only a single flat and banded horn, was of the opinion that it was practically intact and that the bands represented annual growth ("Utraque pars lateralis parum latior est, vixdum incrassata, illa rotundata, hacce acutior, nec detrita, sed integra; rugae transversae 19 numerantur ut itaque totidem annorum bestia fuisse probabile sit.") Fischer (1836:17) also thought that the bands were produced by differential growth, but did not specifically relate them to years. Although he figured both flat and rounded horns, he did not comment on the differences.

Brandt (1849:203) considered all flat horns to have been secondarily damaged and divided his 10 horns into two categories, "cornua integra" and "cornua mutilata," corresponding to the two horns figured by Pallas (1769, pl. X). Brandt (1849:214) mentioned Eichwald's idea that the banding might represent annuli only to dismiss it on the grounds that such are unknown in Recent rhino horns. Instead he offered the explanation that they were produced somehow by "time and physical agencies, namely water, heat and decomposition" (Brandt, 1849:214; my translation). Brandt (1849:211) also considered Cuvier (1834:125) to have been mistaken in thinking that the elongated bony horn bases of *Coelodonta antiquitatis* skulls indicated that the horns had been strongly compressed laterally. (Admittedly, Cuvier thought that both nasal and frontal horns had been flat, but the feat is still impressive, at

least unless he knew of the flat Siberian horns, which he does not mention.)

There are two main difficulties attached to Brandt's interpretation of the flat shape as secondary. First, all the largest horns are flat, so that none of the supposedly intact, smaller horns could possibly be used to manufacture any but the smallest of the flat ones (compare lengths and anteroposterior diameters in Tables 1 and 2). Secondly, and perhaps more conclusively, if the largest flat horns were really circular in cross section originally, they were far wider than the nasal bones themselves and almost as broad as the frontals, which are much broader than the frontal horn base (compare anteroposterior basal diameter in Table 1 with nasal width in Table 3). Between them, these two difficulties make Brandt's interpretation untenable. Whether compared with the rounded horns or with the skull, the flat horns are simply too large. They may still have been altered to some extent, and some probably have, but that alone is not sufficient to explain the occurrence of two types of horns, so that the argument loses much of its force.

Eichwald (1835:751) noted the longitudinal groove in the base of his horn (see Fig. 1b) and tried it on a skull, where it fitted perfectly on the corresponding ridge on the nasals. Before reading Eichwald's paper, I had made exactly the same experiment with the Helsinki horn, and with the same result. When fitted on a skull in this manner, the anterior edge of the horn reaches almost to the tip of the nasals and leaves the skull at an open angle, inclined strongly forward in much the same manner as it is depicted in paleolithic paintings and carvings (see below and Fig. 5). Admittedly, the horn was never attached directly to the bone, but, as in all rhinos, to a pad of connective tissue resting on the rugose bony base. Fortunately, this structure was preserved in the second Starunia specimen and described in detail by Nowak et al. (1930:31): "The base of the first nasal horn is oval-shaped; it is turned with its wider end toward the back of the skull and

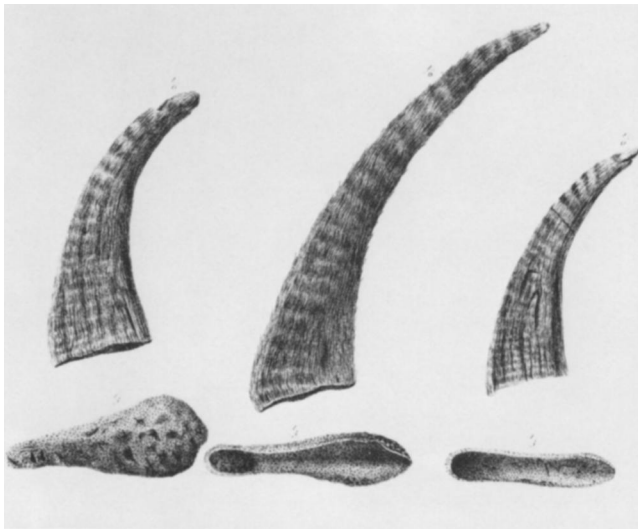


FIGURE 2. Nasal horns of *Coelodonta antiquitatis*, from Brandt (1849, pl. IX). From left to right Brandt's "cornua mutilata" four, one, and six. Dimensions in Table 1.

with the sharper end it reaches the beginning of the nasal bone. From the surface it delineates itself sharply, due to a distinct raising and across it there passes from the rear end to the front end a convexity in the shape of a roll 1 cm wide. This roll as well as the whole area occupied by the horn base is distinctly delineated on the nasal bones due to the existence of large and numerous wart-like appendages."

A horn with a longitudinal groove in its base may thus be fitted on the nasal bones more or less unambiguously. It is interesting that all the "intact" horns figured by Brandt (1849, pls. VII, VIII; Fig. 4 of this paper) have a funnel- or bowl-shaped depression in the base, not a groove. Likewise, the bony frontal horn base lacks any kind of a ridge, and is essentially a rough and evenly elevated convexity above the orbits. This strongly supports the interpretation of the flat horns as nasal and the rounded horns as frontal. Incidentally, Brandt (1849:219ff) made much of this distinction, arguing that it proved the horns with the longitudinal groove to be frontal ones and those with a funnel-shaped depression to be nasal horns (sic!), specifically rejecting Eichwald's opposite interpretation. He based this rather surprising conclusion on analogy with *Dicerorhinus sumatrensis* and *Diceros bicornis*, in which he found the nasal horn to have a funnel-shaped base, while the frontal horns were more compressed laterally. He declined to elaborate on the remarkable coincidence that all the frontal and none of the nasal horns had been damaged.

From the evidence discussed above it seems that the flat and banded horns are definitely nasal, and that their shape has been at most only moderately altered. This, however, seems to present a new problem: If the horns were really as flat as it appears, how could they

be firmly attached to the skull? Particularly lateral forces acting on the horn (from horn wiping or wrestling, for example) would seemingly be disastrous with such a narrow area of attachment.

I believe that two factors confuse the issue. The first is that although the attachment area itself seems to have been of the same elongated shape as the base of the horn (this is very clear in Schrenck's, 1880, plate III, which shows the horn bases of the Yana River specimen), it was probably buttressed at the sides by a collar of connective tissue and skin, so that the area supporting the horn may have been wider than the horn base itself. The second confusing factor is that one automatically tends to think of a flat object as flattened. This is not quite correct in the present case. Compared with any hypothetical ancestral horn that would still fit the by no means abnormally narrow nasals of *Coelodonta antiquitatis*, the change is more a lengthening than flattening. Adding to this the unusual ridge-in-groove structure of attachment (which increases the lateral extension of the contact surface), it seems that the horn may well have been just as strongly attached as that of any living rhinoceros.

Finally, the large size of the horns may seem problematical. The nasal horns are almost invariably longer than the skull (compare Tables 1 and 3), and a meter long horn acting as a lever will cause considerable stress at the attachment. But the African rhinos have long horns, too: the record for *Diceros bicornis* is 106.7 cm, and for *Ceratotherium simum* several horns exceeding 150 cm in length are known (Groves, 1971:248f). Clearly, rhinos can and do have long horns. Perhaps some of the stress is absorbed by the neck muscles and ligaments? It is somehow suggestive that the occipital crest was unusually strong in *Coelodonta antiquitatis*,

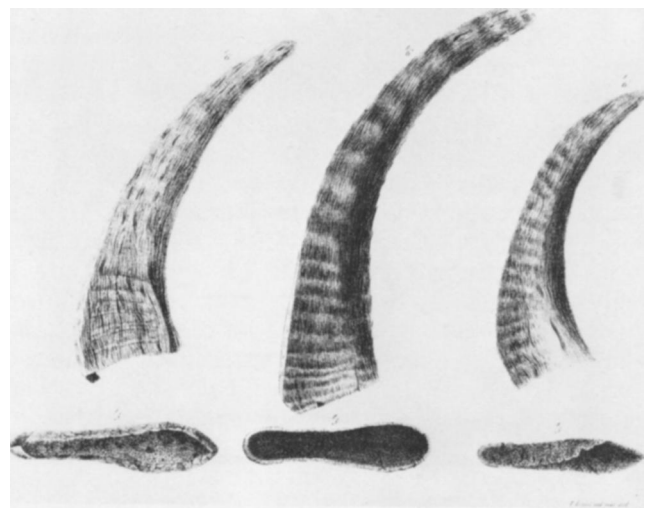


FIGURE 3. Nasal horns of *Coelodonta antiquitatis*, from Brandt (1849, pl. X). From left to right Brandt's "cornua mutilata" three, two, and five. Dimensions in Table 1.

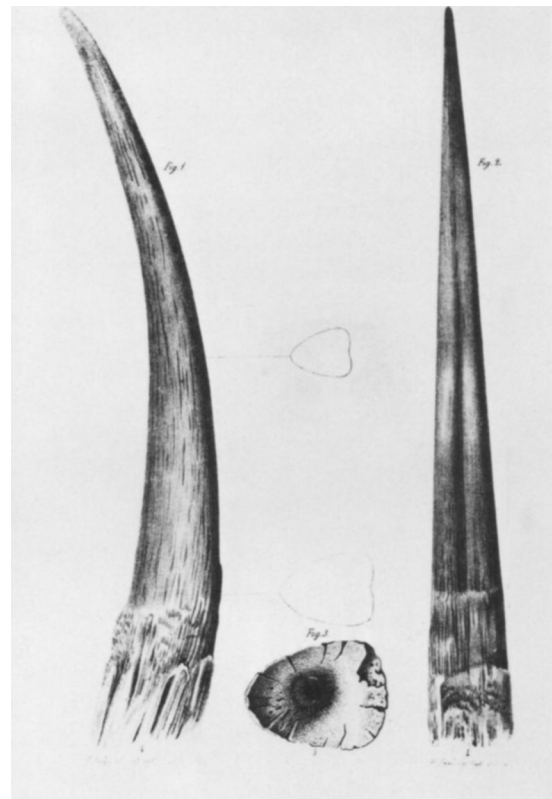
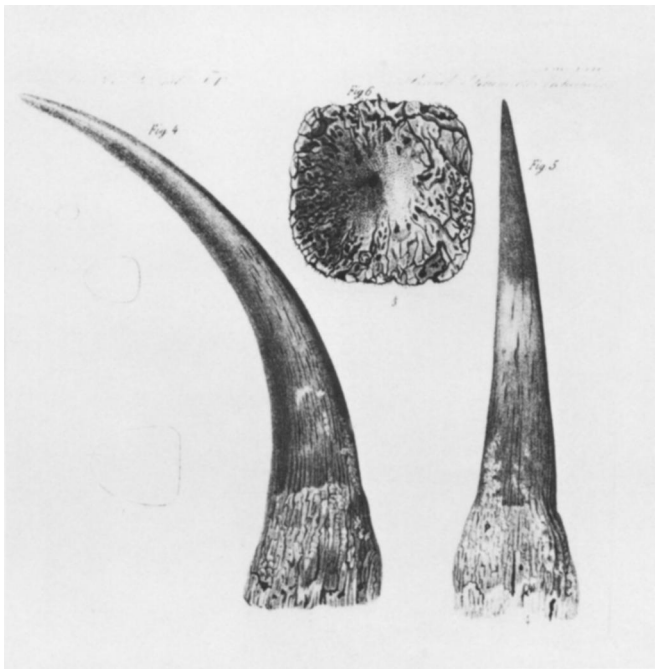
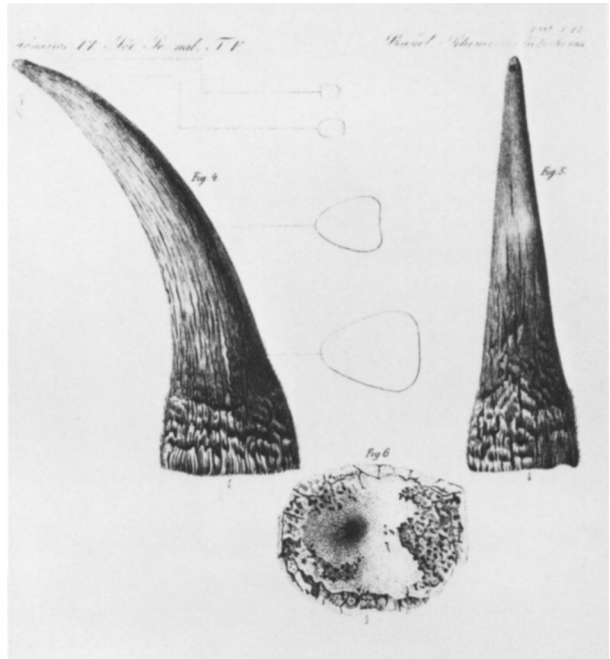
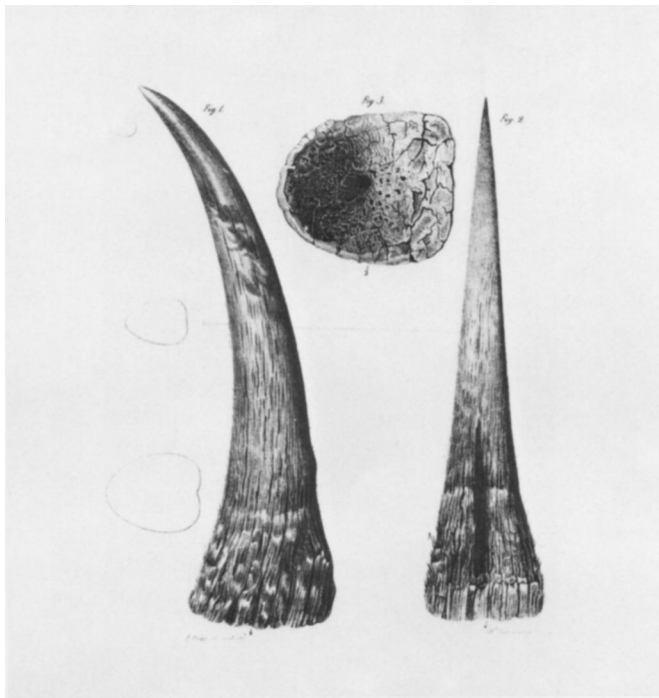


FIGURE 4. Frontal horns of *Coelodonta antiquitatis*, from Brandt (1849, pls. VII, VIII). Upper left to lower right Brandt's "cornua integra" one, two, three and four. Dimensions in Table 2.

TABLE 2. Dimensions (in cm) of frontal horns of *Coelodonta antiquitatis*. B1–B4 = Brandt's (1849:205ff) "cornua integra" one to four. Dimensions converted as in Table 1. ^a, Length of anterior curvature; ^b, length of posterior curvature.

Dimension	B1	B2	B3	B4
1. Length from anterior margin of base to tip	84 ^a	65	80	99
2. Length from posterior margin of base to tip	78 ^b	57	72	96
3. Anterioposterior diameter at base	19	17	17	13
4. Transverse diameter at base	16	13	17	10
5. Anteroposterior diameter at midpoint	9	8	8	8
6. Transverse diameter between midpoint and tip	7	5	5	6
7. Circumference at base	89	50	57	41
8. Circumference at midpoint	28	22	23	22

and that more muscles seem to have been inserting on the linea nuchae than in living rhinos (Zeuner, 1934: 53).

PALEOLITHIC REPRESENTATIONS

An obvious source of information regarding the external appearance of the woolly rhino is cave art. Powers & Stringer (1975:294f) listed and figured 27 profiles, while the rhinoceros in cave art was treated in more detail by Nougier & Robert (1957). Although there is considerable variation in both quality and technique, the general impression is definitely that of a compact and powerful, short-legged animal with a prominent shoulder hump and long, forward pointing horns. Figure 5 shows a drawing (kindly executed by Ms. Rosemary Powers) based on the famous murals from Font de Gaume and the "grande frise" of Rouffignac, which are representative of the best paintings. The Font de Gaume animal seems to be standing in an alerted posture, with head raised, while the Rouffignac animals appear to be grazing peacefully. From some of the representations it even appears that the artist has indicated the ventral wear facet on the nasal horn, however unlikely that may seem. The most striking example is one of the rhinos from the "grand plafond" at Rouffignac (Nougier & Robert, 1957:43, fig. 7).

In other cases, however, the animals are depicted rather differently, with smaller and more vertical horns. Whether this should be taken to indicate the presence of several species, considerable variation in horn shape, or simply inaccuracy of representation is unclear, although the first is perhaps least and the last most likely. Figure 6 shows a reconstruction of *Coelodonta antiquitatis* by Mr. Hubert Pepper, based on skeletal evidence as well as soft anatomy and paleolithic art, with the horns in what we believe to be the correct position.

FUNCTIONAL ASPECTS

There is an old opinion of uncertain origin, but undoubtedly based on the presence of the anterior wear facet, that *Coelodonta antiquitatis* used its nasal horn to brush away snow from the ground while feeding in the winter (see e.g. Haase, 1914:147). The woolly mammoth, *Mammuthus primigenius*, is thought to have used its tusks for this purpose, mainly because of areas showing transverse wear on the ventral surfaces of the tusks (Garutt, 1964:105). Although regarded as fanciful by Loose (1975:24), the reconstructions of the woolly rhino "... with its nasal horn horizontal, ploughing the snow before its head in search of food ..." are quite reasonable, if the "ploughing" is not taken too literally.

Garutt (1964:105f) thought that the characteristic spiral curving of the tusks of all *Mammuthus* species originally evolved in relation to this snow-sweeping behaviour, because spirally curved tusks are more strongly attached in the alveoli and less easily rotated than straighter ones. Be that as it may, a tusk growing in spiral fashion out of its alveolus is severely constrained to a circular cross section, and no departure from this is known among mammoths. A rhino horn, however, growing from a flat basal pad, is not subject to any such constraint. Thus, while the tusks of the mammoth remained cylindrical, the horn of the woolly rhino was free to evolve towards a functionally more advantageous shape. A cylindrical tusk (or horn) has the distinct disadvantage of compressing as well as displacing the material that is being swept over; a narrow structure with a distinct edge minimizes compression and maximizes removal.

At least in the Helsinki specimen, the anterior wear facet is keeled, i.e. it consists of a right and a left wear facet (first noticed by Prof. Ernest L. Lundelius, Jr.,

TABLE 3. Some cranial measurements (in cm) from four samples of *Coelodonta antiquitatis*. Modified from Borsuk-Białynicka (1973:25, table 16). P, Poland; ER, Eruepe; USSR, mixed sample from the entire area of the Soviet Union; S, Siberia.

Dimension	Sample	N	\bar{X}	s	O.R.
1. Maximum length (dorsal)	P	15	74.2	3.94	67–81
	ER	34	76.8	5.22	65–87
	USSR	53	76.3	5.20	68–87
	S	9	78.7	2.89	76–86
2. Basal length	P	14	63.2	2.68	58–68
	ER	30	64.6	3.38	58–71
	USSR	43	64.2	2.86	59–71
	S	6	65.0	2.18	63–69
3. Width of nasal bones	P	14	15.4	1.25	14–19
	ER	34	16.2	1.57	14–20
	USSR	52	15.8	1.79	13–19
	S	9	16.4	0.91	15–18

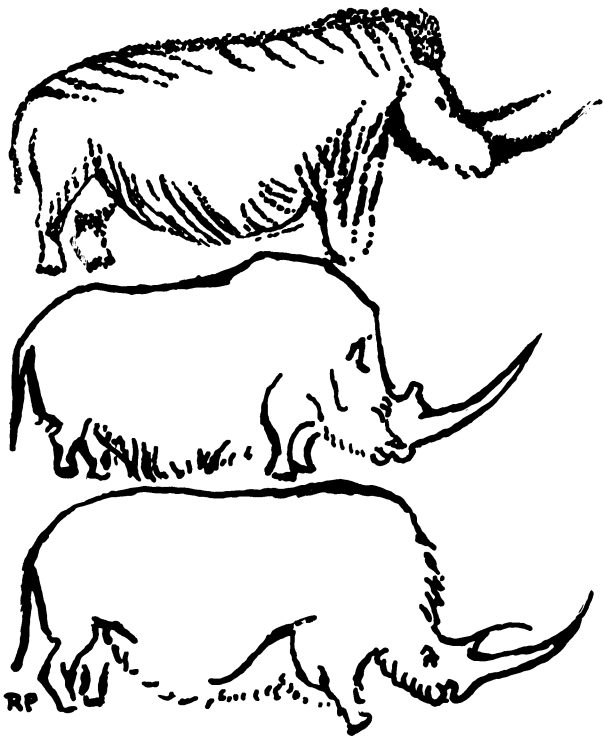


FIGURE 5. Paleolithic paintings of woolly rhino. Top Font de Gaume, middle and bottom Rouffignac. Drawing by Ms. Rosemary Powers. Further comments in text.

pers. comm. 1978). This indicates that it was produced by active, side-to-side strokes rather than by passive abrasion. The sweeping was probably performed with the horn inclined away from the direction of movement, the “keel” acting as the leading edge and the lateral edge trailing. This would explain the clean and sharp appearance of the lateral edges, which obviously have not been subject to much direct head-on wear (I am indebted to Prof. Björn Kurtén for this point). Pushing in this manner seems more plausible than pulling with the horn inclined towards the direction of movement, as the former will minimize compression of the material—man-made snow ploughs are inclined backwards for the same reason. The great anteroposterior elongation (i.e. “flattening”) of the horn is thus explained functionally as an adaptation to prevent snow from spilling over during sweeping.

As to the origin of the behaviour, a comparison with the white rhino, *Ceratotherium simum*, is suggestive. The two species have very similar teeth (unusual among rhinoceroses), with the serial arrangement of the cutting edges that goes with grass eating in non-ruminants (Fortelius, 1981:156, 1982:179), and, as the white rhino, the woolly rhino was almost certainly a grazer. Both species also have the backwards inclined occiput characteristic of grazers on low growing grass (Zeuner, 1934: 42, 52ff; Loose, 1975:9, 23ff). This arrangement gives a low slung head posture and brings the lips, and the

nasal horn, close to the ground. “Horn wiping,” involving transverse rubbing movements, is a behavioural characteristic of territorial white rhino males (Owen-Smith, 1975:372), and may well have been present in the woolly rhino or its ancestors as well. A grazing rhino stands with its head well to the front of its fore feet, and it is not very difficult to imagine how the horn-wiping motor pattern might be taken over by snow sweeping behaviour, as digging with the feet would be very awkward. Even *Bison bison* uses its muzzle to push away snow while grazing (R. Dale Guthrie, pers. comm. 1980), and a rhino with blunt hooves (Pallas, 1773:591f; Brandt, 1849:187ff; Nowak et al., 1930:39f) and short legs (Fortelius, 1979:23ff) would certainly have even more reason to “use its head” in the same situation. Incidentally, horns have been present in both sexes from the beginning in almost all Old World rhinos that developed them, which may indicate that they did not originally evolve for intraspecific combat and display but for other purposes, possibly connected with feeding (Janis, 1982:42f). Also, Norman Owen-Smith (pers. comm. 18.10.1982) suggests that the tandem-horned condition may have arisen in connection with branch breaking during browsing. Thus, a function involved in feeding, such as suggested here for woolly rhino horns, is not necessarily unusual or far-fetched for a rhinoceros.

Digging and brushing away snow to uncover the forage is an important behaviour in many boreal ungulates, and I believe that snow sweeping was as normal and perhaps even as vital to the woolly rhino as cratering is to reindeer. On the other hand, it is doubtful whether the woolly rhino could have been successful in particularly snowy areas, such as the present-day taiga. With its short legs and high load-on-track it would have been practically immobilized by deep snow. Loose’s (1975:28) woolly mammoth and rhino, which, together “... in a howling blizzard ... plough their way through an arctic landscape consisting of endless plains filled with deep snowbanks ...” are indeed as outrageous as they were intended to be, but prove nothing one way or the other about the behaviour of these animals in relation to lesser amounts of snow.

Needless to say, the interpretation of the flat shape of the nasal horn as a snow shoveling specialization in no way presumes that the horns were not used for combat and display as well, just as they are in living rhinos (although the blunt tip argues against effectiveness in actual stabbing). The spectacular size of the horns recalls other Pleistocene boreal ungulates, such as *Megaceros giganteus*, *Bison priscus* and *Mammuthus primigenius*, all of which had large display structures. As a matter of fact, there is some evidence that the horns of *Coelodonta antiquitatis* had a sexual function as well, as will be discussed below.

HORN GROWTH AND PALEOECOLOGY

Apart from its flatness, the most striking feature of a woolly rhino nasal horn is its banding. The idea that these bands are annual growth zones, originally put

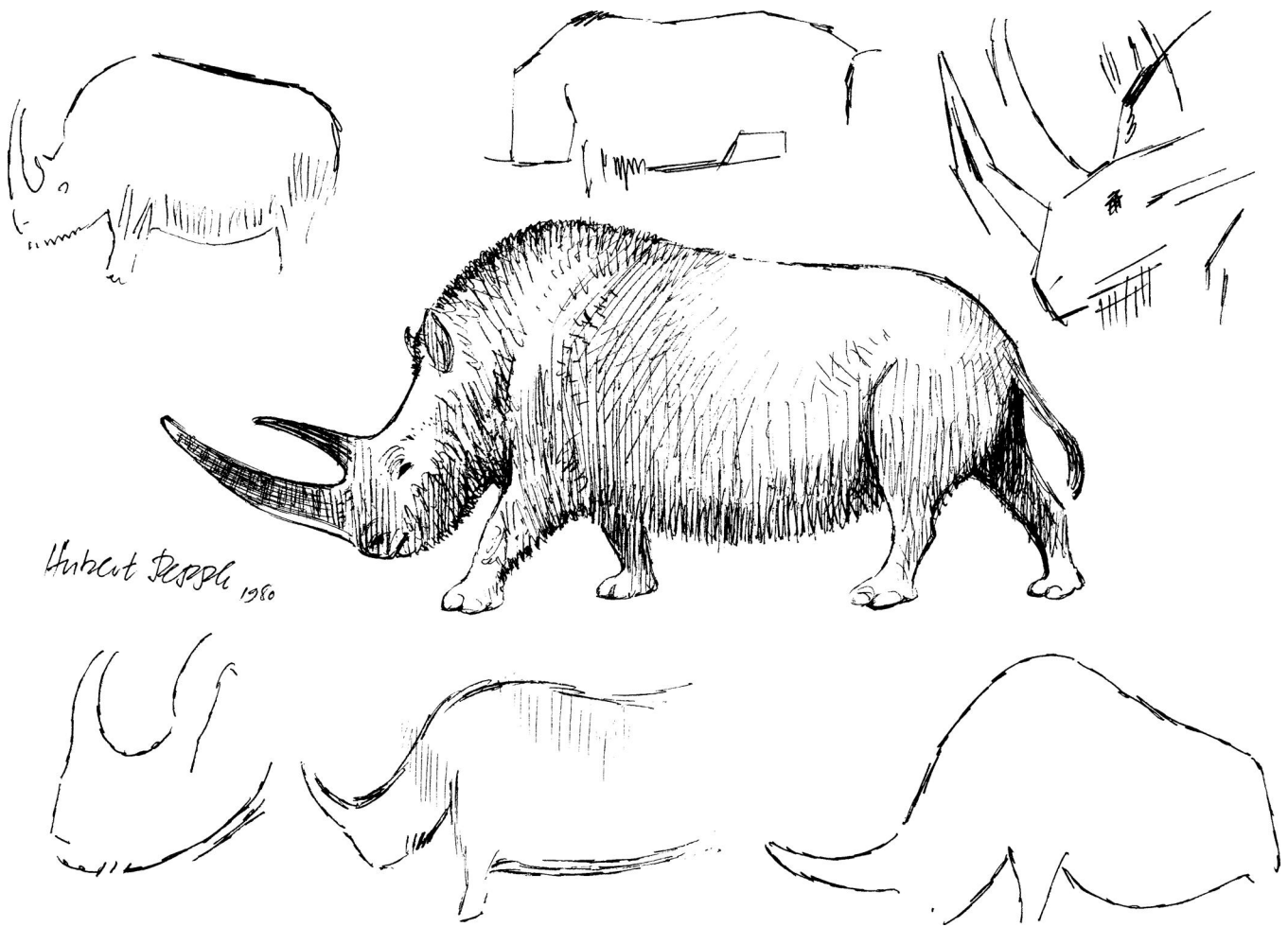


FIGURE 6. Reconstruction of woolly rhino by Mr. Hubert Pepper. Note position of horns and shoulder hump. Surrounding cave art from La Colombière, El Castillo, Les Combarelles, Les Rebières and Rouffignac.

forward by Eichwald (1835:751f) and dismissed off-hand by Brandt (1849:214), is reasonable and fits the facts well. Annual incremental lines are produced in the bone, dentine, and cementum of several large boreal mammals (Klevezal' & Kleinberg, 1967:11ff), and similar lines are found in the fossil teeth of *Mammuthus primigenius* and *Coelodonta antiquitatis* (R. Dale Guthrie, pers. comm. 1980, and personal observation; see also Osborn, 1912). It is generally agreed that the Pleistocene "mammoth steppe" was a strongly seasonal environment (cf. Geist, 1974), and, therefore, the presence of annual growth zones in a rapidly growing structure such as a large rhino horn is not surprising. Why such zones developed only on the nasal and not on the frontal horns is a nagging question that must remain unanswered at present—perhaps the zones are related to the more rapid growth rate of the larger nasal horn?

The average number of bands where they can be counted from published figures, and including the Helsinki specimen, is 21.5 (Table 1), with an observed

range of no more than 18–24. The first 5–11 bands are usually broad and the remaining are narrow, although the transition is more or less gradual (Figs. 1–3). The length distribution (but not the distribution of basal parameters) seems to be bimodal (Table 1). In the long horns the number of broad (distal) bands seems to be higher than in the short horns, but the difference is almost impossible to quantify without access to the specimens. It is suggestive, however, that there is no significant correlation between the length of the anterior curvature and the number of bands for the horns in Table 1 ($r = 0.21$). All this indicates, although it does not prove, that the long horns are long because they had a longer period of rapid growth rather than because they come from older individuals.

Of the living rhinos, only *Ceratotherium simum* and *Rhinoceros unicornis* are sexually dimorphic in body size (Laurie, 1982:334). In both species males take longer to mature than females (Owen-Smith, 1975:340; Colin P. Groves, pers. comm. 1982), which suggests that the proximate cause for dimorphism is a dif-

ference in duration of high juvenile growth rates. The same mechanism would explain the difference between the long and the short nasal horns of *Coelodonta antiquitatis*, and I suggest that the long horns are those of males, whereas the short horns belonged to females. Although Borsuk-Białynicka (1973:26ff) found dimorphism in skull size of woolly rhinos; dimorphism in body size has not yet been demonstrated, but may well be expected.

According to Laurie (1982:332), all living rhinos are sexually dimorphic for skull and horn size, though this dimorphism is not very pronounced, and at least in African species is unusual in that females have longer but more slender horns than males (Groves, 1971:251). Without appropriate experimental data it is difficult to evaluate these differences, but they do not seem to be of the kind usually associated with sexual dimorphism in ungulates, i.e. large horns in males and small or no horns in females. Perhaps African rhino females use their long horns to protect their offspring, while males use their stouter horns in intraspecific combat (Norman Owen-Smith, pers. comm. 18.10.1982)?

Sexual dimorphism in body size is characteristic of the large, grazing, herd-living bovids of Jarman's (1974) ecological category E, in which males establish a dominance hierarchy determining access to females (see also Janis, 1982:268). Of the living rhinos, at least *Ceratotherium simum*, *Diceros bicornis* and *Rhinoceros unicornis* are territorial to some extent, even though details vary between areas and species (Owen-Smith, 1975:345ff; Laurie, 1982:336), and adult males are solitary, although cows and subadults may form small groups (Owen-Smith, 1975:341f; Laurie, 1982:316). All of them are also non-migratory, at least in the sense that they do not have seasonal migrations and inhabit tropical regions where the "boom-and-bust" seasonal change from superabundance of high-quality food to severe shortage (cf. Geist, 1974) characteristic of boreal regimes is much subdued. As a member of the "mammoth steppe" fauna of the later Pleistocene, *Coelodonta antiquitatis* on the other hand, may well have been both non-territorial, herd-living, and migratory (for migration in boreal ungulates see e.g. Nasimovich, 1955). In boreal "boom-and-bust" ecosystems ungulates tend to restrict male interactions to a short and intense rutting season, which saves time for feeding during the short period of superabundance of food (Geist, 1974). Elaborate display organs and marked sexual dimorphism are part of the same pattern, and large, sexually dimorphic horns might well be expected in the woolly rhino, too. The evidence presented in this paper is admittedly slender, but, if it can be supplemented, I would predict that dimorphism will be found also for body size in *Coelodonta antiquitatis*.

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