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Paleontologia. — *Ethological inferences on Pleistocene rhinoceroses of Europe.* Nota di Paul Mazza, presentata (*) dal Socio A. Azzaroli.

Abstract. — The skulls of the five living species, *Diceros bicornis* (L.), *Ceratotherium simum* (Burchell), *Rhinoceros unicornis* L., *R. sondaicus* Desmarest and *Dicerorhinus sumatrensis* (Fischer) are carefully examined to recognize the characters which may give evidence on specific life habits. The state of these characters is analysed in the skulls of Pleistocene rhinocerotids of Europe, namely *Stephanorhinus etruscus* (Falconer), *S. hundsheimensis* (Toula), *S. kirchbergensis* (Jäger), *S. hemitoechus* (Falconer), *Coelodonta antiquitatis* (Blumenbach) and *Elasmotherium sibiricum* Fischer. *S. etruscus* and *S. hundsheimensis* lived in relatively open environmental conditions, somewhat similar to those of the present day black rhinoceros, and seem to have been poorly aggressive rhinoceroses, or had realised a high ritualization of their contentions. They were apparently equipped with a strong, prehensile upper lip. The skulls of *S. hemitoechus* and *C. antiquitatis* show evidence of the occurrence of a weak, semi-prehensile upper lip, whereas *S. kirchbergensis* seems to have been a grazing «square-lipped» rhinoceros like the present day *Ceratotherium simum*. It is suggested here that *Coelodonta* may not only have used horn sweeping for seeking food, but also as part of fighting ritualisation. *E. sibiricum* apparently had a strong, prehensile upper lip. The most convincing explanation of the use of the great front horn of this species is sexual display. The possible reasons for the ossification of the nasal septum are also investigated. The strengthening of the nasal area was probably needed to support the efforts of intense and frequent horn-sweeping, a habit which could have been quite diffused among Pleistocene rhinoceroses, rather than to support the weight of the nasal horn.

Key words: Rhinocerotidae; Perissodactyla; Mammalia; Pleistocene; Eurasia.

Riassunto. — *Inferenze sull'etologia di rinoceronti pleistocenici d'Europa.* I crani delle cinque specie viventi, *Diceros bicornis* (L.), *Ceratotherium simum* (Burchell), *Rhinoceros unicornis* L., *R. sondaicus* Desmarest e *Dicerorhinus sumatrensis* (Fischer) sono esaminati in dettaglio per individuare i caratteri che riflettano specifiche abitudini di vita. Lo stato di questi caratteri è osservato nei crani di rinocerotidi pleistocenici europei, *Stephanorhinus etruscus* (Falconer), *S. hundsheimensis* (Toula), *S. kirchbergensis* (Jäger), *S. hemitoechus* (Falconer), *Coelodonta antiquitatis* (Blumenbach) ed *Elasmotherium sibiricum* Fischer. *S. etruscus* e *S. hundsheimensis* vissero in ambienti relativamente aperti, in qualche modo simili a quelli dell'attuale rinoceronte nero, e sembrano essere stati rinoceronti poco aggressivi, o avevano raggiunto un alto livello di ritualizzazione delle loro contese. Apparentemente avevano un labbro superiore forte e prensile. I crani di *S. hemitoechus* e *C. antiquitatis* mostrano evidenze della presenza di un labbro superiore debole e semiprensile, mentre *S. kirchbergensis* sembra essere stato un rinoceronte pascolante «a labbro squadrato» come l'attuale *Ceratotherium simum*. È avanzata l'ipotesi che in *Coledonta* lo spazzare il terreno con il corno servisse non solo per la ricerca del cibo, ma fosse anche parte del rituale di combattimento. *E. sibiricum* era apparentemente dotato di un labbro superiore forte e prensile. Viene ipotizzato che l'enorme corno frontale di questa specie avesse il solo scopo di parata sessuale. Sono inoltre ricercate le possibili ragioni dell'ossificazione del setto nasale in queste specie. L'irrobustimento dell'area nasale era probabilmente imposto dalla necessità di sopportare gli sforzi legati all'intenso e frequente uso di spazzare il terreno con il corno anteriore, un'abitudine che doveva essere alquanto diffusa fra i rinoceronti pleistocenici, piuttosto che quelli dovuti al peso del corno nasale.

(*) Nella seduta dell'11 novembre 1992.

INTRODUCTION

Although a rich literature has concerned their characters and phyletic relations, the Pleistocene rhinoceroses of Europe are still poorly known. It is the writer's convinction that a deeper understanding of their possible life habits and relations with the environment may usefully contribute to resolve many questions which lay still open.

Living species are carefully examined to find the cranial characters related to specific life habits. A major problem is that the present ranges of extant species are controlled by the pressure of poaching and agricultural demands, and therefore that some habits and some relations with the environments are probably unnatural.

LIVING RHINOCEROSES (figs. 1, 2)

Unfortunately, rhinoceroses today are endangered animals. Their present dispersal is a faint residue of their past distribution and in most cases they survive in very limited numbers in national parks or in reserves under conditions far from the ones congenial to them. The following data on present day rhinoceroses are drawn from Walker (1964), Morris (1965), Gzimek *et al.* (1968), Laurie (1982) and Penny (1987).

Inhabiting very different environments, the two African tandem-horned species, *Diceros bicornis* (L.) and *Ceratotherium simum* (Burchell), and the three Asian ones, *Rhinoceros unicornis* L., *R. sondaicus* Desmarest, and *Dicerorhinus sumatrensis* (Fischer), necessarily have distinct life habits.

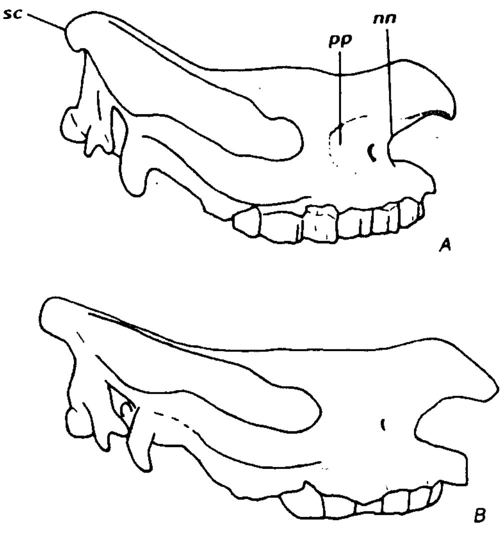

Fig. 1. – Right lateral views of rhinocerotid skulls (all figures about 1/9 nat. size). A: *Diceros bicornis*; B: *Ceratotherium simum*; *nn*-narial notch; *pp*-preorbital pit; *sc*-supraoccipital crest.

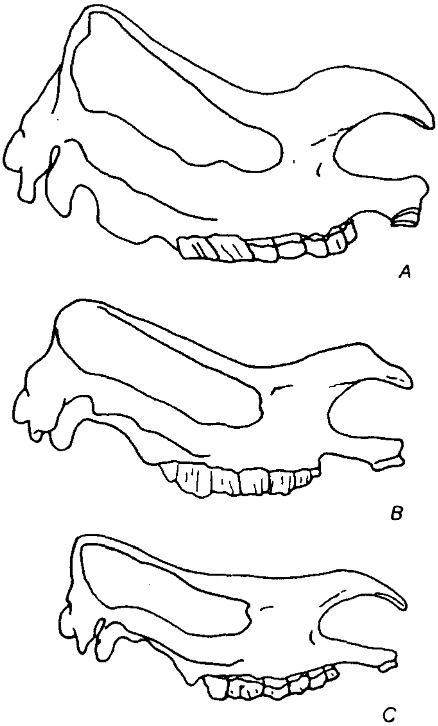

Fig. 2. – Right lateral views of rhinocerotid skulls (all figures about 1/9 nat. size). A: *Rhinoceros unicornis*; B: *Rhinoceros sondaicus*; C: *Dicerorhinus sumatrensis*.

The black rhinoceros, *D. bicornis*, is a browser which lives in open scrub woodlands and at the margins of small woods. It mainly feeds on leaves, shrubs, twigs, and occasionally fruits; therefore on plants at a certain level above the ground. The head is borne fairly uplifted. *D. bicornis* is provided with a pointed and very mobile prehensile upper lip which makes it immediately distinct from the «square-lipped» white rhinoceros.

All this is reflected by the cranial and dental characters of this species. The occiput is subvertical and the supraoccipital crest is moderately projected backwards. The dorsal profile of the skull is markedly concave, which contributes to the raising of the muzzle. The cheek teeth are typically brachyodont. The occurrence of well developed naso-labial, maxillo-labial and dilatator nasi muscles, which altogether form the prehensile upper lip, is indicated in the skull by two shallow preorbital pits, sometimes rimmed dorso-posteriorly by slight rugosities, and by the structure and rugosities of the lateral and anterior edges of the nasals. The latter are generally sharp and rough.

Black rhinoceroses are solitary. The territorial boundaries of neighbour males sometimes overlap; they tend to form clans whose members tolerate each other. On the contrary, outsiders are fiercely challenged. The strategy commonly adopted by black rhinoceroses is to tend to keep out of sight of each other. Fights are usually ritualised, but in periods of drought black rhinoceroses turn very aggressive, and some individuals may be killed.

Ceratotherium simum is a grazer. Unlike all other living rhinoceroses, it lacks the highly mobile, pointed upper lip of *Diceros bicornis*; its broad, mobile upper lip is suited to collect grass. In normal station, the white rhinoceros bears its head drooping. In the skull, the supraoccipital crests stretch far backward, there is no evidence of a preorbital pit, the region in front of the orbit being uniformly convex and smooth, and the edges of the nasals are rounded. The check teeth are high-crowned and covered by thick cementum; their lophs are strongly oblique.

As a grazer, the white rhinoceros typically inhabits open grasslands. The open spaces and the high amount of food supports larger densities of populations as compared to black rhinoceroses. White rhinoceroses are thus more territorial than black ones and their fights are highly ritualised, to a point where contendants seldom get in contact with one another.

Only dominant white rhinoceroses hold a territory, which they mark with urine-sprays and dung-heaps. Subsidiary males are allowed to feed in the territory of a dominant male if they make submissive signals to the resident bull.

Rhinoceros unicornis is the best known of the Asian species. It is a grazer. It typically inhabits swampy areas and grassy river banks, but it is also reported from more arid grasslands. Since it usually grazes hidden in 3 m tall elephant grass, which assures it shelter and food, *R. unicornis* developed a territoriality different from that of its African cousins. The Indian rhinoceroses have private areas, where single individuals feed and breed, and public wallowing areas, where up to about ten individuals may gather. Fights are limited by keeping out of each other's sight; however, any possible intrusion is fiercely attacked. Indian rhinoceroses do not use their weak horn as defence-offence weapon, but rather fight biting and stabbing the opponent with their lower tusks. *Rhinoceros unicornis* feeds mainly on buds and newly grown plants, and often causes great damage to crops. Also bamboo shoots are enclosed in its diet. It is equipped with a semi-prehensile upper lip. Like the other two Asian rhinoceroses, *R. unicornis* bears its head considerably uplifted over the ground. This may be somehow related to the fact that these rhinoceroses live in heavily forested environments, but also to their peculiar way of fighting. Consistently, the skull is characterized by a distinctly concave dorsal profile, which gives it a typical saddle-like appearance, and by a forward inclined occiput. The preorbital pits which house the upper lip muscles are shallow and barely marked by weak dorso-posterior rugosities; they are less developed than in *D. bicornis*. Conversely, the anterior tusks are well developed, especially the lanceolate second lower incisors. On the whole *R. unicornis* is markedly brachycephalic, as the orbits are very advanced and the muzzle is short.

R. sondaicus and *Dicerorhinus sumatrensis* are browsers, have a prehensile upper lip and well developed anterior tusks. Like *R. unicornis, R. sondaicus* and *D. sumatrensis* apparently tend to avoid confrontations and fight using their anterior tusks as main defence-offence weapons. The skull of *R. sondaicus* recalls that of *R. unicornis*. On the contrary, *D. sumatrensis* has a more elongated skull, a less concave dorsal profile and a more vertical occiput. In the skulls of both these species the preorbital pits for the upper lip muscles are slightly developed and shallow.

Rhinoceroses have a rather poor sight, good hearing and excellent sense of smell. Most, if not all, of their social relations are regulated by scent. African rhinoceroses always mark their territory with urine-sprays and dung-heaps. The Asian species do not seem to mark their feeding, breeding or resting territories in any particular way; however, individual Indian rhinoceroses contribute to form huge communal dung-heaps near pools and wallows, to advertise about their presence. In all the five living species, females in oestrus often spray urine to advertise males about their condition. The good sense of smell of these animals is reflected, in the skulls, by the elongation of the muzzles, by the broad narial openings and by the wide foramina which pierce the ethmoidal laminae. On the contrary, the orbital ducts and fissures are rather small. African rhinoceroses, especially *Ceratotherium simum*, have skulls more dolichocephalic than the Asian species.

PLEISTOCENE SPECIES OF EUROPE (figs. 3, 4)

For reasons given by Groves (1983), and successively followed by Fortelius *et al.* (1993), the Pleistocene species of Europe, previously referred to *Dicerorhinus* Gloger, the type species of which is *D. sumatrensis*, should more suitably be referred to *Stephanorhinus*

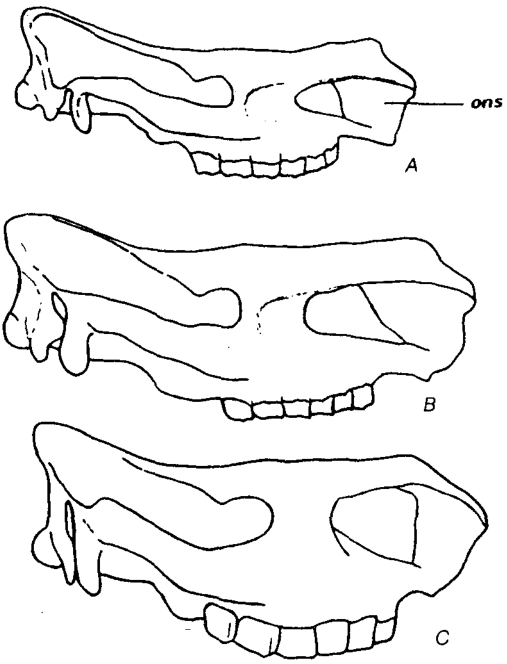

Fig. 3. – Right lateral views of rhinocerotid skulls (all figures about 1/9 nat. size). A: *Stephanorhinus etruscus*; B: *Stephanorhinus hundsheimensis*; C: *Stephanorhinus kirchbergensis*; *ons*-ossified nasal septum.

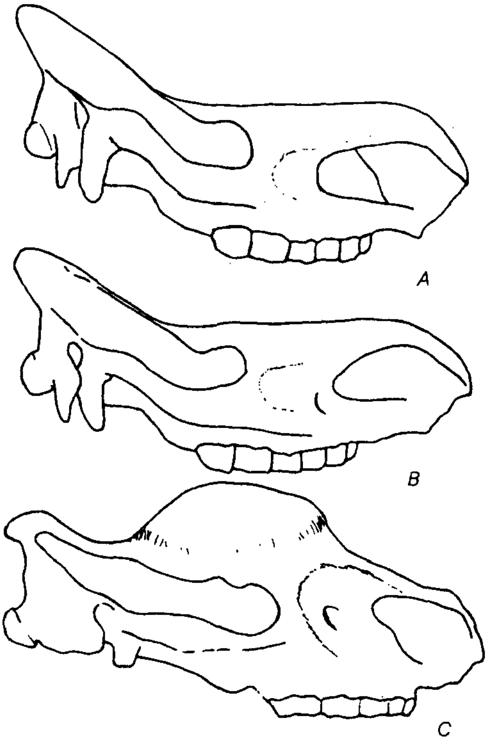

Fig. 4. – Right lateral views of rhinocerotid skulls (all figures about 1/9 nat. size). A: *Stephanorhinus hemitoechus*; B: *Coelodonta antiquitatis*; C: *Elasmotherium sibiricum*.

Kretzoi, with *Rhinoceros etruscus* Falconer, 1868, as type species. With this, the Pleistocene rhinocerotids of Europe are represented by three genera, *Stephanorhinus, Coelodonta* Bronn, and *Elasmotherium* Fischer. *Stephanorhinus* includes the Pliocene species *S. megarhinus* (de Christol) and *S. jeanvireti* (Guérin) and the Pleistocene *S. etruscus, S. hundsheimensis* (Toula), *S. hemitoechus* (Falconer) and *S. kirchbergensis* (Jäger).

The possible environments of life and dietary habits of these fossil rhinoceroses have been inferred by several authors (Zeuner, 1934; Sody, 1941; Hoogerwerf, 1970; Loose, 1975; Owen-Smith, 1975; Fortelius, 1982, 1983) on the basis of their cranial, dental and postcranial characters and of their ecological preferences.

S. etruscus and *S. hundsheimensis* were brachyodont species, with typically low crowned teeth. *S. etruscus* was smaller than *S. hundsheimensis*; both were cursorially built. Cranial characters shared by the two species are the uniform concavity of the dorsal profile, the subvertical, rectangular-shaped occiput, the supraoccipital crests more projected laterally than backward and upward, the high position of the orbits and the occurrence of shallow preorbital pits, sometimes rimmed dorso-posteriorly by a slight rugosity. *S. hundsheimensis* is larger-sized and has a deeper and wider narial notch. The anterior and lateral edges of the nasals are sharp and rugose in both species, but in *S. hundsheimensis* they are more expanded than in *S. etruscus*. Anteriorly the nasals are slightly inclined downwards. In both species the nasal septum is partly ossified.

S. kirchbergensis and *S. hemitoechus* are less brachyodont species, relatively higher crowned than *S. etruscus* and *S. hundsheimensis*. *S. kirchbergensis* was a large-sized rhinoceros; it was graviportal, but relatively more cursorial than *Coelodonta* and *Ceratotherium simum*. The dorsal profile of its skull generally shows a change in slope between the neural and the facial skeletons more evident than in both *S. etruscus* and *S. hundsheimensis*. The facial skeleton is massive. The occiput is vertical, the supraoccipital crest is moderately projected backwards. The orbits are set fairly high, the narial notch very wide and deep. There is no trace of preorbital pits, the walls in front of the orbits being smooth. The edges of the nasals are sharp. The nasals are more bent downwards than in *S. etruscus* and *S. hundsheimensis*. The nasal septum is partly ossified. *S. kirchbergensis* is said to have been a deciduous forest dweller on the basis of its dental characters (Fortelius, 1982).

The skull of *S. hemitoechus* is characterized by a strongly concave dorsal profile, with an abrupt change in slope between the neural and the facial regions. The occiput is vertical, the supraoccipital crest is strongly projected backward. The narial notch is wide and deep. The orbits are placed in a high position. The preorbital pit is very shallow and sometimes is rimmed dorso-posteriorly by slight rugosities. Anteriorly, the nasals are considerably bent downwards; their tips are almost in contact with the premaxillae. The edges of the nasals are rounded and fairly smooth. The nasal septum is partly ossified. On the basis of its cranial and dental characters, *S. hemitoechus* is believed to have inhabited open, grassy environments (Loose, 1975; Fortelius, 1982).

Coelodonta and *Elasmotherium* are hypsodont genera. *Coelodonta* was a medium-sized, graviportal rhinoceros. Its skull is roughly similar to that of *S. hemitoechus*; it differs in having the nasals so inclined downward as to fuse their tips with the premaxillae and in having the nasal septum completely ossified. The woolly rhinoceros fed mainly on grass; its teeth are similar to those of *Ceratotherium simum*. It is therefore believed to be a typical open grassland dweller.

The skull of *Elasmotherium* is characterized by a vertical occiput, supraoccipital crests modestly projected backward, very slender, straight nasals. The nasal septum is often completely ossified. The preorbital pits are deep and broad.

OBSERVATIONS

Stephanorhinus, Coelodonta and *Elasmotherium* share some common characters: they have dolichocephalic skulls, deep narial notches, and have lost their anterior teeth. *Elasmotherium*, and the Pleistocene representatives of *Stephanorhinus* and *Coelodonta* add the tendency, completely realized in *Coelodonta* and in *Elasmotherium*, to ossify the nasal septa. *Stephanorhinus* and *Coelodonta* are tandem-horned rhinoceroses.

Because of their dolichocephalic skulls and of the absence of their anterior teeth, the Pleistocene European rhinoceroses recall present-day African representatives more closely than Asian ones.

Five cranial characters can provide some information on the ethology of these fossil rhinoceroses: the structure of the occipital region, the extension of the narial notch, the development of the foramina of the ethmoidal laminae, the occurrence and development of the preorbital pit and the ossification of the nasal septum.

The subvertically arranged occiput and the supraoccipital crests more extended laterally than in other rhinoceroses, suggests that *S. etruscus* and *S. hundsheimensis* bore their heads and their necks quite high above the ground and that the lateral and rotational movements of the head were favoured against the vertical ones. Asian rhinoceroses, even grazers as *R. unicornis*, bear their heads high above the ground, but this is due to the fact that they live in environments with dense and tall vegetation. The environments which *S. etruscus* and *S. hundsheimensis* are supposed to have inhabited seem to have been more open, judging by their skeletal characteristics and by the faunal contexts in which their remains are commonly found. The structure of the occipital regions of *S. etruscus* and *S. hundsheimensis* suggests that they were poorly aggressive rhinoceroses, or that they developed a high ritualisation of their contentions, maybe with extensive horn-wiping, since fights impose ample vertical movements of the head.

Judging by the architecture of the occipital region of their skulls, the head must have been slightly drooping in *Elasmotherium* and increasingly more in *S. kirchbergensis, S. hemitoechus* and *Coelodonta antiquitatis* (Blumenbach). This is generally connected with the feeding habits of the various species (Zeuner, 1934; Loose, 1975; Fortelius, 1982, 1983).

The enlargement of the narial notch may indicate acute olfaction. Although the fossil skulls are generally so badly preserved as to prevent any detailed observation of the ethmoidal area, in well preserved *S. hemitoechus* skulls the ethmoidal laminae are pierced by wide foramina, as in present-day African rhinoceroses.

Another possibility is that these rhinoceroses may have had the habit to blow the dust off the grass before feeding on it, as Azzaroli (1990) hypothesized for the South American equids *Hippidion* and *Onohippidium*, which are characterized by very deep narial incisures.

Whatever the case, the widening and elongation of the narial notch extends the areas for the insertion of the upper lip muscles. When this is accompained by well developed preorbital pits and by nasals with sharp, rough edges, there is a sound possibility that the animal had a strong, prehensile upper lip. This is exactly the condition shown by *S. etruscus* and *S. hundsheimensis. Elasmotherium* was apparently equipped with a even more developed, strong and prehensile upper lip. On the other hand, *S. hemitoechus* and *C. antiquitatis* may have had a relatively weak, semi-prehensile upper lip, like those of the Indian rhinoceroses, while *S. kirchbergensis* may have been a «square-lipped» rhinoceros as *Ceratotherium*.

The relatively strong, prehensile upper lip, the brachyodont dentition and the slender, subcursorially structured limbs suggest that *S. etruscus* and *S. hundsheimensis* probably inhabitated environments similar to those in which *D. bicornis* lives today. However, the ways of life of *S. etruscus* and *S. hundsheimensis* might have been slightly different from the black rhinoceros. In both *S. etruscus* and *S. hundsheimensis* the hornbase rugosities, especially the nasal one, are more developed than in *D. bicornis*; according to Loose (1975) this should indicate a more extensive use of these structures. Other significant differences are the supraoccipital crests less projected backwards and more extended laterally, the higher position of the orbits and the lesser concavity of the dorsal profile.

In a previous paper (1988), the writer observed that, judging by its limb bones, *S. etruscus* probably was a relatively swift moving animal, and that its slender, delicate nasal bones probably would have not supported a full-speed impact, although rhinoceros horns are rather elastically implanted on the skull and in these forms the nasals were strengthened by the ossification of the septum. The writer also excluded that horns could be used for sexual display, but rather for feeding. It is likely that these Pleistocene species used their horns to perform more than a single function. The black rhinoceros uses its horns for fights, either ritualised or effective, but also for breaking the branches or twigs on which it feeds. The high position of the orbits in *S. etruscus* and *S. hundsheimensis* suggests that among these species male confrontations may have been more ritualised than in present day black rhinoceroses. During ritualised fights, contenders evaluate each other's body mass, strength and horn development; white rhinoceroses sweep the ground with their front horn to display their weapons and to simulate an attack. Hornwiping was probably adopted also by *S. etruscus* and *S. hundsheimensis*, as part of fight ritualisation and/or as a habit connected with feeding.

Fortelius (1983) observed that *Coelodonta antiquitatis* horns are not cylindrical, but laterally flattened and sometimes anteriorly keeled, and show two lateral wear facets. The Author concluded that woolly rhinoceroses used their horns to sweep the snow looking for food, and observed that horn-wiping is performed also by territorial *Ceratotherium* males. Though recognizing that the two species show several morphological similarities, as already observed by Guérin (1980), Fortelius excluded, because of their so different ecological preferences, that the boreal *Coelodonta* could be territorial and sedentary like the tropical *Ceratotherium*.

I find Fortelius' conclusions very convincing. Nevertheless I would not exclude that horn sweeping in *Coelodonta* may have been also part of fight ritualisation, which was perhaps restricted to the short breeding periods when males may well have been territorial.

As browers, black rhinoceroses disperse on very broad areas and bulls hold wide territories. The fact that *S. etruscus* and *S. hundsheimensis* bore their heads uplifted and that their orbits are placed in a high position suggests that they too probably held wide and fairly open territories which they watchfully defended from invasions.

In most mammals, as the animal ages the nasal septum may partly ossify; the ossification progresses from the crista galli forwards. In the Pleistocene European rhinoceroses the opposite is the case. According to Thenius (1955) the nasal septum progressively ossified to support the pressure of an increasingly larger front horn. Loose (1975) rightfully questioned why there is no ossification of the nasal septum in present day forms which bear considerably large front horns. Thenius' hypothesis is plausible, in consideration of the fact that, unlike extant African forms, Pleistocene European rhinoceroses are characterized by the contrasting combination of unusually slender, elongated and delicate nasals and very developed hornbase rugosities. As a matter of fact, the nasal septum is completely ossified in *Coelodonta antiquitatis*, which had a long, powerful front horn; however it was also in *Elasmotherium sibiricum* Fischer, which, on the other hand, lacked a nasal horn. Incidentally, in the rhinoceros-like *Arsinoïtherium zitteli* Beadnell, which bore two enormous nasal horns, there is just a thin, delicate bony rod which connects the tip of the nasals with the premaxillae. *E. sibiricum* apparently bore an enormous front horn, as suggested by the great bumpy hornbase on its forehead. I doubt that such a horn could be used for fights, given its position, and given the structure of the occipital region of this species. In rhinoceroses which use horns for fights, the main weapon is shifted forwards so to best utilize all the impulsion given by the neck muscles, and the supraoccipital region is stretched upward and backward in order to elongate the power arm of the muzzle-occipital condyles-supraoccipital crest lever system. For this reason I believe that confrontations may have been highly ritualised in *Elasmotherium*. Muzzle-wiping may therefore have been part of the ritualised disputes; but muzzle-wiping or muzzle-pushing may well have played an important role also in the feeding habits of this peculiar rhinocerotid. I find that the most reasonable use of the forehead horn of *Elasmotherium sibiricum* is sexual display. Unfortunately, I had the opportunity to examine only one skull at the Natural History Museum of London, and therefore I have no idea of the possible sexual dimorphism of this species.

In my view, muzzle-pushing and muzzle- or horn-wiping were the rule, rather than the exception, among most Pleistocene rhinoceroses, and they may well have been connected with feeding and/or fight ritualisation.

Stephanorhinus hemitoechus and *Ceratotherium simum* are distinguished by evident dental differences, which reflect different habitat preferences. The hypothesized occurrence of a semi-prehensile upper lip in *S. hemitoechus* would further distinguish it from the «square-lipped» white rhinoceros. On the other hand, the two species also share a number of common characters: they both have dolychocephalic skulls; supraoccipital crests strongly projected backwards; orbits placed in a high position; ethmoidal laminae pierced by wide foramina. Both are also graviportal species. In my opinion, the *S. hemitoechus* populations were probably regulated like the present day white rhinoceros; they perhaps were sedentary and territorial rhinoceroses, which based most of their social relations on smell. Contentions were probably ritualised, although the structure of their skull suggests that effective fights may have occurred, as happens among white rhinoceroses today.

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