

On the Holsteinian? and Saalian mammal fauna from the ice-pushed ridge near Rhenen (The Netherlands)

T. VAN KOLFSCHOTEN*

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SAMENVATTING

In de afgelopen jaren zijn in de groeven Leccius de Ridder, Vogelenzang en Kwinteloijen, die liggen in de gemeente Rhenen, vele fossielen van grote zoogdieren gevonden. Deze fossielen zijn veelal in het bezit van amateur verzamelaars en velen van hen, onder andere de in 1980 overleden A. P. DE KLEUVER, hebben het materiaal voor onderzoek beschikbaar gesteld aan de afdeling Stratigrafie/Paleontologie van de Rijksuniversiteit Utrecht. Daarnaast is er door medewerkers van die afdeling, in de groeve Leccius de Ridder een klei-lens bemonsterd, wat een collectie kleine zoogdieren opgeleverd heeft. Zowel de kleine als de grote zoogdieren worden in dit verhaal behandeld, te beginnen met de kleine zoogdieren.

In de klei-lens werden naast schelpen fossielen van de volgende dieren aangetroffen: karperachtigen, kikkers, spitsmuizen (*Neomys* spec., waarschijnlijk de waterspitsmuis *Neomys fodiens*), de mol (*Talpa europaea*), de watermol of desman (*Desmana moschata*), de rosse woelmuis (*Clethrionomys glareolus*), de woelrat (*Arvicola terrestris*), aard- en/of veldmuizen (*Microtus arvalis/agrestis* groep) en de bosmuis (*Apodemus sylvaticus*).

Alle soorten, met uitzondering van de watermol, komen ook nu in Nederland voor wat er op wijst dat er een gematigd klimaat heerste in de periode waarin de klei is afgezet. Omdat de klei-lens in gestuwd sediment werd aangetroffen, is de minimale ouderdom van de fauna Midden-Saalien. Op grond van het voorkomen van de recente woelrat (*Arvicola terrestris*) zal de fauna niet veel ouder zijn dan Midden-Saalien. De fauna wordt dan ook geplaatst in een interstadiaal in het Saalien.

Fossielen van grote zoogdieren zijn afkomstig uit grindrijke niveau's in alle drie groeven. Het merendeel van het bestudeerde materiaal is verzameld in de groeven Vogelenzang en Leccius de Ridder.

Bijna de helft van de fossielen is afkomstig van de mammoet (*Mammuthus primigenius*). Van de "bos" olifant (*Elephas namadicus*) (= *antiquus*) zijn slechts een paar fragmenten van kiezen bekend. Het fossiele paardenmateriaal vertoont erg veel variatie. Er is onder andere een onderkaakskies gevonden die zoveel verschilt van de andere onderkaakskiezen dat het hier waarschijnlijk twee soorten paarden betreft (*Equus* spec. a en spec. b). Om welke soorten

* Instituut voor Aardwetenschappen Budapestlaan 4, 3508 TA Utrecht, The Netherlands

het gaat is nog onduidelijk. Van neushoorns zijn tot nu toe weinig fossielen gevonden. Toch kan er op grond van de beschikbare stukken geconcludeerd worden dat er drie soorten aanwezig zijn, namelijk de "bos" neushoorn (*Dicerorhinus kirchbergensis*) de "steppe" neushoorn (*Dicerorhinus hemitoechus*) en de wolharige neushoorn (*Coelodonta antiquitatis*). Van het wilde zwijn (*Sus scrofa*) is alleen een hoektand bekend, welke duidelijk groter is dan de hoektanden van recente mannelijke wilde zwijnen. Zeer opmerkelijk is de aanwezigheid van het nijlpaard (*Hippopotamus* c.f. *amphibius*) waarvan een stuk onderkaakshoektand gevonden is. Op grond van meerdere stukken gewei is het duidelijk dat er twee soorten herten voorkomen het reuzenhert; (*Cervus (Megaceros) giganteus*) en het edelhert (*Cervus elaphus*). Van de muskus os (*Ovibos* aff. *moschatus*) is slechts één onderkaakskies gevonden. De aanwezigheid van de steppe wisent (*Bison priscus*) wordt gebaseerd op de vondst *in situ* van een fragment van een hoornpit.

Een aantal soorten (de mammoet, de wolharige neushoorn, de muskus os, het reuzenhert en de steppe wisent) duidt op een koud klimaat en bos-arme streken. Andere soorten (onder andere het nijlpaard, de "bos" olifant en het varken) duiden op een veel gematigder klimaat met veel bos. Een verklaring voor het voorkomen van deze, in een verschillend klimaat levende soorten kan zijn dat tijdens de afzetting een faunaverandering plaatsvond die het gevolg is van een snelle klimaatsverandering. Op grond van de overeenkomsten met wat bekend is van Steinheim (West-Duitsland) is het aannemelijk dat deze faunaverandering heeft plaatsgevonden tijdens de overgang Holsteinien — Saalien. Echter op grond van dateringen met behulp van petrologische gegevens is een faunaverandering aan het einde van een interstadiaal in het Saalien waarschijnlijk.

Ondanks het feit dat de stratigrafische posities van de faunas niet precies bekend zijn, geven de faunas veel informatie over de zoogdieren uit het bovenste deel van het Midden-Pleistoceen, een periode waarover op het gebied van de fossiele Nederlandse zoogdieren weinig bekend was.

SUMMARY

For many years now larger mammal fossils have been found by amateur collectors in three pits in the ice-pushed ridge near Rhenen. Part of these fossils has been studied and is described in this paper. Small mammals have been collected from a clay lens in one of the pits.

The collection of small mammals contains the following species: carplike fish, frogs, *Neomys* spec., *Talpa europaea*, *Desmana moschata*, *Clethrionomys glareolus*, *Arvicola terrestris*, *Microtus agrestis/arvalis* group and *Apodemus sylvaticus*. This fauna association indicates a temperate climate during deposition of the clay. It is considered to be a fauna from an interstadial in the Saalian.

The larger mammal fauna is composed of the following species: *Elephas namadicus*, *Mammuthus primigenius*, *Equus* spec. a and spec. b, *Dicerorhinus kirchbergensis*, *Dicerorhinus hemitoechus*, *Coelodonta antiquitatis*, *Sus scrofa*, *Hippopotamus* c.f. *amphibius*, *Cervus (Megaceros) giganteus*, *Cervus elaphus*, *Ovibos* aff. *moschatus* and *Bison priscus*. The assemblage consists of one group of species which indicates cold, glacial conditions and another group which indicates temperate conditions. An explanation for the co-occurrence of these two groups could be that deposition of the fossils took place during shifting of the biotope in response to rapidly changing climate. This fauna change might be placed at the Holsteinian-Saalian transition on the basis of the correlations between the situation in Rhenen and what is known from Steinheim (Western Germany). But the sediment-petrological data make it more likely that the fauna transition occurred at the end of an interstadial in the Saalian.

The Rhenen assemblage gives, in spite of its doubtful stratigraphical position, new information about the mammals lived in The Netherlands during a thusfar badly known interval of the upper part of the Middle Pleistocene.

1. INTRODUCTION

For many years now mammal fossils have been found in the three sand-and-gravel pits on the southern part of the ice-pushed ridge, the "Utrechtse Heuvelrug" near Rhenen. Amateur collectors have found most of the material and one of them, the late Mr. A. P. DE KLEUVER, assembled a large private collection. Part of the fossil material has been exhibited in the office of the Vogelenzang brick-yard. KORTENBOUT VAN DER SLUIJS (1955) already mentioned some of these fossils in his article about the Pleistocene elephants from The Netherlands. This material, together with other large fossil mammals from school collections and from the private collection of Mr. A. P. DE KLEUVER, was made available to Dr. P. Y. SONDAAR of the State University Utrecht for study purposes and is described here.

The amateur archeologists Dr. C. J. H. FRANSSSEN, Mr. B. VAN IJMEREN, Mr. R. VAN BAREN and Mr. L. LIEUWEN also gave the author permission to study their collections from the three pits and part of their material is also described in this paper.

The material mentioned above consists only of fossils of larger mammals. In addition to the larger mammal material small animals were collected from a clay lens in the east slope of the Leccius de Ridder pit by Dr. P. Y. SONDAAR, Dr. A. J. VAN DER MEULEN and Mr. J. LUTTEYN in 1966. First the localities and the methodology will be described, then the smaller mammals will be discussed and thereafter the larger mammals found in the three pits will be treated.

No attention will be paid in this paper to the clearly re-incorporated Cetacean vertebrae and to the bone tools, which have been made by human beings.

2. LOCALITIES

There are two sand-and-gravel pits on the south slope of the Grebbeberg (the southern part of the "Utrechtse Heuvelrug") called Vogelenzang and Leccius de Ridder. The third pit, Kwinteloijen, is situated NW of the Grebbeberg (ZANDSTRA, this volume, fig. 1.). The fossils of the smaller mammals were collected in 1966 from a clay lens in the east slope of the eastern pit, Leccius de Ridder, i.c. clay lens IV, as described by DE JONG (this volume).

Most of the larger mammals treated in this paper come from the Vogelenzang pit and were all collected before 1965 when the work in the pit was stopped. According to Mr. DE KLEUVER the fossils came from a level of coarse gravel. Workmen informed us that the large mammals from the Leccius de Ridder pit also came from a coarse level. Concerning the lithology of the ice-pushed sediments, it is probable that the larger mammals came from sediments belonging to units 5, 6 and 7 (RUEGG, this volume). In the Kwinteloijen pit work is still going on.

Part of the sediment was transported to the Vogelenzang brick-yard where it was riddled. Fossils were found among the large components. But besides these finds and some isolated finds in the pit itself, fossils were also found in sediments at the base or just above the base of unit 5 and in sediments of units 6/7.

3. METHODOLOGY

Because the material obtained from Mr. DE KLEUVER, collected in the Vogelenzang and Leccius de Ridder pits, had not been separated, all the fossils from these pits were encoded with RV and a number. The fossils from the Kwinteloijen pit were given the code RK. Material belonging to private collectors has been encoded according to their own system. The "DE KLEUVER"-collection and the smaller mammal fossils from the clay lens are stored in the Instituut voor Aardwetenschappen (I.v.A., = Institute of Earth Sciences) of the State University Utrecht.

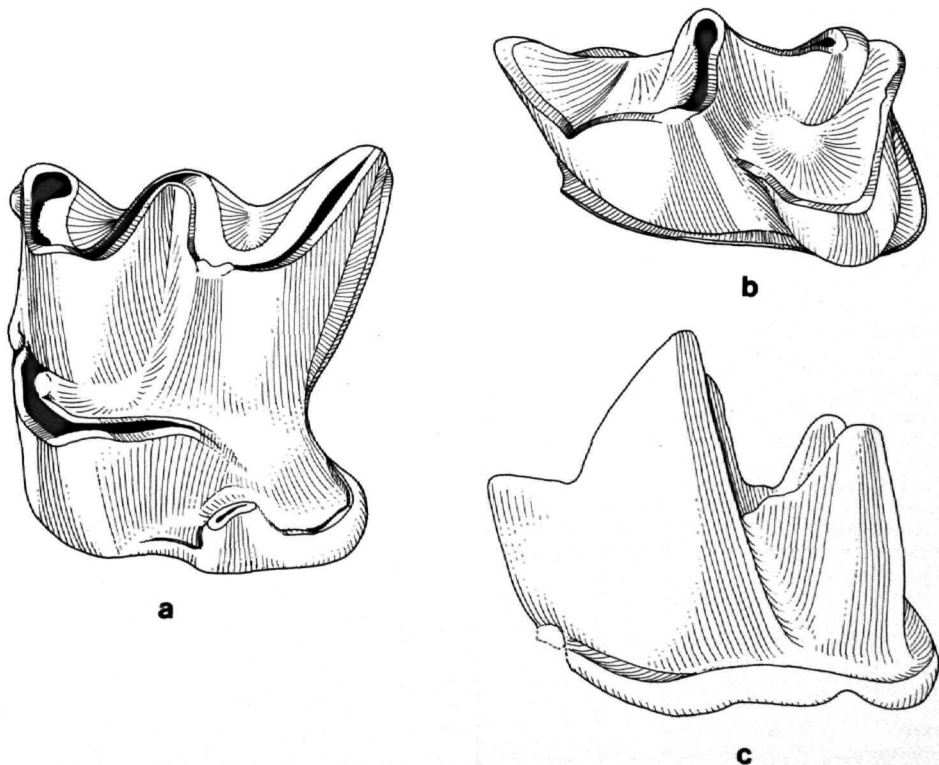


Fig. 1. *Neomys spec.*: a: occlusal view of M^1 sin. (RV 401); b: occlusal view of M^1 sin. (RV 403); c: buccal view of M^1 sin. (RV 403). Enlargement of all figures about $\times 40$.

4. THE SMALLER MAMMAL FAUNA FROM THE CLAY LENS

4.1. DESCRIPTIONS

Among the fossil material from the clay lens there are several pharyngeal teeth of carp-like fish (*Cyprinidae*) and a few bones of frogs. The mammals are represented by the following species:

INSECTIVORA
SORICIDAE

Neomys spec.
(fig. 1a — c)

Material: I inf. dext., M¹ sin., M₁ sin. and M₂ sin.
Measurements: (excluding the cingulum); (in mm)

length incisor	4.36
length M ¹	1.59
width M ¹	1.70
length M ₁	1.67
length trigonid M ₁	1.00
width trigonid M ₁	0.74
width talonid M ₁	0.92
length M ₂	1.53
length trigonid M ₂	0.89
width trigonid M ₂	0.85
width talonid M ₂	0.90

The *Neomys* from Rhenen is about the same size as *Neomys fodiens*. The incisor has only one cusplule on its crown, which is characteristic for the genus *Neomys*. The upper molar (M¹) has a well-developed hypocone which is separated from the protoloph by a deep valley. The protoloph in our fossil upper molar is longer and the posterior emargination is a little stronger than in the M¹ of the extant *Neomys fodiens* (water shrew) from the collection of Drs. L. MEIJER. The lower molar (M₁) has a more elongated trigonid than the M₁ of *Neomys fodiens*. The M₂ is smaller than the M₁ and the trigonid is relatively shorter. Moreover its protoconid is situated more buccal than at the M₁. The M₂ of *Neomys fodiens* has the same characters but is relatively much shorter.

Other species known from the Pleistocene, such as *N. newtoni*, *N. browni* and *N. anomalus*, are all smaller than *N. fodiens* (HINTON 1926; RZEBIK 1968).

However, in view of the observed differences between the species found in Rhenen and *N. fodiens* and the incompleteness of our material, a specific determination cannot be made.

TALPIDAE

Talpa europaea (Linnaeus, 1758)
(mole)
(fig. 2)

Material: M¹ dext.

Measurements: M¹; length 2.72 mm, width 1.49 mm.

The molar has an exceptionally long parastyl. There is no tubercle on the posterior end of the metastyl.

The M¹ is morphologically similar to the M¹ of *Talpa europaea*.

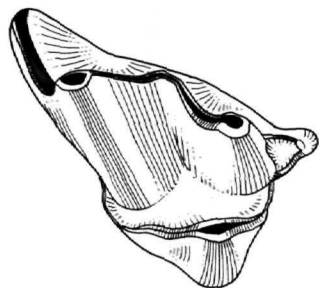
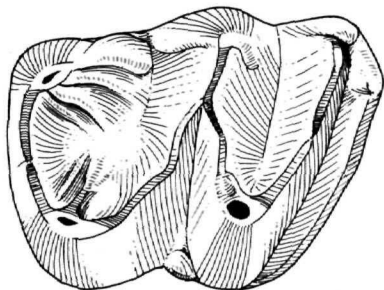
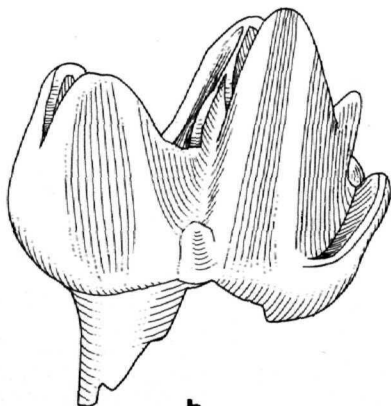


Fig. 2. *Talpa europaea* (Linnaeus): occlusal view of M¹ dext. (RV 411). Enlargement about x 20.



a



b

Fig. 3. *Desmana moschata* (Pallas): a: occlusal view of M₁ (RV 424); b: buccal view of the same specimen. Enlargement about x 20.

Desmana moschata (Pallas, 1831)
(desman)
(fig. 3)

Material: I₁ dext., I₃ sin., C₁ sin., M₃ dext.
Measurements: M₃; length 3.13 mm, width (max.) 2.31 mm, width trigonid 2.04 mm.

The M₃ is morphologically similar to the M₃ of the living *Desmana moschata* and, according to the measurements given by SCHREUDER (1940) is about the same size. It is too big to belong to the other species known from the Pleistocene of Europe.

RODENTIA
ARVICOLIDAE

Clethrionomys glareolus (Schreber, 1780)
(bank vole)
(fig. 4a, b)

Material: M² dext., 4 M² sin., 3 M³ dext., 4 M³ sin., 3 M₁ dext., 3 M₁ sin., M₂ dext., 3 M₃ dext.

Measurements:

M³ length: 1.43-1.66 mm (mean 1.52 mm)
width: 0.69-0.79 mm (mean 0.74 mm)
M₁ length: 2.07-2.25 mm (mean 2.16 mm)
width: 0.95-1.05 mm (mean 0.99 mm)

Molars of adult specimens have two roots each. The elements of young specimens are rootless and have thinner enamel. The re-entrant folds of the molars are partly filled with crown cementum.

The M₁ has 4-5 closed triangular fields and 5 lingual and 4 buccal salient angles. The M³ have a complicated form with 4 salient angles internally and 3 externally (one M³ has 4 salient angles externally) but they do not seem to be complex enough to justify their assignment to *Clethrionomys rutilus* (see OGNEV 1950).

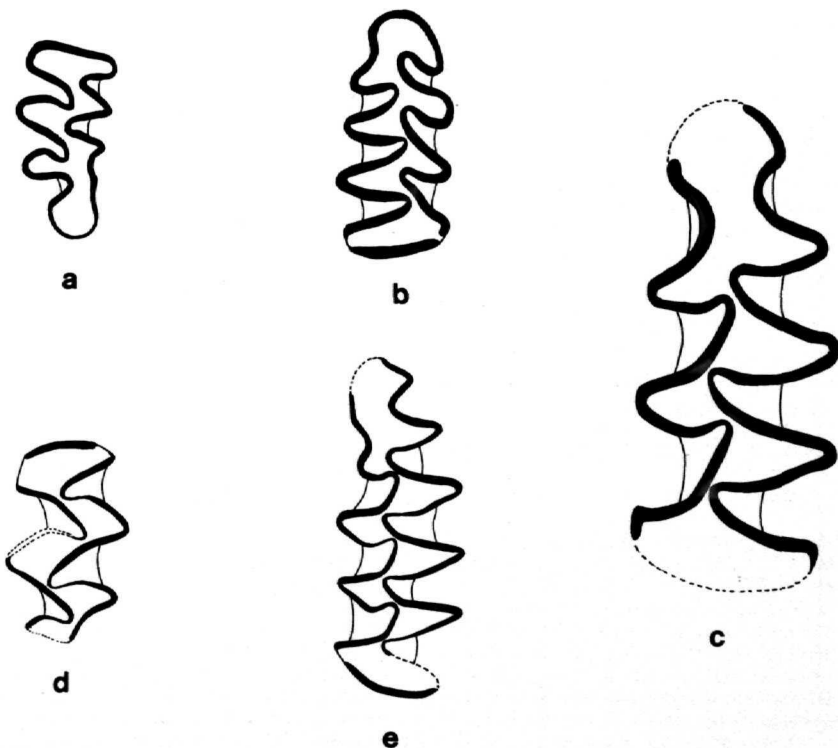


Fig. 4a. and b: *Clethrionomys glareolus* (Schreber): a: M³ sin. (RV 528); b: M₁ dext. (RV 532); c: *Arvicola terrestris* (Linnaeus): M₂ dext. (RV 631); d: *Microtus agrestis* (Linnaeus): M₁ sin. (RV 596); e: *Microtus agrestis/arvalis* group: M₁ sin. (RV 656). Enlargement of all figures about x 20.

Arvicola terrestris (Linnaeus, 1758)
(water vole)
(fig. 4c)

Material: 2 M² sin., 2 M₁ dext., 3 M₁ sin., 2 M₂ sin., M₃ sin.
Measurements: M₁ length: 3.38-3.67 mm (mean 3.53 mm)
width: 1.31-1.78 mm (mean 1.62 mm)

The molars are hypsodont, rootless and their re-entrant folds contain crown cementum. The M₁ has 3 closed triangular fields, 5 internal and 3 external salient angles. The enamel on the convex side of the angle is thinner than on the concave side (see fig. 4c). This type of differentiation of the thickness of the enamel and the size of the material allow the material from Rhenen to be determined positively as *Arvicola terrestris*.

Microtus agrestis/arvalis group
(field and common vole)
(fig. 4d, e)

Material: M² dext., M₁ dext., M₁ sin., M₂ sin., M₃ dext.
Measurements: M₁; length 2.78 mm, width 1.08 mm.

The molars are rootless and the folds contain crown cementum. The single M² has a small salient angle on its postero-internal surface (3 salient angles internally) which is a diagnostic character of *M. agrestis*. The M₁ has 7 closed fields. The ancestor cap has externally a small salient angle in one specimen; in the other it is more rounded.

The lower teeth of *M. agrestis* and *M. arvalis* cannot be clearly distinguished (SUTCLIFFE & KOWALSKI 1976) so it is not clear if *M. arvalis* is present in this fauna.

MURIDAE

Apodemus sylvaticus (Linnaeus, 1758)
(wood mouse)
(fig. 5)

Material: 2 M¹ dext., 3 M¹ sin., 3 M² dext., 2 M² sin., M₁ dext., 3 M₁ sin., 3 M₂ dext., 2 M₂ sin., 2 M₃ dext.

Measurements:

	Length				Width			
	Min.	Mean	Max.	N	Min.	Mean	Max.	N
M ¹	1.62	1.72	1.86	5	0.97	1.07	1.18	5
M ²	1.19	1.29	1.37	5	1.19	1.20	1.22	5
M ³	—	—	—	—	—	—	—	—
M ₁	1.75	1.85	1.94	4	1.03	1.06	1.09	4
M ₂	1.15	1.23	1.27	5	1.02	1.11	1.19	5
M ₃	0.96	0.96	0.96	2	0.90	0.92	0.94	2

In morphology and size our material closely resembles that of *Apodemus sylvaticus*.

4.2. COMPOSITION

The relative frequency, based on the number of molars, is given behind the species names.

Carplike fish	
Frogs	
<i>Neomys</i> spec.	3.75%
<i>Talpa europaea</i>	1.25%
<i>Desmana moschata</i>	1.25%
<i>Clethrionomys glareolus</i>	27.50%
<i>Arvicola terrestris</i>	13.75%
<i>Microtus agrestis/arvalis</i> group	18.75%
<i>Apodemus sylvaticus</i>	33.75%

4.3. THE HABITATS OF THE SPECIES
ACCORDING TO VAN DEN BRINK (1967)

The species best represented in this fauna, *Apodemus sylvaticus*, mainly inhabits open country and fringes of woods. They rarely live in woods. *Clethrionomys glareolus* indicates woods, for it mainly inhabits deciduous woods and fringes of woods. *Microtus agrestis* prefers moist areas like high, rough pastures, peat-moors etc. The habitat of *Microtus arvalis* is open country like pastures, meadows etc. *Arvicola terrestris* is more or less tied to water and mainly inhabits densely overgrown banks of brooks, ditches and lakes but it can also live far away from water. *Talpa europaea* has a wide range of habitats in all kinds of soils. The other species are aquatic mammals.

4.4. THE CLIMATE

Except for *Desmana moschata*, all species still inhabit The Netherlands. Therefore we assume that the assemblage indicates a temperate climate during deposition of the clay.

4.5. THE STRATIGRAPHICAL POSITION

The genus *Arvicola* appears in Europe in the Late Biharian (possibly during the Elsterian). *Desmana moschata* is not known in The Netherlands from the Holocene. So the fauna association indicates an age between Elsterian and Holocene. The genus *Arvicola* has been used for a more detailed zonation of the interval Elsterian — Eemian (VON KOENIGSWALD 1973). He distinguishes four faunal types, each characterized by an association of various small mammal species. The primitive *Arvicola cantiana* is present in his "Arvicola Faunas Type 1 and part of 2", which he correlates to the later part of the Elsterian, Holsteinian and possibly the Saalian. This species is replaced by the *Arvicola cantiana — terrestris* transitional form present in the younger associations of "Arvicola Fauna Type 2", and in the older association of "Arvicola Fauna Type 3". Von Koeningswald equates this interval with the Eemian. The advanced *Arvicola terrestris* replaces the *Arvicola cantiana — terrestris* transitional form during the Eemian (VON KOENIGSWALD 1973).

There is a discrepancy between his correlation and the presence of *Arvicola terrestris* in sediment that has been

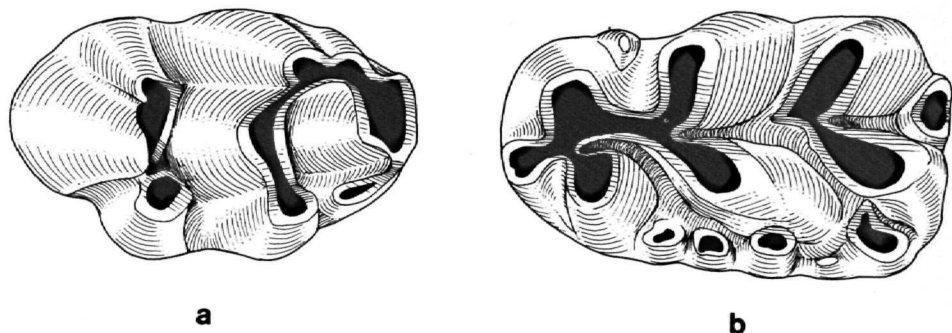


Fig. 5. *Apodemus sylvaticus* (Linnaeus): a: M¹ sin. (RV 686); b: M₁ sin. (RV 717). Enlargement about x 40.

pushed by the Saalian inland ice. There are no indications for dating the fauna as Holsteinian or even older. It is more likely to be an interstadial fauna in the Saalian.

For the pollen-analytical investigation of the clay lens the reader is referred to de JONG (this volume).

5. THE LARGER MAMMALS

5.1. DESCRIPTIONS

ELEPHANTIDAE

Elephas namadicus (Falconer and Cautley, 1845)
(= *Elephas antiquus*)
(Straight-tusked elephant)
(plate 1, fig. 1a, b)

Material: Fragment of an upper molar (coll. Vink);
fragment of M₂/M₃ sin. (RV 1).

Measurements:	upper molar	lower molar
number of plates	+ 5 +	+ 3 +
length	135 +	117 +
width	108	68.0
height	—	115.5
lamellar frequency	4.5	5.50
enamel thickness	2.5-3.5 (X = 3.0)	2.0-3.3 (X = 2.4)

The upper molar

On the basis of its width it is thought that the fragment belongs to an M³. The occlusal surface of the molar is broken off. The enamel is strongly folded and the lamellar frequency is low.

The lower molar

According to the measurements of *E. namadicus* (MAGLIO 1973) the lower molar fragment may be part of an M₂ or an M₃.

The enamel is strongly folded and the enamel figures, rising above the cement, are slightly lozenge-shaped, near-

ly touching each other at the mid-line. On the lingual and buccal side the plates are visibly bent and their lower parts point in the posterior direction. The molar is smaller than the lower molars of *Mammuthus primigenius*.

The lower molar was found in the Leccius de Ridder or the Vogelenzang pit. An almost identical fragment was found in the Kwinteloijen pit and is part of the collection belonging to the hospital in Rhenen.

Mammuthus primigenius (Blumenbach, 1799)
(woolly mammoth)
(plate 1, fig. 2 and 3)

Material: 3 tusk fragments; 2 fragments of M³
dext.; 1 fragment of M³ sin.; 1 fragment
of M² or M³; Mandibula with M₃ dext.;
M₃ dext., M₃ sin.; 3 fragments of lower
molars M₂ or M₃; fragment of a lower
molar indet.

Measurements: See table 1.

The tusk fragments (RV 20, 27 and 28)

The fragments (one (RV 28) with a length of about 75 cm) are from doubly curved tusks. Hence they do not belong to the straight-tusk elephant *Elephas namadicus*.

Molars

There are only fragmentary remains of upper molars. On the basis of the measurements they are determined as M² or M³. The enamel is rather thin and the lamellar frequency is high. One upper molar (RV 10) is very high (200 mm). The lower molars are better preserved than the upper molars. There is only one complete lower molar; it has 20 plates. The enamel of the lower molars is 1.45-2.6 mm thick and finely wrinkled. Worn enamel figures are irregular in outline and there are no medial enamel loops. The crown is heavily invested with cement.

In addition to these molar fragments many indeterminate plate fragments with thin enamel were found in the Kwinteloijen pit.

element	Number of			width	height	lamellar frequency	enamel thickness		
	plates	length					min.	mean	max.
M ³ (sin. ?)	(RV 4)	11+	128+	71.6 ³	185 ¹¹	8.9	1.4	1.5	1.7
M ² or M ³	(RV 7)	+ 4+	100+	68.2 ¹	157 ³	± 8.0	1.8	2.1	2.5
M ³ dext.	(RV 9)	9+	130+	76.0 ¹	140 ¹	8.5	1.2	1.5	1.8
M ³ dext.	(RV 10)	+ 12+	142+	92.5 ⁷	200 ¹	9.0	1.2	1.5	2.0
M ₃ dext.	(RV 16)	20	220	74.2 ⁶	—	9.5	1.8	2.0	2.2
M ₃ dext.	(RV 8)	14+	230+	96.5 ¹	148 ⁷	± 7.5	1.4	1.6	1.8
M ₃ sin.	(RV 2)	13+	166+	78.0 ⁵	160 ¹⁰	9.0	1.3	1.45	1.7
M ₃ /M ₂ (?) sin.	(RV 3)	+ 9+	95+	85.5 ²	111.5 ⁹	9.4	1.4	1.5	1.6
M ₃ /M ₂ (?) dext.	(RV 5)	+ 8	107+	66.9 ¹	149 ¹	8.2	1.8	2.0	2.2
M ₂ (?) sin.	(RV 11)	+ 12+	215+	84.0 ³	107 ⁸	6.5	2.0	2.2	2.6
Lower Molar	(RV 12)	+ 3+	66+	78.0 ²	99 ¹	6.4	1.6	1.8	2.0

Table 1: Measurements of the upper and lower molars of *Mammuthus primigenius* from Rhenen (made according to the method described by MAGLIO, 1973).

The elements differ clearly from those of *Elephas namadicus*, especially as far as the lamellar frequency is concerned. There is also a large variation in the lamellar frequency of the molars. In one upper molar (RV 7) and two lower molars (RV 11, 12) the lamellar frequency is very low for *M. primigenius* and the enamel in some molars is very thick for *M. primigenius*. The values agree more with those of *M. armeniacus* (= *E. trogontherii*) from which *M. primigenius* is descended (MAGLIO 1973). The basic structure of the molars of these two species is similar but in general the molars of *M. primigenius* are less high, have thinner enamel and higher lamellar frequency. Hence these must be very primitive specimens of *M. primigenius* or progressive specimens of *M. armeniacus*. Because most of the material has thinner enamel and a higher lamellar frequency the first possibility is the more likely one.

ELEPHANTIDAE INDET

Post-cranial bones, such as a distal fragment of a scapula (RV 19), an acetabulum of a left pelvis (RV 21), a medial fragment of an ilium (RV 22), a caput costae of a left rib (RV 23) and a diaphysis of a femur from a young individual (RV 26) have not been determined at specific level. This applies also to two mandibular symphyses (RV 24 and 25).

EQUIDAE

Equus spec. a and spec. b
(horses)
(plate 2, fig. 1-5)

Material:

- 22 upper (pre-)molars (coll. I. v. A., VAN BAREN, FRANSSEN and VAN IJMEREN)
- 9 lower (pre-) molars (coll. I. v. A., VAN BAREN, FRANSSEN en VAN IJMEREN)
- first phalanx ant. (coll. VAN IJMEREN)
- distal part of metacarpus (coll. VAN BAREN)
- distal part of a tibia (coll. FRANSSEN)
- calcaneum (coll. I. v. A.)
- metatarsus (coll. I. v. A.)

- distal part of metatarsus (coll. VAN IJMEREN)
- first phalanx (coll. I. v. A.)

Measurements: See description.

Only a brief description of the equine fossils is given because recently many equine fossils have become available and these have not been studied yet. In this paper only a few preliminary notes on a few specimens of the genus *Equus* are given. The material list shows that many teeth and bones have been collected. A few of these fossils are figured on plate 2. There is a great variation in the morphology and the size of the teeth. The M³ (RK 102), figured on plate 2 (fig. 1) has on its posterior side a well-developed metastyl and a double-ribbed hypostyl with edges of the same size. However, this character is variable and is different in the other upper third molars.

One lower molar (RV 105), probably an M₂, is so much smaller than the other lower (pre-)molars that it is hard to believe that they belong to the same species. On the basis of this molar in particular we conclude that we are dealing here with two different species *Equus* spec. a and spec. b.

The metatarsus (RV 107) has a length of 283 mm and the width of the diaphysis is 40 mm. The metatarsus from Rhenen is shorter and has a broader diaphysis than the metatarsus of the recent horse *E. caballus* (coll. I. v. A., rec. 13 f). Also the posterior first phalanx has a broader diaphysis and is clearly shorter than the posterior first phalanx of the recent horse.

RHINOCEROTIDAE

Dicerorhinus kirchbergensis (Jäger, 1839)
(Merck's rhinoceros)
(plate 3, fig. 1a, b)

Material: Calcaneum sin. (RV 153).

Measurements:

length	152.8
proximal width	± 63
proximal ant. — post. diameter	69
width diaphysis	49.5
ant. — post. diameter diaphysis	64.2
maximum width	70.5
distal width	39.8
distal ant. — post. diameter	47.7

The calcaneum is not quite complete. The tuber

calcaneum is damaged especially on the posterior side and the anterior process of the tuber calcaneum is broken off. The medial part of the sustentaculum tali is also missing. The calcaneum is heavily built, and is far too heavily built to belong to *Dicerorhinus bemitoechus* or *Coelodonta antiquitatis*, the other rhinoceros-species present in this fauna. The distal part is short and its axis is not parallel to the axis of the tuber calcaneum but points in the posterior direction. The axis of the groove on the lateral side of the calcaneum at the same height as the sustentaculum tali is not perpendicular to the axis of the tuber calcaneum. In the calcaneum of *D. bemitoechus* the axis is perpendicular (GUÉRIN 1973).

The proximal part of the upper lateral facet (for articulation with the astragalus) is very globular and extends a long way in the proximal direction. The distal part of this facet gradually becomes concave. Proximal of this facet there is no facet for the tibia. Between the proximal and distal facet on the lateral part of the anterior side there is a wide groove which is smaller than in the calcaneum of *C. antiquitatis* (DE LUMLEY 1959). The facet for articulation with the cuboid is slightly concave.

Dicerorhinus bemitoechus (Falconer, 1868)
(steppe rhinoceros)

(plate 3, fig. 2a — c; plate 4, fig. 2a — c, 3a — c)

Material:	P ¹ dext. (RV 151)	
	M ₁ sin. (RV 152)	
	astragalus dext. (RV 154)	
Measurements:		
(in mm) P ¹	length	45.6
	width	62.0
	height	61.5
M ₁	length	47.0
	width trigonid	28.2
	width talonid	29.4
	height trigonid	55.7
astragalus	width	84.8
	height	82.7
	ant. — post. diameter medial side	56.2
	distal width articulation facet	78.5
	ant. — post. diameter distal art. facet	45.0
	distance between the crests	62
	maximum width of the distal part	81
	upper lateral facet; diameter vertical	40.5
	width	43
	lower medial facet; diameter vertical	37
	width	30
	lower lateral facet; diameter vertical	12.4
	width	± 25

The P¹

Because of its length/width ratio the tooth has been determined as a P¹. It is slightly worn. The enamel is finely rugose and looks a little leathery. On the buccal side of the ectoloph, between the paracone and the metacone, there are two more or less parallel grooves running from

the top of the crown to the base. The P¹ of *D. kirchbergensis* has only one groove between these cones (STAESCHE 1941).

The crochet is well-developed but there is no crista. So there is no medifossette, a character which is found in the upper molars of *Coelodonta antiquitatis*. Also the presence of the hypostyl is a character in which this premolar differs from the same element of *C. antiquitatis*. On the anterior, lingual and partly on the posterior side there is a well-developed cingulum. There is no cement on the enamel layer.

The M₁

Its measurements agree most with those of an M₁ (GUÉRIN 1973). The molar is slightly worn. The trigonid has a round shape and the buccal side of it is rather flat. The talonid is crescent-shaped. Between these two parts there is on the buccal side a deep groove from the base to the top of the crown. In the lower molars of *C. antiquitatis* this groove is only deep and clear in the upper part of the crown (STAESCHE 1941).

The enamel is finely rugose and looks a little leathery. There is no cement. On the anterior and lingual side there is a very small cingulum.

According to GUÉRIN (1973), isolated lower teeth of *D. bemitoechus* and *D. kirchbergensis* are very difficult to determine. This means that the element can belong to *D. kirchbergensis*, although STAESCHE (1941) says that the buccal side of the trigonid is flat in the premolars and molars of *D. bemitoechus* and round in the same elements of *D. kirchbergensis*.

The astragalus

The astragalus is complete. The measurements agree most with those of *D. bemitoechus* and are too small to be the astragalus of *D. kirchbergensis* and *C. antiquitatis* (GUÉRIN 1973). The trochlea is asymmetrical but less so than the astragali of the other two species, in which the lateral part is far larger than the medial part. The angle between the internal sides of the two crests is more acute in this astragalus than it is in astragali of *D. kirchbergensis* and *C. antiquitatis*, figured by GUÉRIN (1973).

On the posterior side there are three facets, the upper lateral one being for articulation with the calcaneum. The upper part of this facet is very concave and the lower part is convex. The medial facet has an irregular shape and its larger upper part is a little convex in transverse and vertical direction, which is in contradiction with the characters of the astragalus of *D. bemitoechus* given by GUÉRIN (1973). He says that the facet is concave in the astragalus of *D. bemitoechus* and convex in the astragali of *D. kirchbergensis* and *C. antiquitatis*. The lower part of this facet is concave in the vertical direction. The lower lateral facet is broad.

The distal articulation surface has a trapezoid shape with a straight anterior side, which is characteristic for *D. bemitoechus* (GUÉRIN 1973).

The medial side of the astragalus shows that the medial

crest of the trochlea extends very far in the posterior and proximal direction, which is also characteristic for *D. bemitoebus*.

Coelodonta antiquitatis (Blumenbach, 1807)
(woolly rhinoceros)
(plate 4, fig. 1a-c)

Material: M² sin. (coll. FRANSSSEN, R. I.)
mandibula sin. with M₂ and M₃ (RV 155)
MT III dext. (coll. VAN IJMEREN no. 52)

Measurements:	(in mm)	
mandibula	height at the internal side	
	under M ₁ -M ₂	± 96
	under M ₂ -M ₃	100.5
	width under M ₁	68.2
	width under M ₂	62.4
	width under M ₃	50.3
M ₂	length	51.5
	width	33.0
	height	48
M ₃	length	53.8
	width	± 28
MT III	proximal ant. — post. diameter	42
	width diaphysis	40
	ant. — post. diameter of the diaphysis	23.5

The M²

Only a fragment of the upper molar was found. The anterior and lingual enamel layer of the protoloph and part of the metaloph are missing in addition to the posterior buccal part of the molar. At the buccal side there is a deep groove between paracone and mesostyl from the top of the crown to its base. The valley between the protoloph and the metaloph (the medisinus) extends very far in the buccal direction. The narrow crochet and crista have grown together to form a large more or less triangular lifossette (diameter max. 13.6 mm, min. 10.2 mm). This fossette is characteristic for *C. antiquitatis* and is not present in the upper molars of *D. kirchbergensis* and *D. bemitoebus*.

The mandibula

The anterior part of the mandibula, the premolars and the M₁ are absent. The measurements of the mandibula agree with those of the mandibula of *C. antiquitatis* given by GUÉRIN (1973). Compared to these measurements, the mandibula is relatively narrow below the M₃.

The M₂ and M₃

The M₂ is slightly worn, the M₃ unworn. The molars are hypsodont. The trigonid of the molars is rectangular with clear angles. The talonid is crescent-shaped. On the buccal side of the M₂ between the trigonid and the talonid there is a groove from the top of the crown to about 10

mm above the base. In the M₃ only the upper part of this groove is visible. On the anterior side of the entoconid of the M₃ there is a little tubercle which is also present but very small in the M₂. The enamel looks leathery and not as smooth as the enamel of the elements described under *D. bemitoebus*. There is cement in the valleys, on the anterior side and on the bases of the lingual and buccal sides. A cingulum is absent or nearly absent.

The mandibula is determined as *C. antiquitatis* because of the hypsodont M₂, the rectangular shape of the trigonid of the two molars and the leathery and rugose enamel all of which are characters from *C. antiquitatis*, according to BOUCHUD (1966) and GUÉRIN (1973).

The metatarsus (MT III)

The distal part and, the lateral part, at the proximal end are broken off. The shapes of the facets on the proximal medial side (for articulation with the MT III) are not clear because they are damaged.

The MT III is too small to be an MT III of *D. kirchbergensis*. The measurements agree in the mean with those of the MT III of *C. antiquitatis* and *D. bemitoebus* (GUÉRIN 1973), although this MT III is slender and has a relatively large diameter in the anterior — posterior direction. In cross-section it is clear that the medial part of the diaphysis has the largest ant. — post. diameter and that the medial side is almost perpendicular to the posterior side, which is characteristic for the MT III of *C. antiquitatis* (GUÉRIN 1973).

RHINOCEROTIDAE INDET

A few post-cranial bones such as an atlas, two incomplete humeri, two pelvic fragments and two incomplete tibias have not been determined at specific level because the material is not complete enough or the differences between these bones of the three species are too poorly known.

The atlas (RV 158)

The transverse processes and the lower distal part of the atlas are missing. The vertical diameter of the cranial articulation surface is 109 mm and the transverse diameter 145 mm. Because of its size and the morphological resemblance of the cranial articulation surface with the occipital processes of the skull of a woolly rhinoceros it is determined as an atlas of a rhinoceros.

The humeri (RV 156, 157)

Both are fragments of a left humerus. One (RV 157) is the middle part of a diaphysis (min. transverse width 82.5 mm). The other is more complete, but the proximal half and the anterior and lateral part of the distal end are missing. Its measurements are; min. width of the diaphysis 86.7 mm, distal width ± 160 mm and the ant. — post. diameter at the distal end is ± 130 mm. These measurements agree with those of the humeri of

Coelodonta antiquitatis (GUÉRIN 1973).

The humerus is short, broad, with a flat anterior diaphysis surface and a deep olecranon groove. All are characters of the humerus of rhinocerotidae (BOUCHUD 1966).

The pelvis fragments (RV 160, 161)

The fragments are two almost identical pieces of the pubis of left pelvises. They resemble morphologically the pubis of the pelvis of *C. antiquitatis*.

The tibia fragments

From one of the two fragments, namely a fragment of a left tibia (coll. VAN BAREN no. 3), the proximal part and the lateral distal part are missing. The measurements are; min. transverse width of the diaphysis 51.2 mm, ant. — post. diameter at the height of the min. width 51.5 mm, min. ant. — post. diameter of the diaphysis 46.8 mm and the ant. — post. diameter on the medial distal side is 63.0 mm. The tibia is very slender, too slender to belong to *C. antiquitatis* (GUERIN 1973). The medial distal part of the posterior surface is vertically very convex, which is characteristic for *D. kirchbergensis* and *C. antiquitatis* and which is not found in the tibia of *D. hemitoechus*.

The other fragment (coll. FRANSSEN) is of a right tibia. From that tibia only the distal part, with only a section of the distal articulation surface, is left. This tibia is more heavily built than the one described above. The ant. — post. diameter on the distal medial side is 71 mm.

SUIDAE

Sus scrofa (Linnaeus, 1758)
(Eurasian wild hog)
(plate 5, fig. 1)

Material: C. sup. sin. (coll. VAN IJMEREN no. 7).
Measurements: length along the anterior surface 82 mm
length along the posterior surface 67 mm
height 29.7 mm
ant. — post. diameter 24.5 mm

The canine is bent and has a strip of enamel 20 mm wide only on the lower part of its anterior surface. The enamel is finely grooved in the longitudinal direction. The oblique wearing facet cuts off the enamel obliquely. The presence of the enamel only on the anterior surface and the oblique wearing facet are characters of a canine of a pig. The canine is much larger than the canine of a male of the recent Eurasian wild hog. Because the Pleistocene form was markedly larger than the recent one (KURTEN 1968) the canine probably belongs to *Sus scrofa*.

HIPPOTAMIDAE

Hippopotamus cf. amphibius (Linnaeus, 1758)
(hippopotamus)
(plate 5, fig. 2a-c)

Material: Fragment of C. inf. dext. (RV 201).
Measurements: height ant. ± 41 mm
height post. ± 25 mm
ant. — post. diameter at the top 28.1 mm
ant. — post. diameter at the base 32.5 mm
transverse diameter at the top 20.9 mm
transverse diameter at the base 23.2 mm

The fossil is part of the top of a right lower canine from a juvenile hippopotamus. The top and the lower part of the canine are broken off. About 3/4 of the fragment is coated with enamel. There is no enamel on the posterior side. In the enamel, which is about 1.2 mm thick, we observe fine longitudinal grooves with a warty micro-structure. The dentine is 4-5 mm thick, surrounding a pulp cavity, visible at the upper and lower surface and partly filled with sediment. On the mesial side there is a wide longitudinal groove in the enamel surface which becomes less deep towards the top of the canine.

This canine is similar to the canines of recent *Hippopotamus amphibius* in many aspects, e.g. the shape, the longitudinal grooves and the wide mesial groove. In the recent species the longitudinal grooves are sometimes more pronounced than in the fossil from Rhenen and the wide mesial groove is not always as clear as in the described fragment.

CERVIDAE

Cervus (Megaceros) giganteus (Blumenbach, 1803)
(giant deer)
(plate 5, fig. 5; plate 6, fig. 1)

Material: pedicle of a left antler (coll. VAN IJMEREN)
pedicle of a right antler (coll. FRANSSEN)
fragment of a left antler (RV 51)
fragment of a right antler (coll. FRANSSEN, R II, o.a.)
metacarpus sin. (RV 52)
astragalus dext. (RV 63)
2 astragali sin. (RV 67, 68)

Measurements:

	pedicle (coll. FRANSSEN)	pedicle (coll. V. IJMEREN)
Antler		
transverse diameter of the rosary	± 90	—
ant. — post. diameter of the rosary	± 95	59
	RV 51	antler (coll. FRANSSEN)
transverse diameter of the rosary	85	72
ant. — post. diameter of the rosary	77	54

metacarpus	
proximal width	65.7
proximal ant. — post.	43.8
diameter	
width of the diaphysis	43.2
ant. — post. diameter of the diaphysis	37.9

astragalus	RV 63	RV 67	RV 68
lateral length	88.9	93.4	90.2
medial length	84	84.7	84
proximal width	55.5	58.4	55.6
distal width	57.6	59.0	53.8
ant. — post. diameter on the medial side	49.5	50.0	47.5

The pedicles and the antlers

On the pedicles there are only fragments of the rosary and at the base of the pedicles there is only part of the frontal bone. The pedicles differ greatly in size but not in height.

Both of the antler fragments are basic parts of shed antlers. The right antler consists of a short piece (length about 300 mm) of a beam with the rosary and the remnants of a browtine and the second anterior tine. The angle between the rosary and the beam is about 45°. A little way behind the rosary and partly grown together with it is the base of the browtine. At the terminal end of the fragment there is a flat part of the second anterior tine. The other fragment is from a smaller right antler. The browtine is broken off and the second tine is missing. Its terminal fracture surface is flat. The length of the fragment is about 170 mm.

The metacarpus

Only the proximal half of the metacarpus is left. The ridge on the proximal articulation surface between the lateral and medial facet is short. On the posterior side of the metacarpus there is a deep, wide groove and on the anterior side a small, shallow one. These are characters of the metacarpus of a Cervidae (HEINTZ 1970). The metacarpus is about the same size as a metacarpus of *Cervus (Megaceros) giganteus* and is too large to be a metacarpus of *Cervus elaphus*.

The astragali

The astragali differ from the astragalus of *Bison priscus* in some respects:

- they are more slender (they are of about the same length but are smaller);
- their distal articulation surfaces are less symmetric (the external part is broader than the internal part);
- the distal medial grooves are asymmetric because of the presence of a ridge on the anterior medial side of the external part of the articulation surface.

These characters are more or less typical for the astragalus of Cervidae (HEINTZ 1970) and because of the

large size of the astragali they probably belong to *Cervus (Megaceros) giganteus*.

Cervus elaphus (Linnaeus, 1758)

(red deer)

(plate 5, fig. 3a, b and 4)

Material: 4 antler fragments (coll. I. v. A. RV 55, 56, 57, RK 51)
2 antler fragments (coll. LIEUWEN 9a, V 4)
1 antler fragment (coll. VAN BAREN)
1 antler fragment (coll. FRANSSEN)
anterior part of a P₄? dext. (RV 54)

Measurements:

Antler fragment	RV 55	RV 56	fragm. (coll. FRANSSEN)
max. diameter of the rosary	60	57	81
min. diameter of the rosary	42	46	70

The antler fragments

There are 4 basic fragments, one beam fragment and 3 terminal ends of a tine. One basic fragment is from a shed antler. The other fragments have the pedicle attached.

All the basic parts show the presence of a rosary with a browtine and a beztine at a short distance behind. This is characteristic for the more developed antlers of *Cervus elaphus* (SCHMID 1972). The beam fragment is more or less circular in cross section, with a diameter of ± 45 mm, which indicates that it belonged to a large antler. This fragment and the three terminal ends have a rugged surface. The rugged surface is characteristic for *C. elaphus* but is not characteristic for *Rangifer* (SCHMID 1972).

The P₄? fragment

This is a fragment of a brachio-selenodont lower (pre-)molar. The measurements are: height at the buccal side ± 14 mm, width at the base ± 14 mm. It closely resembles the anterior lobe of a right P₄ of *Cervus elaphus*.

BOVIDAE

Ovibos aff. moschatus (Zimmermann, 1780)

(musk ox)

(plate 6, fig. 2a-c)

Material: M₂ dext. (coll. VAN IJMEREN no. 9).

Measurements: See table 2.

	M ₂		<i>Ovibos moschatus</i> recent Coll. R. N. H. Leiden				
	Rhenen	N ^o	M ₁		M ₂		
			mean	min.-max.	N	mean	min.-max.
length	33.9	6	24.51	23.6-25.6	5	31.96	29.2-33.6
width ant. lobe at the top	14.7	5	13.28	11.9-14.5	5	12.72	11.7-13.9
at the base	19.9						
width post. lobe at the top	15.7	4	14.33	13.5-15.0	5	13.66	12.7-14.5
at the base	20.8						
height	± 40.5						

Table 2: The measurements of the M₂ of *Ovibos* aff. *moschatus* from Rhenen and of the lower molars (M₁ and M₂) of recent specimens of *O. moschatus* (Collection Rijksmuseum voor Natuurlijke Historie Leiden) (N^o = number of measured molars).

The molar is nearly complete. It is broken off above the roots and on the base of the posterior side the enamel and a part of the dentine is missing. The molar is hypsodont. The lingual side is rather flat. The metastylid is absent or nearly absent and the parastylid is not well-developed. The parastylid and the entostylid diverge at the base of the crown but at the top they even converge. There is no or only very small ectostylid and no cingulum. The occlusal surface is rather flat.

The molar is too hypsodont for it to belong to a Cervidae and differs greatly from the lower molars of the genus *Bos* and *Bison*.

Morphologically it corresponds more to the lower molars of a sheep, which belongs to the same subfamily as *Ovibos* (subfam. Caprinae).

Although it is the same size as the M₂ of the recent *O. moschatus* (see table 2) and has the same morphological characters, there are some differences between the M₂ from Rhenen and the M₂ of the recent specimens. These differences are: in the recent specimens:

- the protoconid and the hypoconid are broader;
- the lingual side is not so flat;
- the parastylid is better developed;
- the parastylid and entostylid diverge up to the top of the crown;
- a "pli antérieur" is present;
- the occlusal surface is not so flat, and more pointed.

The second lower molars of close related genera like *Præovibos* and *Soergelia*, also greatly resemble the molar from Rhenen, but they are smaller (SCHAUB 1951; KAHLKE 1963). So it is more likely that the molar belongs to the genus *Ovibos* and probably to *Ovibos moschatus*.

Bison priscus (Bojanus, 1828)
(steppe wisent)
(plate 6, fig. 3-6)

Material: fragment of a left horn core (Coll. R. G. D., Haarlem)
M² sin. (Coll. VAN IJMEREN no. 8)
M₂ sin. (Coll. FRANSEN)
M₃ dext. (distal part; RV 64),
humerus dext. (fragment of the diaphysis; RV 66)
humerus sin. (distal part; RV 65)
astragalus (RV 59)

Measurements:

horn core: See description

teeth	M ²	M ₂	M ₃
length at the top of the crown	34.0	35.3	33.6
length at the base of the crown	—	30.8	42.5
width at the top of the crown	23.3	16.6	11.8
width at the base of the crown	30.4	20.6	14.0

humeri	RV 64	RV 65
distal width of the articulation surface	103.5	113
ant. — post. diameter on the distal lateral side	—	113

astragalus	
lateral length	93.6
medial length	84.9
proximal width	62.0
distal width	64.7
ant. — post. diameter on the medial side	51.0

Apart from the horn core and the astragalus, the material could belong to *Bos primigenius* because it is very difficult to distinguish the teeth and nearly all the postcranial bones of this species from those of *Bison priscus* (BONIFAY 1966). Because the presence of *Bos primigenius* has not yet been proved, the teeth and the humeri are described as *Bison priscus*.

The horn core

Only the proximal part of the horn core is present and is badly fossilized. The upper part of the frontal bone and of the very proximal end of the horn core are absent. The core is broken at about 12 cm from its base. The total length of the horn core fragment is about 25 cm. It has a large diameter (max. 94 mm). The diameter at the broken terminal end is 74 mm and the ant. — post. diameter at the base of the horn core is 96 mm.

The horn core is a little bent and almost perpendicular to the skull, but is not bending backwards. The horn core has a very rugged surface.

Short, little bent horn cores with a rugged surface are characteristic for the genus *Bison* (BONIFAY 1966) and

because of its size this specimen is determined as *Bison priscus*. It concerns an *in situ* find (RUEGG this volume).

The M₃

The molar is broken off above its roots. The upper part of the entostyl and the lingual posterior and the anterior face are absent. The molar is hypsodont. The para-, meso- and metastyl are well-developed and there are deep grooves between the para- and hypocone and these styli. The entostyl is large.

The M₂

The M₂ is a hypsodont molar broken off above its roots. This molar is completely different from the M₂ of *Ovibos aff. moschatus*, especially its lingual surface (see plate 6, fig. 2 and 5). The parastylid is well-developed, the entostylid less. The ectostylid is also well-developed.

The M₃

The M₃ is almost unworn. The molar is very hypsodont (height 62 mm). It has a well-developed para- and entostylid. A metastylid is absent. An ectostylid is present from the base of the crown up to about 18 mm from the top of the crown.

The humerus fragments

These are remains of large broad humeri. The articulation surfaces of the distal parts show that they are from Bovidae and not from Cervidae (acc. to HEINTZ 1970), because their median grooves are not at the same level as the lateral parts of the articulation surfaces.

The astragalus (see also the description of the astragali of *Cervus (M.) giganteus*)

The astragalus is broad and its distal articulation surface is more or less symmetric. On its plantar surface the astragalus has a groove between the articulation surfaces for the calcaneum and the navicuboid which is clearly visible on the lateral side. This groove is nearly absent in the astragalus of *Bos primigenius* (SCHERK 1936) and the astragali of *Cervus (M.) giganteus*. The relatively flat shape of the lateral surface and the shape of the plantar articulation facets also agree with the characters of the astragalus of *Bison priscus* (SCHERK 1936).

5.2 COMPOSITION

Abbreviations of the names of the pit in which fossils from the species are found, are given behind the species names:

<i>Elephas namadicus</i>	VZ, LdR, K
<i>Mammuthus primigenius</i>	VZ, LdR, K
<i>Equus spec. a</i> and <i>spec. b</i>	VZ, LdR, K
<i>Dicerorhinus kirchbergensis</i>	VZ, LdR
<i>Dicerorhinus hemitoechus</i>	VZ, LdR
<i>Coelodonta antiquitatis</i>	VZ, LdR

<i>Sus scrofa</i>	LdR
<i>Hippopotamus c.f. amphibius</i>	VZ
<i>Cervus (Megacerus) giganteus</i>	VZ, LdR, K
<i>Cervus elaphus</i>	VZ, LdR, K
<i>Ovibos aff. moschatus</i>	K
<i>Bison priscus</i>	VZ, LdR, K

The differences between the assemblages from the different pits are due mainly to the rareness of certain species. The material will be treated as a single assemblage.

The relative frequency of the species is not given because only part of the available fossils have been described and some private collections have not been seen at all. Nevertheless it seems likely that *Mammuthus primigenius* is the most abundant species, because half of the material belongs to it. The genus *Equus* is well represented too. *Elephas namadicus*, *Dicerorhinus hemitoechus*, *Coelodonta antiquitatis*, *Cervus (M.) giganteus*, *Cervus elaphus* and *Bison priscus* are much rare. So far the presence of *Dicerorhinus kirchbergensis*, *Sus scrofa*, *Hippopotamus c.f. amphibius* and *Ovibos aff. moschatus* is indicated by a single specimen.

5.3. THE BIOTOPES OF THE DIFFERENT SPECIES

Mammuthus primigenius, *Coelodonta antiquitatis* and *Ovibos moschatus* are known to prefer a cold climate and open areas (tundra and steppe). *Cervus (M.) giganteus* and *Bison priscus* are often found in association with these species. Other species such as *Elephas namadicus*, *Dicerorhinus kirchbergensis*, *Sus scrofa* and *Cervus elaphus* prefer a more temperate climate and woods. *Dicerorhinus hemitoechus* and *Equus* prefer a steppe-biotope. *Hippopotamus amphibius* is tied to water and lives today in a sub-tropical climate.

There is one group of species (*Mammuthus primigenius*, *Coelodonta antiquitatis*, *Ovibos moschatus*, *Cervus (M.) giganteus* and *Bison priscus*) which indicates cold, glacial conditions, and another group, the remainder of the species, which indicates temperate conditions.

In view of the good preservation of virtually all specimens, neither of the groups seems to have been re-deposited. Only one astragalus (? *Cervus elaphus*) and two? *Bison* molars from Vogelenzang are rounded, and therefore may have been re-incorporated and/or transported over a large distance.

Explanations for the co-occurrence of the two groups can be:

a. that the biotope indications of the different species are not right. This possibility is discarded because there are more species indicating the same biotope and it is very unlikely that all the species lived in the same biotope, for they are rarely found together.

b. that this is due to seasonal differences. This is also very unlikely because the different groups prefer a different landscape. One group prefers an open area, the other prefers woods and parkland.

c. that re-deposition took place after transport over a very short distance, and this had no visible erosive effect on the re-deposited fossils. This is doubtful but the relative

dating method, based on the contents of fluorine and nitrogen in skeletal material (OAKLEY 1980) may give more information about the possibility of re-deposition.

d. that deposition of the fossils took place during shifting of the biotope in response to the rapidly changing climate. This is possible if there was slow or irregular sedimentation.

5.4. THE STRATIGRAPHICAL POSITION OF THE "FAUNA"

There are many correlations between the situation in Rhenen and what is known from Steinheim (Western Germany) where 4 levels each with a different fauna, have been distinguished (ADAM 1954). In the Rhenen assemblage species from the two middle levels, "antiquus-Schotter" and "trogontherii-primigenius-Schotter" are present. These two levels are dated as Holsteinian and Saalian, respectively. Figure 6 shows that there is no abrupt fauna change at the transition from the "antiquus-Schotter" level to the "trogontherii-primigenius-Schotter" level, which means that the fauna changed gradually. Adam places this fauna change at the beginning of the Saalian (Riss-glaciation), and not at the end of an interstadial in the Saalian, because of the resemblances between the Elephantidae from the "trogontherii-primigenius-Schotter" and from other faunas like Markkleeberg, the stratigraphical position of which is well known. In addition Adam also mentioned other indications for the stratigraphical position of the fauna-transition.

On the basis of the correlations with the situation in Steinheim, the stratigraphical position of the Rhenen assemblage might be at the Holsteinian — Saalian transition. But this is in contradiction with the petrological data, which indicate a Middle Saalian age for the sediment in which the fossils were found. This makes it more likely that the fauna-transition occurred at the end of an interstadial of the Saalian.

The Rhenen-fauna can be placed in the upper part of the Middle Pleistocene. This interval is badly known, at least as far as the fossil mammals from The Netherlands is concerned. The famous Tegelen-fauna give us a lot of information about the Early Pleistocene and from the Late Pleistocene a lot of fossil remains are known from *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Cervus (Megaceros) giganteus*, *Bison priscus* and *Cervus elaphus*. The Rhenen "fauna" indicates that these species also lived during the Saalian together with *Ovibos aff. moschatus*. Of this species only 4 specimens are known from several places and all of them are probably of Weichselian age (ERDBRINK & KORTENBOUT VAN DER SLUIJS 1961).

Elephas namadicus, *Dicerorhinus kirchbergensis* and *Cervus elaphus* are known from Holsteinian (=Needian) deposits from The Netherlands (VAN DER VLERK & FLORSCHÜTZ 1950). Whether the Rhenen "fauna" covers part of the Holsteinian interval or not, it gives us a lot of information about the temperate fauna which lived in The Netherlands during an interval of the upper part of the Middle Pleistocene.

The occurrence of *Hippopotamus amphibius* is all the more remarkable because ZEUNER (1959) states that the

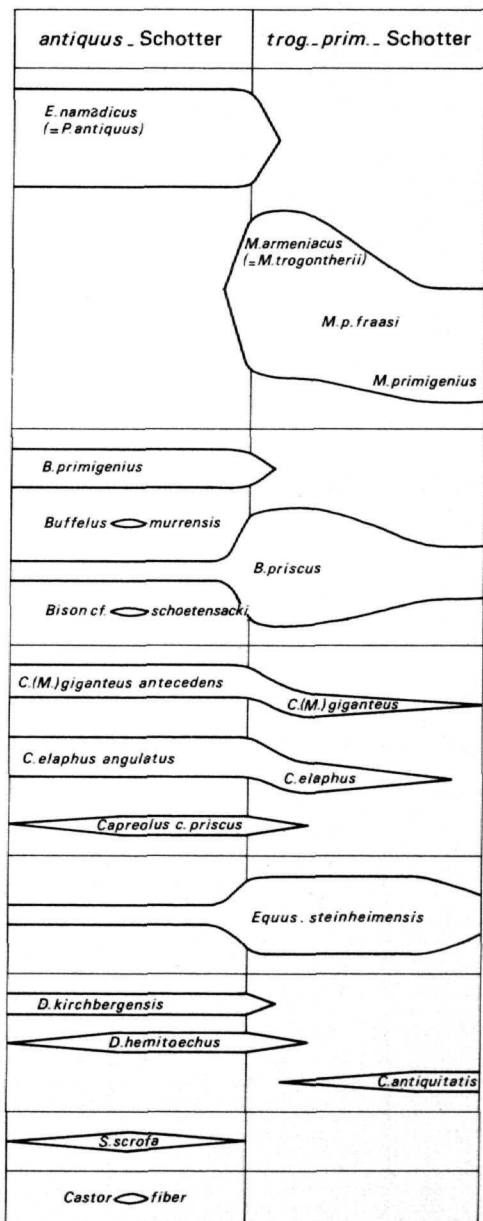


Fig. 6. Distribution of the larger mammals (with the exception of the Carnivora) in the "antiquus" — and "trogontherii-primigenius-Schotter" of Steinheim (Western Germany) (after ADAM 1954).

Hippopotamus did not survive the Elsterian glacial time in the Rhine area. In the light of the occurrence of *Hippopotamus amphibius* in Rhenen this statement is unlikely to be true.

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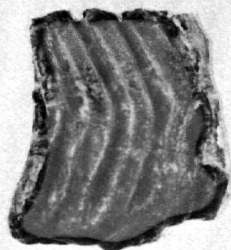
Plates

PLATE I

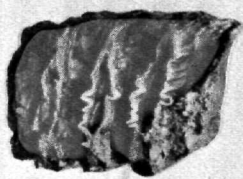
Fig. 1. *Elephas namadicus* (Falconer & Cautley): M_2/M_3 sin. (RV 1): a: lingual view; b: occlusal view.

Fig. 2. *Mammuthus primigenius* (Blumenbach): part of a right mandibula with an M_3 (RV 16): a. occlusal view; b: lingual view.

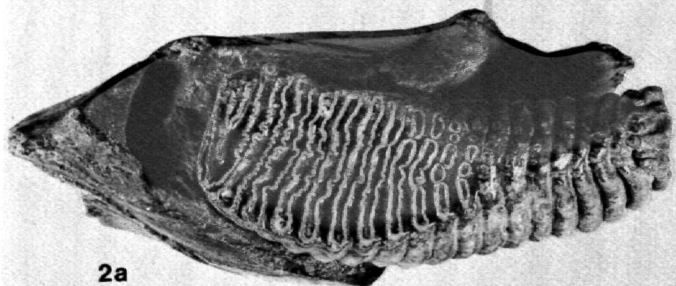
Fig. 3. *Mammuthus primigenius* (Blumenbach): fragment of a tusk (RV 28).



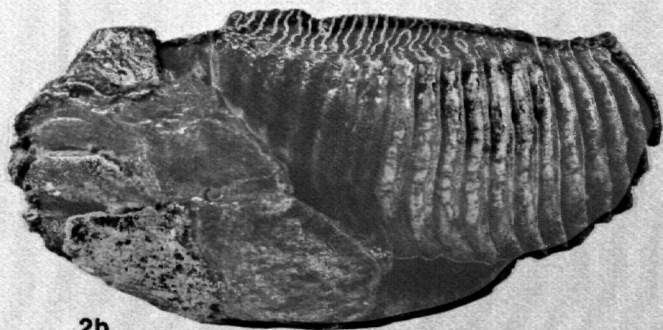
1a



1b



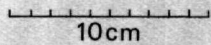
2a



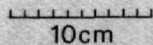
2b



3



10cm



10cm

PLATE 2

Equus spec. a and b

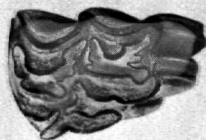
Fig. 1. M^3 sin. (RK 102); a: occlusal view; b: posterior view.

Fig. 2. P_3/P_4 sin. (Coll. VAN IJMEREN no. 25); a: occlusal view; b: buccal view; c: lingual view.

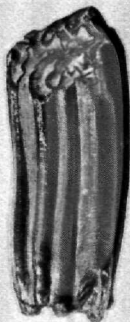
Fig. 3. M_2 (?) sin. (RV 105); a: occlusal view; b: buccal view; c: lingual view.

Fig. 4. Metatarsus dext. (RV 107); anterior view.

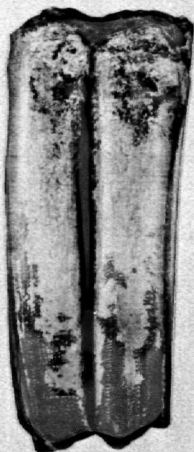
Fig. 5. First phalanx (of a right hindleg) (RV 106); anterior view.



1a



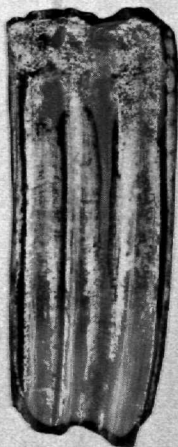
1b



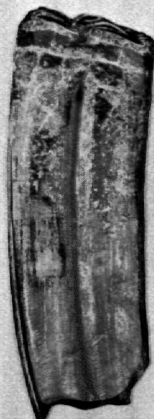
2b



2a



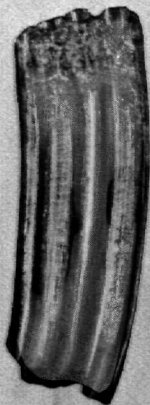
2c



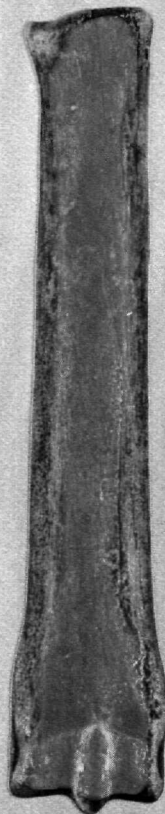
3b



3a



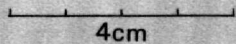
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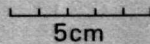
4



5



4cm

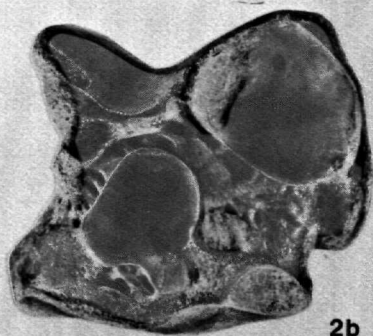
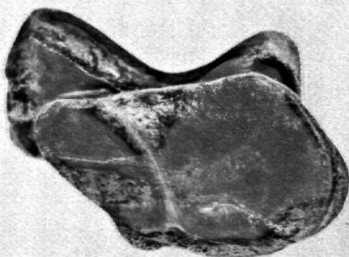


5cm

PLATE 3

Fig. 1. *Dicerorhinus kirchbergensis* (Jäger); calcaneum sin. (RV 153); a: medial view; b: lateral view.

Fig. 2. *Dicerorhinus bemitoechus* (Falconer); astragalus dext. (RV 154); a: anterior view; b: posterior view; c: distal view.



5cm

A horizontal scale bar with a central vertical tick and four smaller vertical ticks on either side, indicating a length of 5 centimeters.

PLATE 4

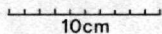
Fig. 1. *Coelodonta antiquitatis* (Blumenbach): mandibula sin. with M_2 and M_3 (RV 155); a: occlusal view; b: buccal view; c: lingual view.

Fig. 2. *Dicerorhinus hemitoechus* (Falconer): P^3 dext. (RV 151); a: occlusal view; b: buccal view; c: posterior view.

Fig. 3. *Dicerorhinus hemitoechus* (Falconer): M_1 sin. (RV 152); a: occlusal view; b: buccal view; c: anterior view.



1a



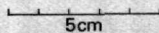
1b



1c



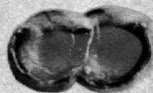
2a



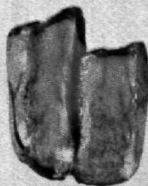
2b



2c



3a



3b



3c

PLATE 5

Fig. 1. *Sus scrofa* (Linnaeus) ♂: canine sup. sin. (Coll. VAN IJMEREN no. 7); anterior view.

Fig. 2. *Hippopotamus* cf. *amphibius* (Linnaeus): fragment of a canine inf. dext. (RV 201); a: proximal view; b: medial view; c: lateral view.

Fig. 3. *Cervus elaphus* (Linnaeus): basic part of a right antler (RV 55); a: medial view; b: lateral view.

Fig. 4. *Cervus elaphus* (Linnaeus): fragment of an antler (RV 57).

Fig. 5. *Cervus (Megaceros) giganteus* (Blumenbach): basic part of a left antler (RV 51); a: ventro-lateral view; b: medial view.

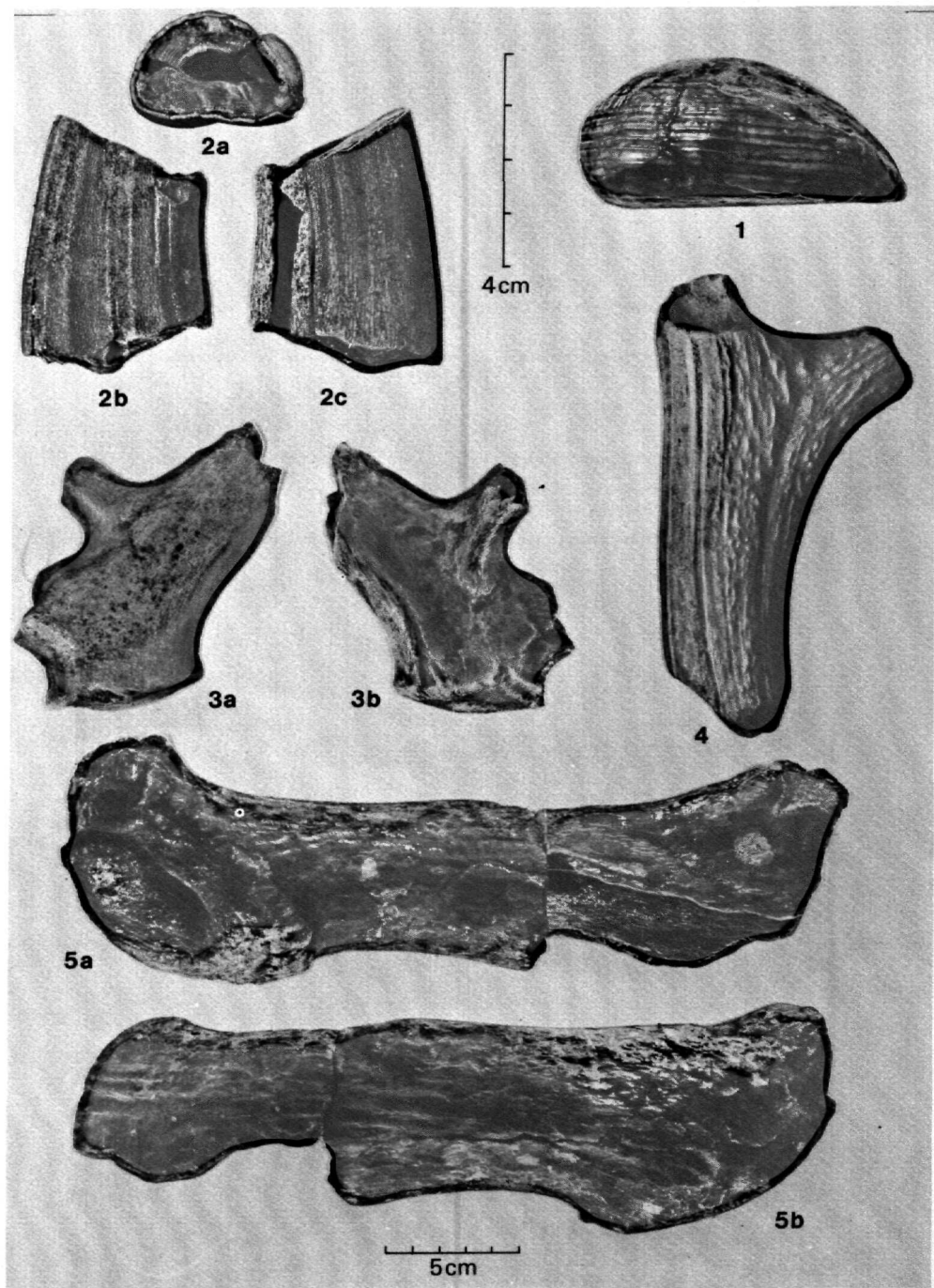


PLATE 6

- Fig. 1. *Cervus (Megaceros) giganteus* (Blumenbach); astragalus dext. (RV 63); a: anterior view; b: posterior view.
- Fig. 2. *Ovibos* aff. *moschatus* (Zimmermann); M₂ dext. (Coll. VAN IJMEREN no. 9); a: occlusal view; b: buccal view; c: lingual view.
- Fig. 3. *Bison priscus* (Bojanus); astragalus dext. (RV 59); a: anterior view; b: posterior view; c: lateral view.
- Fig. 4. *Bison priscus* (Bojanus); M₃ dext. (Coll. FRANSSEN); a: occlusal view; b: buccal view.
- Fig. 5. *Bison priscus* (Bojanus); M₂ sin. (Coll. FRANSSEN); a: occlusal view; b: buccal view; c: lingual view.
- Fig. 6. *Bison priscus* (Bojanus); basic part of a left horn core (Coll. R. G. D.); ventral view.



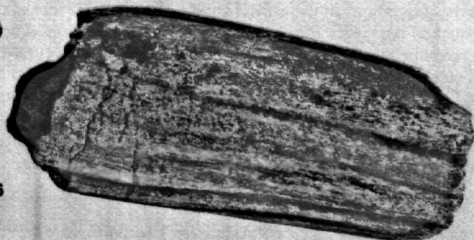
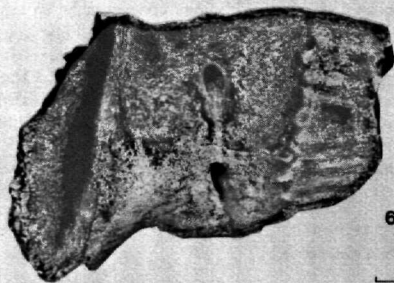
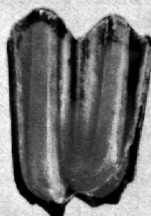
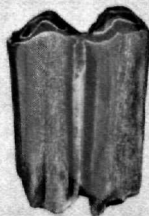
5cm



4cm



4cm



5cm