THE EVOLUTION OF THE MAMMAL FAUNA IN THE NETHERLANDS AND THE MIDDLE RHINE AREA (WESTERN GERMANY) DURING THE LATE MIDDLE PLEISTOCENE

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ABSTRACT

In this paper a biozonation of the continental Middle Pleistocene in N.W. Europe is presented. This zonation is based on a number of fossil mammal assemblages, usually referred to as "faunas", from different localities in The Netherlands and Western Germany. Because of the importance for the mutual correlation of these faunas and the correlation of mammal zones with the Dutch standard subdivision of the Pleistocene, a review of the geological setting and the stratigraphy of the discussed localities is given in Chapter 1.

The recently discovered mammal fossils from Neede are described. In addition a review of previously described faunas (Wageningen - Fransche Kamp, Rhenen, Maastricht-Belvédère 1-5 and Ariendorf) is presented; this review is amplified by the description of new material recovered from these localities. Furthermore, provisional lists of recently collected and/or briefly investigated faunas from Maastricht-Belvédère (The Netherlands), Miesenheim I and Plaidter-Hummerich (Western Germany) are discussed.

Special attention is given to the genus *Arvicola* because of its relevance for the biostratigraphy of the Middle and Late Pleistocene. The taxonomy of *Arvicola* is revised and the author proposes to include all hitherto described fossil species, except for *Arvicola sapidus*, as subspecies of *Arvicola terrestris*.

Finally a new biozonation of the late Middle Pleistocene, valid for N.W. Europe, is proposed. The correlation between this zonation and the Dutch Standard subdivision of the Pleistocene is discussed.

ZUSAMMENFASSUNG

In dieser Arbeit wird eine Gliederung des kontinentalen Mittelpleistozäns in Nordwest-Europa vorgeschlagen. Diese Gliederung basiert auf der Untersuchung einer Reihe von Sammlungen fossiler Säugetiere (Faunen genannt) von verschiedenen Fundplätzen in Holland und der Bundesrepublik Deutschland. Um die verschiedenen Fundkomplexe untereinander vergleichen und in die holländische Standardgliederung einordnen zu können, wird in Kapitel 1 ein Überblick über die geologische Einbettung und die Stratigraphie der entsprechenden Fundstellen gegeben.

Erstmals werden die vor kurzem gesammelten fossilen Säugetierreste von Neede beschrieben. Weiter wird eine Überblick über schon vorgelegte Faunen (Wageningen - Fransche Kamp, Rhenen, Maastricht-Belvédère 1 - 5 und Ariendorf) gegeben. Dieser Überblick wird durch eine Beschreibung von neu entdeckten Funden vervollständigt. Es werden vorläufige Faunenlisten von neu entdeckten oder untersuchten Fundkomplexen, Maastricht-Belvédère (Holland), Miesenheim I und Plaidter Hummerich (Bundesrepublik Deutschland) behandelt.

Das Genus *Arvicola* wird wegen ihrer Wichtigkeit für die Gliederung des Mittel- und Spätpleistozäns besonders beachtet. Der Autor schlägt eine revidierte Taxonomie von *Arvicola* vor: Mit Ausnahme von *Arvicola sapidus*, sollten alle bis heute beschriebenen fossilen Arten, als Unterart von *Arvicola terrestris* aufgefasst werden.

Basierend auf den vorgestellten Säugetierfaunen, wird schliesslich eine Gliederung des späten Mittelpleistozäns in Nord-West-Europa vorgeschlagen. Die erarbeitete Giederung wird mit der holländischen Standardgliederung verglichen.

INTRODUCTION

Our knowledge of the Pleistocene in The Netherlands has considerably increased during the last 30 years, due to the application of palynological, sediment-petrological, malacological and other stratigraphical techniques. This has resulted in a detailed subdivision of the Plio-Pleistocene, which is often applied as a standard for N.W. Europe. In this paper, this subdivision is used as the Standard to which the proposed biozonation will be correlated. The calibration of the European mammal stratigraphy to the Standard Division is, however, incomplete.

In his Ph. D. thesis, Rutten (1909) presented a review of the Dutch Pleistocene mammals and made a correlation between his faunal units and the then existing subdivision. Van der Vlerk and Florschütz did the same in 1950, utilizing, among others, Schreuder's (1936, 1943) and Bernsen's (1930-1934) studies of Dutch Pleistocene mammals.

Since 1950 the presence of many mammal fossils, including species unknown so far in The Netherlands, has been noticed and described by, amongst others, Hooijer (1959), Kortenbout van der Sluijs (1960), Erdbrink (1972) Freudenthal *et al.* (1976) and Van der Meulen & Zagwijn (1974).

However, the overall correlation between the most up-to-date subdivision of the Pleistocene system and many of the earlier described Dutch fauna-associations, except for the faunas from Tegelen (Freudenthal *et al.*, 1976) and Neede (Hooijer, 1959) and the faunal material from the Brielle borehole (Van der Meulen and Zagwijn, 1974; Suc and Zagwijn, 1983), remained uncertain or unknown. Therefore, it is very difficult to correlate the European Pleistocene mammal "zonations" (Kretzoi (1965), Kretzoi and Pécsi (1979), Fejfar and Heinrich (1981) and Chaline (1976)) which have been established for Central Europe or Western Europe, with the chronostratigraphic Standard Division of the Pleistocene as published, for instance, by Zagwijn (1985). To be able to do so would be very useful in order to correlate those fossiliferous layers that do not yield good pollen-spectra with the Pleistocene chronostratigraphic subdivision. This is especially important for archeological research. Many Paleolithic artefacts are collected from deposits where pollen is lacking, but where fossils of mammals do occur. In this context, the mammal fossils should not be useful only for biostratigraphical correlation, but they can also give information about the climate and the environment in which Paleolithic man lived. The increase in the number of Paleolithic localities in The Netherlands and adjacent countries emphasizes the need for more knowledge of the faunal history during the Middle and Late Pleistocene.

The aim of this study is to contribute towards the fulfilment of this need by investigating, in their geological and stratigraphical context, a number of mammal assemblages from The Netherlands (Neede, Wageningen-Fransche Kamp, Maastricht-Belvédère and Rhenen) and from the Middle Rhine area (Western Germany) (Kärlich, Miesenheim I, Ariendorf and Plaidter-Hummerich); the former are relevant because they are obtained from the area which yielded infor-

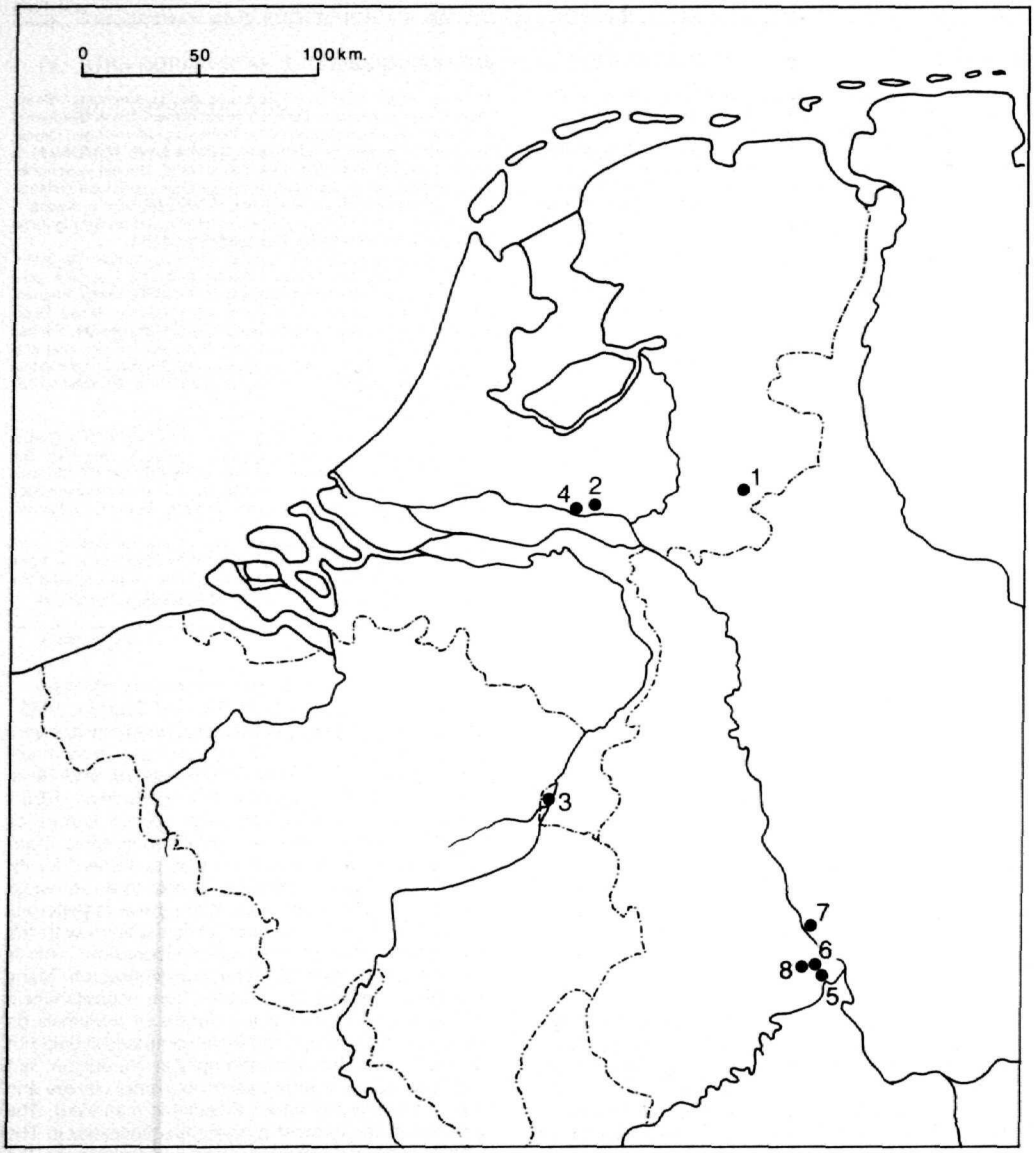


Fig. 1. Geographical position of the localities discussed in this paper. 1 = Neede; 2 = Wageningen - Fransche Kamp; 3 = Maastricht-Belvédère; 4 = Rhenen; 5 = Kärlich; 6 = Miesenheim I; 7 = Ariendorf; 8 = Plaidter-Hummerich.

mation on which the Standard subdivision of the Pleistocene is based, the latter have been included because they supply additional faunistic data.

The first results, from the locality Rhenen, showed that the correlation between the "biozonation" proposed by Von Koenigswald (1973) and the chronostratigraphic subdivision is not quite correct (Van Kolfschoten, 1981). This idea was confirmed later by the results of the investigations of the faunas from the Dutch as well as from the German localities.

The work of Röttger (1986), who studied the living subspecies of the genus *Arvicola*, a genus which plays an important role in the biostratigraphy of the Middle and Late Pleistocene, gives rise to new ideas about the history of *Arvicola* in which migrations prove to play an important role. The paleontological and geological data, obtained from the localities discussed in this paper, supplemented with data ob-

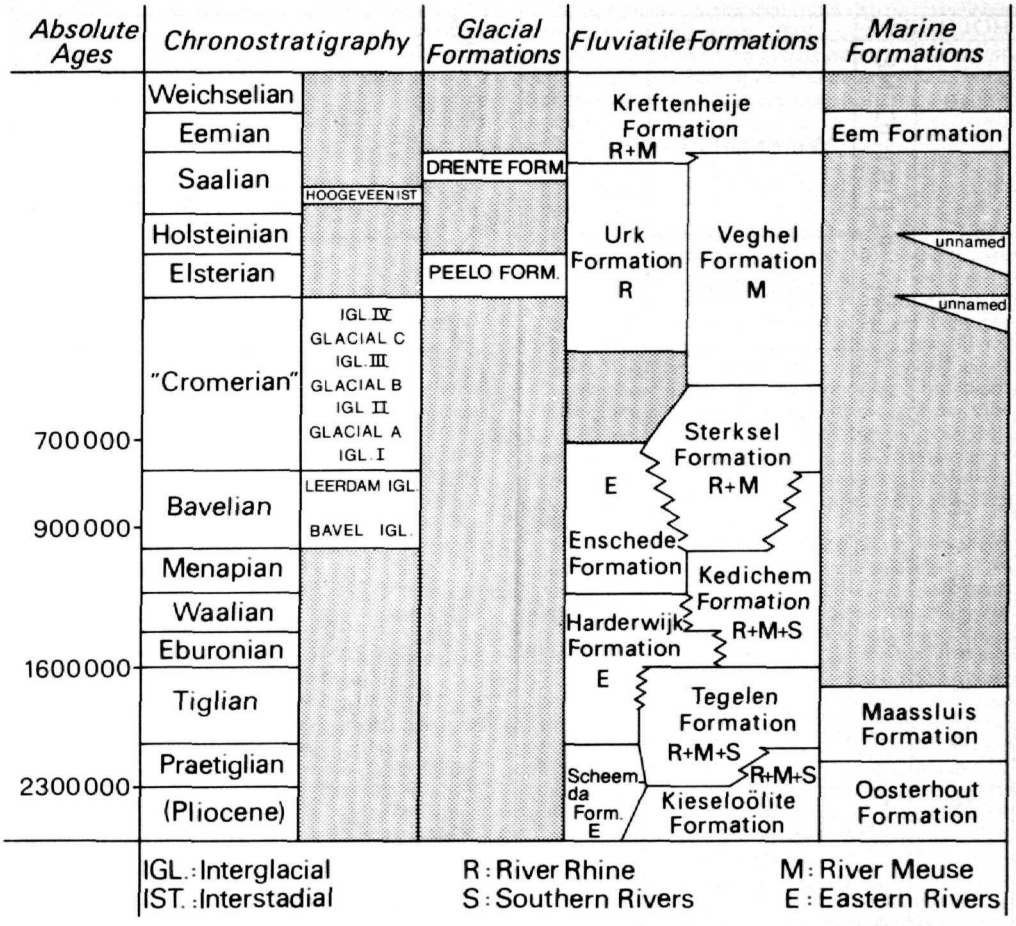


Fig. 2. Chronostratigraphy and lithostratigraphy of the Pleistocene in The Netherlands (after: Zagwijn, 1985).

tained from literature, form the basis of a proposal for the biozonation of the Middle and Late Pleistocene.

Two zones are distinguished: The *Arvicola terrestris cantiana* Range-zone and the *Arvicola terrestris* Partial-range- zone. The former is subdivided into two subzones: The *Arvicola terrestris cantiana* - *Sorex* (*Drepanosorex*) sp. Concurrent-range-subzone and the *Arvicola terrestris cantiana* Partial-range-subzone. The *Arvicola terrestris* Partial-range-zone comprises four groups of faunas of different age, which do not differ in composition so much, that they can be used as the basis for a subdivision of this zone.

In chapter I the geological setting and the stratigraphy of the discussed localities is described in detail because they are relevant for the biostratigraphy and for the correlation between the proposed biozonation and the Dutch Standard Division of the Pleistocene. The geological information is supplemented with a review of the fauna(s) and the description of the paleo-environmental indications obtained from the faunas.

Some of the faunas have already been described and published: Rhenen (Van Kolfschoten, 1981), Maastricht-Belvédère (Van Kolfschoten, 1985), or will be published in the near future: Wageningen - Fransche Kamp (Van Kolfschoten, in press), Ariendorf (Steensma & Van Kolfschoten, in press). Others are still being studied. Therefore, only the mammal fossils from Neede, supplemented with a number of recently collected specimens from Maastricht-Belvédère, are described in chapter II. A number of interesting larger mammal fossils from Rhenen (Kwintelooijen and Leccius de Ridder pits), of unknown stratigraphical provenance and collected in the period after 1981, are described and figured in the appendix.

The taxonomy and evolution of *Arvicola* is discussed in detail in chapter III because of its relevance for the biostratigraphy.

In chapter IV, which deals with the stratigraphical succession of the faunas, a proposal for a new biozo-

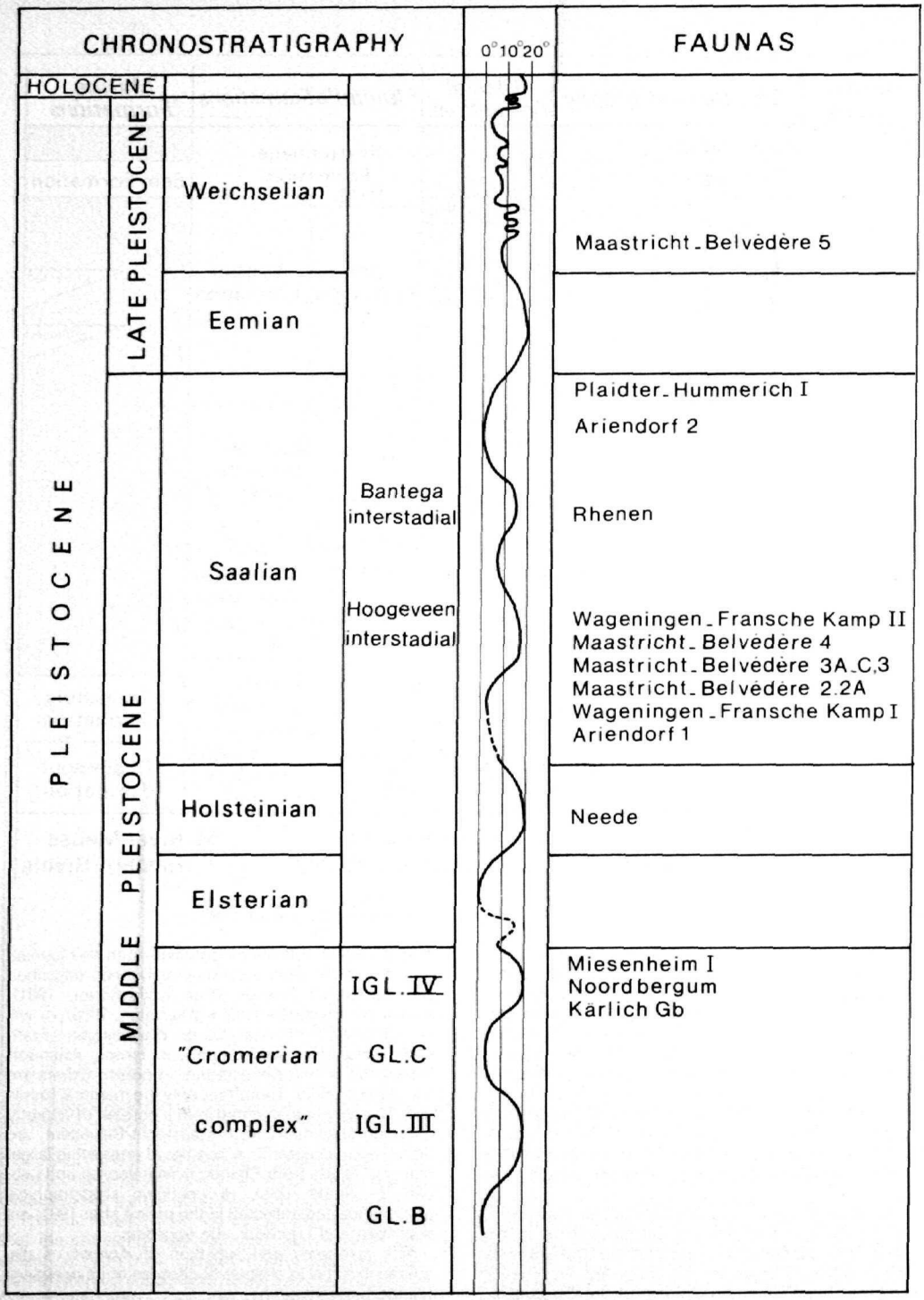


Fig. 3. Chronostratigraphy and the palaeoclimatic curve (estimated mean temperature in July) of the later part of the Quaternary in The Netherlands (from Zagwijn, 1985; slightly modified) and the stratigraphical position of the discussed faunas. IGL.: Interglacial; GL.: Glacial.

nation of the late Middle Pleistocene is presented and discussed. In addition the correlation between the local stratigraphic subdivision of the Middle Rhine Area and the Dutch Standard Division of the Pleistocene is discussed.

I. DESCRIPTION OF THE LOCALITIES AND A REVIEW OF THE FAUNAS

I.1. DUTCH LOCALITIES

I.1.1. Introduction

The mammal faunas from The Netherlands to be considered in this paper are derived from Quaternary deposits exposed in localities which are geographically too far apart (see Fig. 1) to allow a direct and a detailed lithological correlation to be made between them. The faunas from Neede, Wageningen – Fransche Kamp and Rhenen are derived from ice-pushed continental deposits whereas the faunas from Maastricht-Belvédère were obtained from nearly undisturbed fluviatile and loess-like deposits.

The Dutch Quaternary deposits have been grouped in formations (Fig. 2) (Zagwijn & van Staalduinen, 1975) based on their origin, their lithology, their provenance and genesis, and their sediment-petrological characteristics. Correlation of these units with the chronostratigraphical subdivision is based mainly on palynological data.

Part of the fossil material discussed in this paper was collected from deposits assigned to the Urk Formation (material from the localities Neede, Wageningen – Fransche Kamp and part of the material from Rhenen). Deposits assigned to the Veghel Formation yielded the material of the faunas Maastricht-Belvédère 1-4.

Sediments of the Urk Formation were deposited by the river Rhine. The formation consists mainly of coarse sands, sometimes with gravels. Layers of fine sand occur and at certain levels there are clay and peat layers (Doppert *et al.*, 1975). On the basis of its heavy mineral contents the Urk Formation has been subdivided into three zones: the Mixed Mineral Zone (the lowermost one), the Beilen Mineral Zone and the Augite Zone. The Beilen Mineral Zone is correlated with Interglacial IV of the "Cromerian complex" (Zagwijn, 1985; Zandstra, 1981).

The Veghel Formation consists of coarse sands and some gravels deposited by the river Meuse. Clay- and peat-layers occur occasionally (Doppert *et al.*, 1975).

Sediments of the Urk and the Veghel Formation have been deposited during the Middle Pleistocene. The Middle Pleistocene series is, according to Zagwijn (1985), subdivided into a number of stages (see Fig. 3): the "Cromerian complex" with at least four interglacial and three glacial stages; the Elsterian, a glacial stage with probably one cool to temperate phase; the Holsteinian, an interglacial stage; the Saalian, a glacial stage with a temperate phase (the Hoogeveen interstadial) and a cool phase (the Bantega interstadial). The Hoogeveen interstadial could also be classified as an interglacial (Zagwijn, 1985).

The correlation of the faunas with the chronostratigraphical subdivision (Fig. 3) is based on data which are presented and discussed in this chapter and in chapter IV.

I.1.2. Neede

Introduction

The ice-pushed ridge called the Needse Berg, North-northwest of the village of Neede, features a number of abandoned claypits and sand quarries (Fig. 4) which were already in exploitation at the end of the last century. In some of these pits clay, sand and gravelly coarse sand, deposited during the Middle Pleistocene, overlie Miocene-Lower Pliocene sands. On the basis of paleontological data from the Middle Pleistocene clay bed, the Neede Clay, Van der Vlerk and Florschütz (1950) introduced the term Needien, which is a now obsolete name for the Holsteinian Interglacial (Van der Vlerk, 1957). The term Needien is still used by a few authors e.g. Kretzoi and Pecsi (1979).

At the time the pits were still being worked a large number of vertebrate fossils were collected. They consisted mainly of whale vertebrae and shark-teeth, from the underlying marine Miocene deposits. But there are also mammalian fossils which were derived from the Pleistocene deposits exposed in the pits. Part of this material has been described and figured before. Rutten (1909) described fossils of *Cervus elaphus* and the (pre)molar of *Dicerorhinus mercki*. These species are also mentioned by Van der Vlerk & Florschütz (1950). Roding (1953) described and figured molar fragments of *Elephas antiquus*, Hooijer (1959) published the mandibulas of *Trogontherium cuvieri* and Erdbrink (1967) described a femur of *Ursus* cf. *arctos* from Neede.

The Neede Clay is of biostratigraphical interest because it is the only unit in The Netherlands which is reliably correlated to the Holsteinian on the basis of pollen (Van der Vlerk, 1957) and contains a mammal fauna. Unfortunately the mammal material: a) is scattered over various collections; b) does not originate from a single lithostratigraphical unit (see below); c) contains very few small mammals (rodents and insectivores).

Most of the fossils were collected by quarry workers during the last century and the first half of this century. A large number became part of the collection of the late Mr. Ten Bokkel Huinink, who owned some of the pits and quarries. Nowadays the fossils from Neede form part of the collections of a number of museums such as the National Museum of Geology and Mineralogy at Leiden, the Institute of Earth Sciences at Utrecht, the Natural History Museum at Enschede, the museum "Natura Docet" at Denekamp, the collection of the village of Neede and the private collection of Mr. A. Buter from Borne. All the old collections of the Pleistocene material have been re-examined by the author. This has resulted in the recovery of material of a few hitherto unpublished

species (*Equus* sp., *Megaloceros giganteus* and a large bovid). Only those fossils with a clear stratigraphical range which are derived from the Neede Clay will be described in Chapter II.

Field trips, to collect smaller mammals, were organized in 1985 and 1986 and resulted in the recovery of the Neede Clay in the most southerly pit called "Weeskes Gaete" (Fig. 4). The pit is overgrown by plants which cover the originally exposed layers. With the assistance of the Geological Survey of The Netherlands, we were able to locate the clay in the south-western corner of the pit. The clay is overlain by gravelly and sandy deposits. The clay layer is at least two metres thick. A sample of about 2.5 tons of sediment was taken in this corner. The sample yielded only a small number of badly preserved, decalcified molars of *Apodemus* sp. and enamel fragments of *Clethrionomys* cf. *glareolus*, *Arvicola terrestris cantiana* and Microtini.

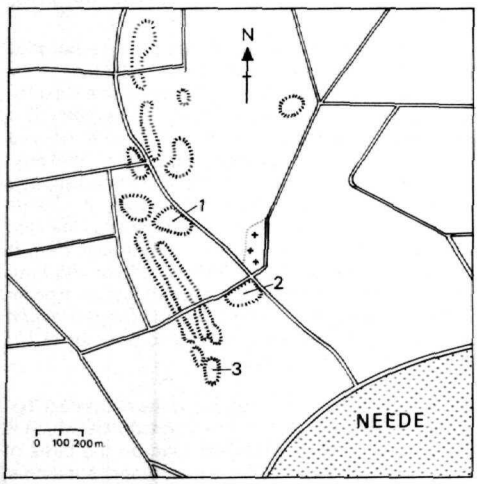


Fig. 4. Location of the abandoned claypits and quarries North-northwest of the village of Neede. 1: the type locality of the Needian; 2: the sand quarry of the firm Ordelman; 3: the Weeskes Gaete pit.

A second sample of about 1 ton of clay was taken from a depth of about 1 metre below the bottom of the pit, 20 metres north of the former sampling locality. This sample contained better preserved material of *Arvicola terrestris cantiana* and *Sorex* cf. *araneus* and a higher concentration of molluscs than the first sample.

The differences between the two samples are considered to be due to chance, since the concentration of the fossils is very low at each sampling site. The two assemblages are therefore treated as a whole.

Geological setting and stratigraphy

The claypits and sandpits of Neede are located in an ice-pushed ridge formed by inland ice during the Saalian Glacial Stage. The western part of the ridge consists of a number of thrust sheets caused by glaciotectonics. These sheets are covered partly with till (Drente Formation) and Weichselian slope deposits of the Twente Formation. The thrust sheets have a north-south directed strike. In these glaciotectonic units the following two formations are distinguished (Van de Meene and Van Houten, 1983; Van de Meene, 1985; pers. comm., 1986) starting from below these are:

– fine and very fine marine sands of the Breda Formation (Miocene and Early Pliocene). These sands yielded a great number of vertebrae of Cetaceae and shark teeth.

– 5 – 10 metres of coarse sands and gravelly coarse sands overlain by the Neede Clay (0.5 – 6 metres thick). These two subunits are of fluvial and lacustrine origin respectively and are assigned to the Urk Formation. Their heavy mineral assemblage contains a high percentage of the volcanic mineral augite, which indicates that these sediments were not deposited before Glacial C of the "Cromerian complex" (Zandstra, 1981). The vertebrate fossils described in this paper are derived from the upper part of this unit, the Neede Clay.

So far no fluvioglacial or till deposits have been recognized in the ice-pushed ridge of Neede.

In addition to the two subunits of the Urk Formation mentioned above, Van der Vlerk and Florschütz (1950) describe "fluviatile sands on top of the Neede Clay". According to Van de Meene (the regional geologist) however, the sands on top of the clay belong to the sandy subunit of the Urk Formation and their position on top of the Neede Clay is due to glaciotectonic overthrusting. The stratigraphy proposed by Van de Meene is not generally accepted (Zandstra, pers. comm., 1986).

Most of the faunal material from Neede was obtained from the Neede Clay, the type deposits of the Dutch "Needien", a name which was abandoned in favour of the terms Holsteinian and Hoxnian (Van der Vlerk, 1957).

Van de Vlerk and Florschütz (1953) published a pollen-diagram of the "Needien" from the type locality, the Ten Bokkel Huinink pit (pit III in Fig. 4). *Abies* is well represented in the diagram, and therefore the clay can be referred to pollen-zone 3 of the Holsteinian (De Jong, pers. comm., 1987). This implies that the sandy deposits below the Neede Clay might have a Holsteinian age but they can also be older.

The clay in Weeskes Gaete pit with the smaller mammals is Holsteinian in age too (De Jong, 1987). It cannot be correlated with a particular pollen-zone because the information obtained up to now is too poor. The Neede Clay which yielded the mammal fauna belongs to the *Arvicola terrestris cantiana* Partial-range-subzone.

The material of two species, *"Elephas antiquus"* and *Ursus* cf. *arctos*, was found in a sandy unit of the Urk Formation.

The fauna from Neede

Because not all the fossils were obtained from the clay-layer the fossils from Neede do not necessarily belong to a single faunal unit, although Van der Vlerk and Florschütz (1950) and Hooijer (1959) suggested they did. The molar fragments which are assigned to *Elephas antiquus* by Roding (1953) and the femur of the bear *Ursus* cf. *arctos* come from sandy deposits, the lithostratigraphical provenance of some specimens, such as the antler fragment of *Megaloceros giganteus* and the phalange of the large bovid, is unknown.

The molar fragments of the elephant show some of the characteristics of *Elephas antiquus*. A side view of one of the fragments shows that the plates are very strongly bent antero – posteriorly. This character occurs rather frequently in the lower molars of *Elephas antiquus* (for instance in the molar from Rhenen (Van Kolfschoten, 1981) and the molars from Maastricht-Belvédère (Van Kolfschoten, 1985)) and is absent or less well developed in molars of *Mammuthus primigenius* or related species. However, one of the fragments from Neede is rather brachiodont and corresponds in this respect more to molars of the Early Pleistocene *Mammuthus meridionalis*. It is therefore not clear whether the molar fragments belonged to *E. antiquus* or to *M. meridionalis*.

The majority of the material has been collected from the Neede Clay. Rutten (1909) explicitly states that the (pre)molar of *Dicerorhinus mercki* was found in the Neede Clay. The clay attached to the metatarsus of the horse *Equus* sp. and to the lower premolar (p4) and some bones of the red deer *Cervus elaphus* and the type of preservation of the mandibulars of *Trogontherium cuvieri* indicate that it is very likely that this material, as well as the pharyngeal teeth of carp – like fish (Cyprinidae) and the smaller mammal fossils, was derived from the clay.

The list of the species collected with certainty from the Neede Clay is:

Pisces Cyprinidae

Mammalia
- Insectivora
  - *Sorex* cf. *araneus*
- Rodentia
  - *Trogontherium cuvieri*
  - *Clethrionomys* cf. *glareolus*
  - *Arvicola terrestris cantiana*
  - Microtini indet.
  - *Apodemus* sp.
- Perissodactyla
  - *Equus sp.*
  - *Dicerorhinus mercki*
- Artiodactyla
  - *Cervus elaphus*

Remarks

The most common species are *Clethrionomys* cf. *glareolus*, *Arvicola terrestris cantiana* and *Cervus elaphus*.

The fauna is assigned to the *Arvicola terrestris cantiana* Partial-range-zone because of the occurrence of *A. terrestris cantiana* and the absence of *Sorex* (*Drepanosorex*) sp. and *Pliomys* sp. (see Chapter IV).

A systematic description of the mammal fossils from the Neede Clay will be given in the next chapter.

Paleo-environmental and paleo-climatological interpretations of the fauna-association

Clethrionomys glareolus prefers a wooded environment. *Trogontherium cuvieri* and *Arvicola terrestris cantiana* are considered to be dependent on the presence of water. Living European Microtini live in an open environment. *Sorex araneus* has a wide range of habitats.

Dicerorhinus mercki has been found most frequently in association with species which prefer a wooded environment such as deer. However, it is also found together with the woolly mammoth, bison and horses (Guérin, 1980). *Cervus elaphus* prefers a wooded environment but is also found in other habitats (Van den Brink, 1978).

The faunal association points to the occurrence of forest alternating with some open areas and interglacial or interstadial conditions during the deposition of the clay.

A pollen diagram of the Neede Clay exposed in one of the pits of Ten Bokkel Huinink (probably Pit 1, see Fig. 4) shows the predominance of *Alnus* and *Pinus*; *Picea* and *Abies* are well represented (Van der Vlerk and Florschütz, 1953) . The pollen diagram points to interglacial conditions.

The mollusc association from the Neede Clay in the old collection of the Institute of Earth Sciences, Utrecht likewise indicates interglacial conditions and a lacustrine environment. Land molluscs are hardly represented in this collection (Meijer, pers. comm., 1987). They are, however, dominant in the assemblage from the second (northern) locality in the Weeskes Gaete pit, and point to a different sub-environment than the one discussed above. The assemblage indicates interglacial conditions and a mainly wooded environment (Meijer, pers. comm., 1987), a conclusion that fits very well with the mammal assemblage.

I.1.3. Wageningen – Fransche Kamp

Introduction

The discovery of a number of molluscs in the sandpit "Fransche Kamp" at Wageningen by Dr. C.J.H. Franssen (Bennekom) in 1983 led to the investigations of the sediments exposed in this pit. The pit is still being worked.

The loam and clay layer at the top of Unit 3 (see below), containing the molluscs, is exposed in the pit at several places. A sample of about 3 tons of clay was taken at the most westerly outcrop of this particular layer (Fig. 5). This sample yielded about 650 identifiable vertebrate fossils (mainly mammals) and a large molluscan fauna. The mammals are described in this paper, together with an incomplete molar of an ele-

phant, found by Mr. G.H.J. Ruegg (Geological Survey Haarlem) also in sediments of Unit 3.

A number of Middle Paleolithic artefacts have been collected in the sandpit. The geological provenance of these finds is unknown, they too are derived most probably from Unit 3 (Rensink & Spieksma, 1987).

Geological setting and stratigraphy

The sand quarry Fransche Kamp is located in the highest part of the ice-pushed ridge situated to the east of Lunteren-Ede-Wageningen, east of the Gelderse Vallei (see Fig. 6). The ridge was formed during the Saalian.

In the pit five (in)complete thrust sheets are exposed. Ruegg (1987) recognizes in the most complete sheet five successive lithostratigraphical units, which from bottom to top are:

Unit 1: greenish-brown and light brown-orange fine and coarse fluviatile sands of the Sterksel Formation. 65-95% of the heavy mineral association consists of instable minerals such as garnet and epidote. The unit is less than 10 metres thick.

Unit 2: greenish-brown fine and coarse fluviatile sands locally with some gravel, about 4 metres thick. The heavy mineral assemblage contains a relatively high percentage of hornblende. This unit is the lower of the three exposed units assigned to the Urk Formation.

Unit 3: gravels and gravelly, coarse sands overlain by 5 metres of sand, loam and clay deposits. The base consists of only one layer of stones with coarse gravel and small stones, from which the elephant molar was collected. The heavy mineral assemblage of the lower part of this unit in particular contains the volcanic mineral augite. Molluscs are present throughout. In some thrust sheets the top of Unit 3 consists of a loam/clay layer which may attain a thickness of more than 1 metre. The smaller mammals were collected from this layer. The whole unit, which has a fluvial origin, may be 10-15 metres thick. It is the middle unit which has been assigned to the Urk Formation.



Fig. 5. Wageningen - Fransche Kamp: View of the northwestern section of the pit. The arrow indicates the location where the samples were taken.

Unit 4: a unit of fluvial origin (4 – 6 metres thick) of brownish gravels, gravelly sands and coarse sands, with a fining upwards tendency. Near the base the unit contains coarse gravel and boulders (the latter especially at the base), a number of which are cracked. The heavy mineral association contains a high percentage of augite. This is the upper unit of the Urk Formation.

The transition from Unit 4 to Unit 5 seems to be more or less gradual.

Unit 5: a few metres to more than 10 metres of light brown, evenly laminated to low-angle laminated sands without gravel. The heavy mineral association is mainly unstable and contains a low percentage of augite. These sediments are considered to be sandr-deposits and are assigned to the Drente Formation.

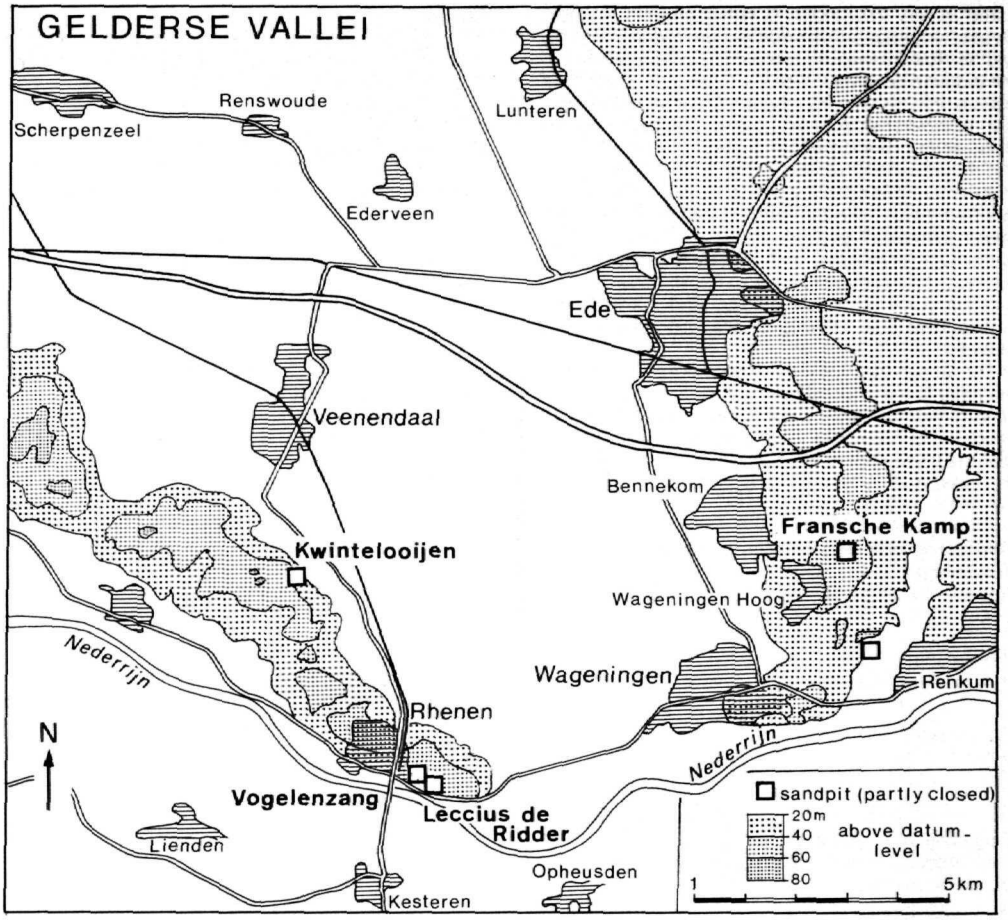


Fig. 6. Geographical position of the Kwintelooijen pits, Vogelenzang, Leccius de Ridder and Wageningen - Fransche Kamp.

All the fossil material has been collected from sediments assigned to Unit 3. This unit contains a high percentage of the mineral augite which indicates that Unit 3 was probably deposited after Interglacial III of the "Cromerian complex". On the other hand deposition must have taken place before stadial III of the Saalian, since the sediments have been pushed by the Saalian inland ice.

Molluscs are obtained from the same layer as the smaller mammal fossils. The molluscs point to deposition during an interglacial period but do not give precise stratigraphical information (Meijer, 1981).

The clay layer at the top of Unit 3 yielded not only faunal remains but also pollen. According to De Jong (pers. comm., 1987) the following remarks can be made. The pollen-diagram indicates interglacial conditions. It shows a dominance of *Pinus* and the presence of *Picea* and notably a great deal of *Tilia* and *Ulmus*. *Abies* and *Alnus* are present in a very low percentage. The clay also contains some Early Pleistocene relicts such as *Tsuga*. These have probably been reworked. The composition of the diagram indicates that we are dealing with the earliest part of a warm phase.

The pollen diagram differs in some respects from the diagrams known from the Saalian Hoogeveen Interstadial published by Zagwijn (1973). *Abies* is quite unknown from that interval. However, the *Abies* pollen in Unit 3 might be reworked. Furthermore the percentages of *Tilia* and *Ulmus* in the pollen diagram from Fransche Kamp are much higher than those in the Hoogeveen-Interstadial diagrams. Even during the climatic optimum of that interval *Ulmus* and *Tilia* only occur in a low percentage.

The pollen diagram of Fransche Kamp indicates interglacial rather than interstadial conditions. However, it cannot simply be referred to the Holsteinian Interglacial. The percentage of *Alnus* in the Fransche

Kamp is very low. *Abies* is either absent, or rarely present whereas in the Holsteinian pollen-zones 2b and 3a *Abies* is well represented. *Taxus* is lacking in the diagram of Wageningen – Fransche Kamp, but is present in the clay from borehole Gelzelaar (Holsteinian pollen-zones 2b and 3a) and is absent from the Holsteinian pollen-zone 2a (Zagwijn, 1973).

In summary it is concluded that the faunal assemblages from Unit 3 postdate Interglacial III of the "Cromerian complex" because the unit contains a high percentage of Augite, and predate the late Saalian because the sediments have been pushed by the Saalian inland ice. The palynological and malacological data do not give more precise stratigraphical information.

The upper part Unit 3 which yielded the smaller mammal fauna is placed in the lower part of the *Arvicola terrestris* Partial-range-zone (see Chapter IV) which is correlated to the Early Saalian. This indicates that the palynological knowledge about the Early Saalian was, until recently, not complete.

The faunas from Wageningen – Fransche Kamp

Wageningen – Fransche Kamp I

A single specimen has been collected from the base of Unit 3.

Proboscidea
Mammuthus primigenius

Wageningen – Fransche Kamp II

The following fauna has been collected from the upper part of Unit 3.

Pisces
Cyprinidae
Esocidae *Esox lucius*

Aves
Passeriformes indet.

Mammalia		Number of specimens		min. no. of individuals
Insectivora				
Sorex araneus	154	25.75%	15	19.74%
Crocidura sp.	4	0.67%	1	1.32%
Rodentia				
Eliomys quercinus	11	1.84%	2	2.63%
Clethrionomys glareolus	164	27.42%	17	22.37%
Arvicola terrestris ssp. A	10	1.67%	2	2.63%
Microtis agrestis	1	0.17%	1	1.32%
Microtus arvalis and/or				
Microtus agrestis	19	3.18%	5	6.58%
Apodemus sylvaticus	223	37.29%	29	38.16%
Apodemus maastrichtiensis	12	2.01%	4	5.26%
	598	100.00%	76	100.01%

Remarks

Amongst the fossils of Fauna II there are pharyngeal teeth of carp-like fish (Cyprinidae), dental teeth of the pike, *Esox lucius* Linnaeus, 1758 and some bones of frogs. A small distal part of an ulna could be identified by Dr. P. Weesie, Utrecht, as a fossil of a perching bird (Passeriformes).

The fauna is correlated to the *Arvicola terrestris* Partial-range-zone because of the occurrence of *A. terrestris* ssp. A (see Chapter IV).

The fossils are described in a paper on the mammal fauna from Wageningen – Fransche Kamp (Van Kolfschoten, in press).

Paleo-environmental and paleo-climatological interpretations of the fauna-associations

Wageningen – Fransche Kamp I

Mammuthus primigenius is very often associated with species such as the woolly rhino *Coelodonta antiquitatis*, the bison *Bison priscus* and the reindeer *Rangifer tarandus* all of which prefer a cold climate and open areas (tundra and steppe).

The presence of *Mammuthus primigenius* in the gravels suggests that at the time of the deposition of the gravels at the base of Unit 3 the climate was cold.

Wageningen – Fransche Kamp II

Two species which are very common in the small mammalian fauna from Fransche Kamp Unit 3: *Clethrionomys glareolus* and *Apodemus sylvaticus* point to the presence of woods. The other abundant species

Sorex araneus has a wide range of habitats. *Eliomys quercinus* prefers to live in deciduous and mixed forests. The living water voles in Western Europe, *Arvicola terrestris terrestris* and *A. t. sherman*, are more or less aquatic.

The presence of open areas is indicated by *Microtus agrestis* and/or *Microtus arvalis*. The habitat of *M. arvalis* is open country such as pasture-land. *M. agrestis* prefers moist areas such as high rough pastures and peat-moors.

The composition of the fauna, notably the relative frequency of *Clethrionomys glareolus* and *Apodemus* as compared to *Microtus*, indicates a predominance of woods alternating with some open areas. The presence of the garden dormouse *Eliomys quercinus* and *Crocidura* sp. leads us to the conclusion that the climatic conditions during the deposition of the clay were like those of today, probably even a little warmer.

The pollen and the molluscan fauna from the same clay layer support this interpretation. The pollen association points to interglacial conditions and a wooded environment and, because of the low percentage of *Alnus*, to rather a dry environment (De Jong, pers. comm., 1987).

The mollusc assemblage from the clay layer is characterized by the dominant occurrence of woodland species (*Cepeae nemoralis, Discus rotundatus* and *Clausilia* cf. *lineolata*). The fresh-water species are represented by *Bithynia tentaculata, Segmentina nitida* and *Corbicula fluminalis*. The mollusc association is characteristic for a mainly forested environment and interglacial conditions (Meijer, 1981).

Briefly one can say that the loam and clay of Unit 3, yielding the smaller mammal fossils, can be considered as overbank deposits of a meandering river system. The banks of the river are covered with forest; open areas occurred at larger distances from the river.

I.1.4. Maastricht – Belvédère

Introduction

The Maastricht-Belvédère loess – and gravel pit is located N.W. of the city of Maastricht (Fig. 7). After W.M. Felder (Geological Survey of The Netherlands, Heerlen) had discovered a paleolithic artefact in one of the loess-sections in this pit, an intensive archeological investigation began. Due to the work of Mr. K. Groenendijk and Mr. J.P. de Warrimont who investigated the sections exposed in the Maastricht-Belvédère pit very intensively and due to the archeological excavations, organized by the Institute of Prehistory, Leiden University conducted by Mr. W. Roebroeks, a large number of mammal fossils have been collected.

The Maastricht-Belvédère research, started as an archeological project, developed into a project involving several disciplines. A review of the results has been published (Van Kolfschoten and Roebroeks eds., 1985).

Large mammal fossils from this pit had already been described by Rutten (1909) and Cremers (1925 and 1926). The old collections have been re-examined; some of the fossils of which the stratigraphical provenance was known with certainty have been described together with material collected from different levels and several sites in the pit, in the period 1980 – 1984 (Van Kolfschoten, 1985). Five different mammal faunas (M-B 1 – 5) have been recognized. In this paper these faunas are reviewed, and provisional faunal lists of the material collected by Groenendijk and De Warrimont in 1985, 1986 and 1987 are given. This material will be described in more detail in a separate paper concerning these faunas in the near future.

Geological setting and stratigraphy

The large Maastricht-Belvédère loess- and gravel pit is located on the left bank of the River Maas (Fig. 7), at the edge of the Caberg Middle Terrace. In this pit mainly Quaternary deposits are exposed. The lower part of these deposits has a fluvial origin, the upper part is aeolian. The base of the Quaternary deposits is irregular due to karstic features and/or erosion. A detailed description of the lithostratigraphy of the sediments exposed in the pit is presented by Vandenberghe *et al.* (1985). However, intensive geological

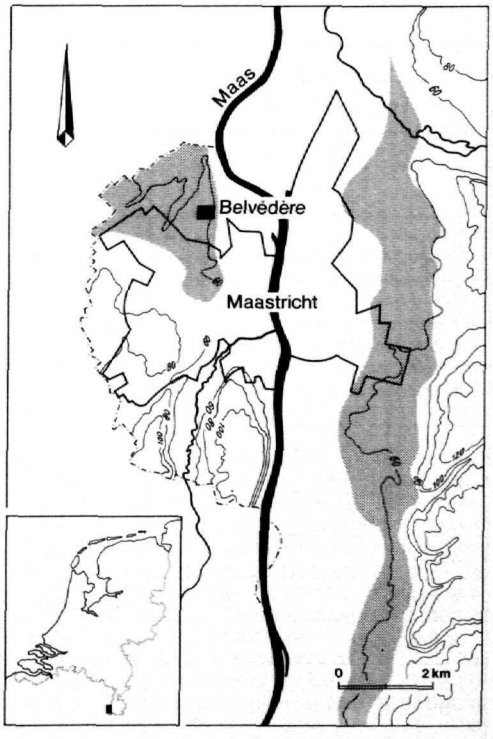


Fig. 7. Location of the Maastricht-Belvédère pit; the grey areas show the distribution of the Caberg Middle Terrace sediments (after: Brueren, 1945; from Vandenberghe *et al.*, 1985).

fieldwork by J. Vandenberghe, K. Groenendijk and J.P. de Warrimont in the period 1985 – 1988 has revealed the existence of a more complex sedimentological system. This has resulted in a modification of the framework presented by Vandenberghe *et al.* (1985).

Seven lithological units are distinguished; some of these units are subdivided into subunits. The characteristics of the lithological (sub)units (after Vandenberghe, Groenendijk, De Warrimont and Roebroeks, pers. comm., 1988; Vandenberghe *et al.*, 1985) can be summarized as follows:

Unit 1: Paleocene chalk deposits of the Houthem Formation forming the subsoil of the pit;

Unit 2: Oligocene clayey sands which locally cover the chalk deposits;

Unit 3: Terrace gravels (up to 7 metres thick): heterogeneous, laminated gravels with lenses of fine to coarse, gravelly sands;

Unit 4: Terrace sands (0.5 – 1.5 metres thick): greyish-white to light greenish sands, with intercalated pebble horizons;

Unit 5: Loams (2-3 metres thick) generally showing a fining upwards sequence from the base (Subunit 5.1) to the top (Subunit 5.2);

Unit 6: Silts and silty loams up to 3 metres thick.

Unit 7: a well-sorted silty loam (up to about 6 metres thick) with at the top phenomena of the Holocene soil formation.

The spatial relationships between the distinguished (sub)units of the Quaternary deposits is presented in figures 8 and 9.

The lateral and vertical transition between the lithological (sub)units can be gradual. But some boundaries (i.e. between 5.1 and 5.2; between 4.5.1 and 4.5.2; between 4.5.2 and 4.5.3) are occasionally marked by an erosional level, which is often characterized by the occurrence of sandy layers or the occurrence of pebbles and cobbles.

Lithostratigraphical units are defined because it is confusing to use the lithological (sub)units to indicate the provenance of artefacts and fossils. Figure 8 shows the grouping of the lithologic in the lithostratigraphic units; the latter are indicated with Roman numerals.

Sediments of Unit 3 were deposited in the central part of a braided river system, while the Subunits 4.1, 4.2

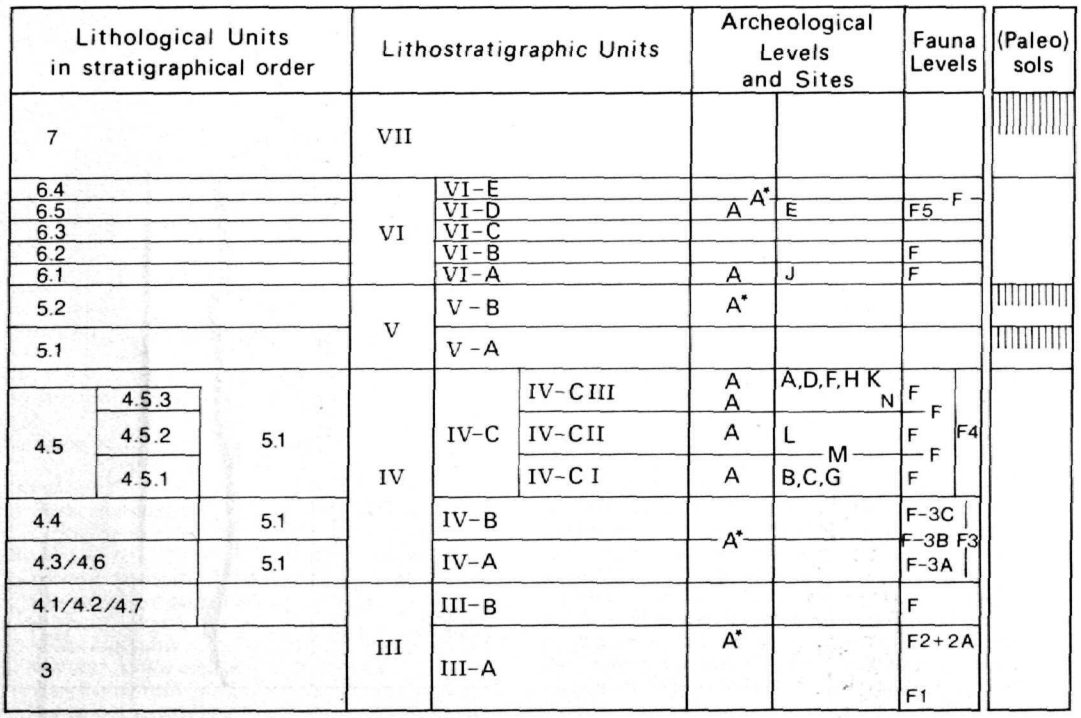


Fig. 8. The stratigraphical relation between the lithologic and lithostratigraphic (sub)units exposed in the Maastricht-Belvédère quarry and the stratigraphical position of the various archeological and faunal levels and the (paleo)sols.

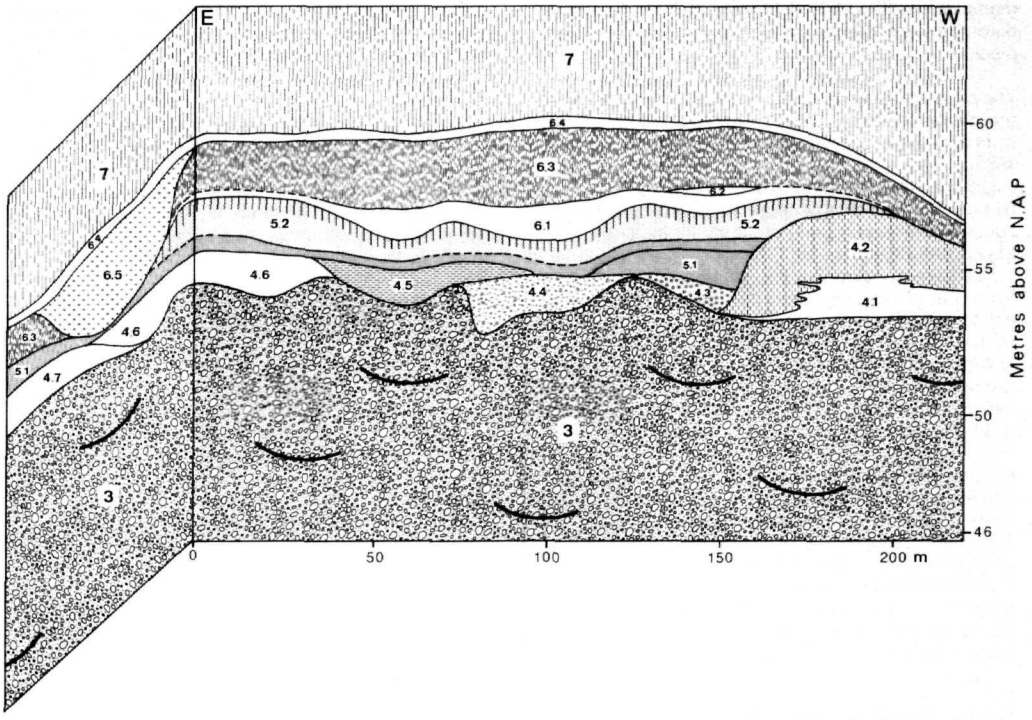


Fig. 9. Schematic drawing of a section exposed in the Maastricht-Belvédère quarry during the summer of 1987 (made by: Edelman and Mommersteeg, Institute of Earth Sciences, Free University Amsterdam). For information about the lithology of the different (sub)units the reader is referred to the text of this paper.

and 4.7 were formed at the margins. The lithological units 4.3, 4.6 and 4.4 also have a fluviatile origin; they are deposited in shallow channels on each side of the main stream of the river. Unit 4.5 is formed in a so-called "backswamp"-like environment and Unit 5.1 is regarded as overbank deposits of a large river system. Unit 5.2 bears a striking resemblance to aeolian loess deposits.

However, micromorphological research (Mücher, 1985) has indicated that the sediment consists of fluviatile deposits and redeposited loess and possibly also with loess in situ. Unit 6 is a loess-derived deposit, reworked by overland flow whereas Unit 7 has a pure aeolian genesis.

Periglacial features such as cryoturbation occur mainly in the lithostratigraphical units III and V-A. Ice-wedges have been observed in sediments assigned to the lithological units 3, 4.1 and 4.7 but minor cryoturbations and ice-wedges also occur in Unit 4.6.

The remnants of two palaeosols are present in the Quaternary sequence; one in the top of Unit V-A and one in the top of Unit V-B (see Fig. 8).

The fluvial Units III and IV belong to the Caberg-Middle Terrace deposits and form part of the Veghel Formation. Paulissen (1973) correlates the gravels of Unit III-A with the Saalian because of the position of the Caberg Terrace within the Maas-terrace sequence. The soil remnants at the top of Unit V-B have been correlated with the Eemian Rocourt palaeosol (Vandenberghe *et al.*, 1985). The calcareous silts of Unit VI-E have been correlated with the so called "Nagelbeek" horizon which according to Haesaerts *et al.* (1981) has an age of ca. 20 ka..

Analysis of heavy minerals in the Unit VI-D deposits indicates that sedimentation of this unit took place during the Middle Weichselian (Meijs, 1985). However, the occurrence of Middle Palaeolithic artefacts (Roebroeks, 1985) and relatively primitive faunal elements (for instance the evolutionary stage of *Dicrostonyx torquatus*)(Van Kolfschoten, 1985) in beds of VI-D indicate a correlation with an earlier part of the Weichselian (see Chapter IV).

The channel filled by sediments of Unit VI-D has cut through the sediments of the Units V-B, VI-A, VI-B and VI-C. This might imply that M-B 5 consists of redeposited fossils from Units VI-A or VI-B. That would explain the unsolved contradiction between the age determinations of Unit VI-D. However, the fact that several flint artefacts from site E could be refitted, and the excellent state of preservation of the

mammal fossils (Van Kolfschoten, 1985) indicate that hardly any transportation of the material has taken place.

The molluscan fauna from Unit IV is to be assigned to the Saalian (Meijer, 1985). The malacological data from Unit VI-D are not suitable for dating (Kuijper, 1985).

Unfortunately these correlations cannot be verified by palynological data because no pollen-bearing horizont has yet been found in the section exposed in the Maastricht-Belvédère pit.

Thermoluminescence (TL) dating of burnt flints from Unit IV-C and Electron Spin Resonance (E.S.R.) dating of molluscs from the same unit yielded absolute dates of 270 ka $\pm 11/\pm 22$ (Ox TL 712k) (Huxtable & Aitken, 1985) and 220 ± 40 ka respectively (Grün & Katzenberg (Köln) pers. comm., 1985). TL dating of sediments of Unit VII indicate an average age of 17.5 ± 3.5 ka (Huxtable and Aitken, 1985).

In summary it is concluded that, on the basis of the above given data the mammal fossils deriving from Units 3 – 7 should have a post-Holsteinian age. M-B 5 has a Weichselian age whereas the other faunas date from the Saalian. These correlations are confirmed by the mammal faunas. The Units III and IV are assigned to the lower part of the *Arvicola terrestris* Partial-range-zone, Unit VI-D to the upper part of the same zone (see also Chapter IV).

The mammal faunas from Maastricht-Belvédère

Nearly all the different lithostratigraphical units yielded fossil material (see Fig. 8) in varying quantities. Generally, the material is rather badly preserved, due to weathering. Especially the larger mammal fossils are very often difficult to identify. The oldest fauna-association (M-B 1) comes from the base of the gravels of Unit III. The most recent material (not regarding the Holocene (sub)fossils from the top layer) was obtained from the base of Unit VII. However, these fossils are so badly preserved that identification is impossible.

The faunas M-B 1, 2, 3, 4 and 5 have been described in detail in van Kolfschoten (1985). New information on these faunas is presented in the remarks on the faunas; some fossils, collected in the years after 1984, will be described in detail in Chapter II.

The recently collected faunas (M-B 2A, 3A, 3B (partly) and 3C) and some isolated finds are mentioned only briefly in this paper.

Maastricht-Belvédère 1

Provenance: the base of Unit III
Faunal list:
Elephas antiquus
(Hippopotamus sp.)

Remarks

The remains of both species were found a long time ago. Cremers (1926) mentioned a molar of *E. antiquus* collected from the base of the gravel in the Maastricht-Belvédère pit. Whether or not *Hippopotamus* has been found is uncertain. Habets (1887) published a report mentioning the recovery, in gravels of the Caberg – Terrace, of *Hippopotamus* fossils consisting of a number of fragments of tusks (canines?), teeth and some molars However, these specimens have been lost for many years (Rutten, 1909).

The stratigraphical position of this fauna is not clear. It might date from the late Early Pleistocene or early Middle Pleistocene.

Maastricht – Belvédère 2

Provenance: the upper 3 metres of Unit III-A
Faunal list:
Mammuthus primigenius
Equus sp.
Coelodonta antiquitatis
Cervus elaphus

Remarks

A nearly complete curved and spirally twisted tusk (about 3 metres long) of *M. primigenius* and some molar fragments from the same species were collected from the gravels in 1985 and 1986. From the same stratigraphical horizon an upper molar of the woolly rhinoceros (*Coelodonta antiquitatis*) and two premolars of a large, robust horse (*Equus* sp.) were obtained (see Chapter II).

The occurrence of *Mammuthus primigenius* and *Coelodonta antiquitatis* indicate that this fauna should be correlated to the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

Maastricht – Belvédère 2A

Provenance: a small lens of coarse sand, intercalated in the coarse gravels of Unit III-A, about 0.5 – 1 metre below the top of the gravel
Faunal list:
Pisces
  Esox lucius
Mammalia
  Insectivora
    Neomys cf. *fodiens*
  Rodentia
    Spermophilus cf. *undulatus*
    Lemmus lemmus
    Clethrionomys sp.
    Arvicola sp.
    Microtus arvalis
  Perissodactyla
    cf. *Coelodonta antiquitatis*

Remarks

The smaller mammal species, except for *Microtus arvalis*, are represented by one or two elements.

A rooted, small m^3 indicates the presence of *Clethrionomys* sp. A specific determination cannot be made on the basis of this single molar. The *Arvicola* remains are poor and are badly preserved. The genus

Microtus is represented by 27 (in)complete molars. The two m1 have a morphology resembling that of the living *Microtus arvalis* and *M. agrestis*. The five M1 and the single M2 have the *M. arvalis* morphology.

The presence of cf. *Coelodonta antiquitatis* in this fauna is indicated by small upper molar fragments with enamel about 2 mm thick and with a shape characteristic for upper molars of Rhinocerotidae. The enamel looks leathery. Therefore the material is assigned to cf. *Coelodonta antiquitatis* and not to *Dicerorhinus mercki* or *D. hemitoechus*, which have molars with smoother enamel.

The fauna represents an association of the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

Equus sp.
Provenance: Unit III-B (lithologically: Unit 4.2)

Recently a metatarsus dext. (Fig. 25.1) of a large and robust horse (*Equus* sp.) was collected from this layer. For more detailed information on this fossil the reader is referred to the systematic description of the material.

Maastricht – Belvédère 3
Provenance: Units IV-A and IV-B
Faunal list:

Pisces
Leuciscus celaphus
Chondrostoma nasus

Mammalia
Insectivora
Talpa europaea
Sorex araneus
Neomys fodiens
Lagomorpha
Ochotona pusilla
Rodentia
Spermophilus cf. *undulatus*
Cricetus cricetus praeglacialis
Clethrionomys glareolus
Arvicola terrestris ssp. A
Microtus gregalis
Microtus arvalis and/or *Microtus agrestis*
Microtus sp.
Apodemus sylvaticus
Apodemus maastrichtiensis

Remarks
The list of the fauna Maastricht-Belvédère 3 as published before (Van Kolfschoten, 1985) is based on a compilation of 5 small assemblages, obtained from layers which are nowadays correlated with the Units IV-A and IV-B (and maybe Unit IV-C). The composite fauna is rather small (105 specimens).

Most of the material assigned to M-B 3 was derived from the transition from Unit IV-A to Unit IV-B and can be correlated to the recently discovered fauna M-B 3B. A small collection formerly asssigned to M-B 3, with e.g. a mandibula of *Neomys fodiens* and some Microtine molars, was collected from Unit IV-A and has about the same age as fauna M-B 3A.

Apodemus sylvaticus and *A. maastrichtiensis* do not occur in the faunas M-B 3A and M-B 3B. The absence indicates that the *Apodemus* molars of fauna M-B 3 might have been collected from a stratigraphically higher level than those from which the faunas M-B 3A and 3B were obtained.

The Units IV-A and IV-B are assigned to the *Arvicola terrestris* Partial-range-zone because of the occurrence of *A. terrestris* ssp. A in M-B 3 (see Chapter IV).

Maastricht – Belvédère 3A
Provenance: Unit IV – A
Faunal list:

Mammalia
Rodentia
Spermophilus cf. *undulatus*
Lemmus lemmus
Arvicola terrestris
Microtus arvalis
Microtus gregalis
Carnivora
Mustela cf. *nivalis*

Remarks
The fossils are badly preserved and rather fragmentary. Most abundant (> 40 specimens) is *Microtus*, represented by two species, *M. arvalis* and *M. gregalis*. The other species are rare (1-3 specimens). The absence of Insectivora and Muridae is remarkable.

The composition of the fauna indicates that Unit IV should be placed in the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

Maastricht – Belvédère 3B
Provenance: a lenticular horizon rich in molluscs and mammal fossils intercalated in the deposits of Unit IV at the transition IV-A to IV-B

Faunal list:
The provisional faunal list is composed of the following species:

Pisces
Cyprinidae
Esox lucius

Mammalia
Insectivora
Soricidae indet.
Lagomorpha
Ochotona pusilla
Rodentia
Spermophilus cf. *undulatus*
Sicista subtilus
Cricetus cricetus

Lemmus lemmus
Clethrionomys sp.
Arvicola terrestris ssp. A
Microtus gregalis
Microtus oeconomus
Microtus arvalis

Remarks
This assemblage is much larger than the assemblages of M-B 2A and 3. However, the material is not so well preserved.

The morphology of the teeth of the insectivores of M-B 3A resembles that of the teeth of *Sorex araneus*. However, the teeth are smaller than those of most of the specimens of *Sorex araneus* from Wageningen – Fransche Kamp and they are larger than the teeth of *Sorex minutus* of M-B 4. The *Cricetus* molars are too large to be assigned to *Cricetulus migratorius* and too small for *Cricetus major*. It is uncertain whether the molars belong to the subspecies *Cricetus cricetus praeglacialis*, because the m1 is missing. The single m3 of *Clethrionomys* cannot be determined at the species level.

The fauna is correlated to the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

Maastricht – Belvédère 3C
Provenance: Unit IV-B
Faunal list:

Mammuthus sp.
Dicerorhinus hemitoechus

Remarks
A nearly complete upper dentition and a large number of articulated bones of a steppe rhinoceros (*Dicerorhinus hemitoechus*), all from one individual, have been collected from deposits assigned to Unit IV-B. The presence of a second, more robust individual is indicated by the occurrence of another ulna (De Warrimont & Groenendijk, 1988; Van Kolfschoten, 1988).

The same unit yielded a spirally twisted tusk of an elephant identified as *Mammuthus* sp.

Maastricht – Belvédère 4
Provenance: Unit IV-C

Faunal list:
Pisces
Leuciscus cephalus
Chondrostoma nasus
Esox lucius

Reptilia
Emys orbicularis

Aves
Anatidae indet.

Mammalia
Insectivora
Erinaceus cf. *davidi*
Talpa europaea
Sorex araneus
Sorex minutus
Neomys fodiens
Crocidura sp.*
Rodentia
Eliomys quercinus
Clethrionomys glareolus
Arvicola terrestris ssp. A
Pitymys cf. *subterraneus*
Microtus oeconomus
Microtus agrestis
Microtus arvalis and/or
Microtus agrestis
Pitymys/Microtus sp.
Apodemus sylvaticus
Apodemus maastrichtiensis
Carnivora
Mustela cf. *nivalis*
Proboscidea
Elephas cf. *antiquus*
Perissodactyla
Equus sp.
Dicerorhinus hemitoechus
Artiodactyla
Cervus elaphus
Megaloceros giganteus
Capreolus capreolus
Bovidae indet. (large bovid)

*Note: In the faunal list published by the author in 1985, *Crocidura* cf. *leucodon* was listed. To prevent confusion about the stratigraphical range of *Crocidura leucodon* it is better to assign the material to *Crocidura* sp., because according to Reumer (1986) the first appearence of *Cr. leucodon* in Europe postdates the Weichselian.

Remarks
Five fossiliferous layers are distinguished within Unit IV-C (see Fig. 8). The lowermost level, Unit IV-C I yielded most of the formerly described material. Exceptions are: the skull of the giant deer *Megaloceros giganteus* which was obtained from the transition from Unit IV-C I to Unit IV-C II; the fossils of the European pond tortoise *Emys orbicularis* were collected from the transitional layer Unit IV-C I/II (the lower *Emys* layer) and the transition Unit IV-C II/III (the upper *Emys* layer) and some roe deer fossils (*Capreolus capreolus*) which have been collected, together with a small micromammal fauna, from deposits of Unit IV-C II.

More material was obtained in the period after 1984. During the summer of 1985 an excavation took place at site G in sediments assigned to Unit IV-C I. This site yielded a number of large mammal fossils. Most of the species concerned were already present in the list of M-B 4. New in the faunal list are *Elephas* cf. *antiquus* and a large bovid. The most relevant specimens from site G (i.e. the fossils of *Elephas* cf. *antiquus, Dicerorhinus hemitoechus, Cervus elaphus,*

Capreolus capreolus and Bovidae indet.) are described in this paper (see: systematic description).

Recently, in 1988, new material of *Emys orbicularis* and a mandibula of *Arvicola terrestris* were collected from the lowermost *Emys* layer. Very badly preserved molars from a horse *Equus* sp. and a mandible with molars of a deer cf. *Cervus elaphus* have been excavated at the archeological site N.

The fauna represents an association of the lower part of the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

Maastricht – Belvédère 5
Provenance: Unit VI-D (Archeological Site E)

Faunal list:
Aves
Nyctea scandiaca

Mammalia
Insectivora
Talpa europaea
Rodentia
Spermophilus (Urocitellus) cf. *undulatus*
Cricetulus migratorius
Dicrostonyx torquatus
Arvicola terrestris ssp. B
Microtus gregalis
Microtus oeconomus
Probosicdea
Mammuthus primigenius
Perissodactyla
Equus sp.
Coelodonta antiquitatis
Artiodactyla
Cervus elaphus
Rangifer tarandus
Cervidae indet. (large deer)
Bos primigenius/Bison priscus

Remarks
From the lowermost Subunit VI-A badly preserved fossils of *Mammuthus primigenius* (from the excavation of site J) have been obtained. Material of *Coelodonta antiquitatis* and *Equus* sp. are also collected from Unit VI-A. A fragment of a radius of an elephant is known from Unit VI-B. The majority of the material from Unit VI has been collected from the base of Unit VI-D (site E). This material has been described in an earlier paper (Van Kolfschoten, 1985).

The fauna is correlated to the upper part of the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

The influence of human activity on the composition of the faunas
A large number of archeological sites, located in the Maastricht-Belvédère pit yielded larger mammal remains as well as flint artefacts. This co-occurrence leads one to believe that in some cases, humans might have been responsible for the presence of mammal fossils at a particular spot. The occurrence of a high percentage of young and very old individuals at sites B, C, E and G supports this hypothesis (Roebroeks, pers. comm., 1987; Roebroeks, in prep.).

Most of the larger mammal fossils from site G, such as the majority of the teeth of *Dicerorhinus hemitoechus, Cervus elaphus, Capreolus capreolus* and the large bovid, are from young, not fully grown individuals. Other specimens such as a lower molar of *Dicerorhinus hemitoechus* and a lower molar of *Capreolus capreolus* are derived from very old individuals. At site E all the identifiable larger mammal fossils belong to young individuals (Van Kolfschoten, 1985).

According to A. van Gijn (pers. comm., 1987) the results of the studies on micro-wear of flint artefacts also suggest a relationship between human activity and the presence of larger mammal fossils. Her investigations indicate that one of the artefacts have been used for butchering mammals with a thick skin. Unfortunately most of the bones are too weathered or too badly preserved to show cut (or butchering) marks. An exception is a metacarpal bone of a horse, (from Unit VI-D) with an oval-shaped hole which might be man-made (Roebroeks, 1985).

Paleo-environmental indications from the Maastricht-Belvédère faunas
Maastricht – Belvédère 2 – 4
The sequence of the faunas M-B 2 + 2A, 3A, 3B, 3C and 4 document faunal changes during the transition from a cold to a warm temperate period (see Table 1).

The smaller mammal assemblage M-B 2A is characterized by the occurrence of the ground squirrel *Spermophilus* cf. *undulatus*, the Norway lemming *Lemmus lemmus*, the short-tailed vole *Microtus arvalis* and the near absence of species that prefer a wooded environment. The faunal composition indicates a tundra/steppe environment and cool climatic conditions. This interpretation is in agreement with evidence from the larger mammals from the same lithostratigraphical horizon.

The presence of *Clethrionomys* in fauna M-B 2A seems to be remarkable, because nowadays *Clethrionomys glareolus* prefers a wooded environment and temperate climatic conditions. The related living species *C. rutilus* and *C. rufocanus* also occur in Europe; they have more northerly distributions (Van den Brink, 1967) but both species are unknown from European Pleistocene faunas (Kowalski, 1977a).

The presence of *Clethrionomys glareolus* in faunas such as those from La Fage (Chaline, 1975), in which it co-occurs with *Lemmus lemmus* and *Dicrostonyx torquatus* indicates that *Clethrionomys glareolus* was less restricted environmentally during the Pleistocene period.

Fauna 3B indicates a steppe-like environment and most probably rather warm and dry climatic conditions. It comprises species such as *Ochotona pusilla, Sicista subtilus* and *Cricetus cricetus*, which prefer a steppe environment. *Lemmus lemmus* is still present.

Fauna M-B 4 has an interglacial character. Wood-

	FAUNAS						
	2	2A	3A	3B	3C	3	4
Erinaceus cf. *davidi*	.	.	.	.	.	.	+
Talpa europaea	.	.	.	.	.	+	+
Sorex araneus	.	.	.	.	.	+	+
Sorex minutus	.	.	.	.	.	.	+
Neomys fodiens	.	O	.	.	.	+	+
Crocidura sp.	.	.	.	.	.	.	+
Soricidae indet.	.	.	.	+	.	.	.
Ochotona pusilla	.	.	.	+	.	+	.
Eliomys quercinus	.	.	.	.	.	.	+
Spermophilus undulatus	.	O	O	O	.	O	.
Sicista subtilus	.	.	.	+	.	.	.
Cricetus cricetus praeglacialis	.	.	.	O	.	+	.
Lemmus lemmus	.	+	+	+	.	.	.
Clethrionomys sp.	.	+	.	+	.	.	.
Clethrionomys glareolus	.	.	.	.	.	+	+
Arvicola sp.	.	+	.	.	.	.	.
Arvicola terrestris ssp. A	.	.	+	+	.	+	+
Pitymys subterraneus	.	.	.	.	.	.	O
Microtus gregalis	.	.	+	+	.	+	.
Microtus oeconomus	.	.	.	+	.	.	+
Microtus agrestis	.	.	.	.	.	.	+
Microtus arvalis	.	+	+	+	.	.	.
Microtus arvalis and/or *Microtus agrestis*	.	.	.	.	.	+	+
Apodemus sylvaticus	.	.	.	.	.	+	+
Apodemus maastrichtiensis	.	.	.	.	.	+	+
Mustela nivalis	.	.	O	.	.	.	+
Elephas antiquus	.	.	.	.	.	.	+
Mammuthus primigenius	+	.	.	.	O	.	.
Equus sp. (robust type)	+	.	.	.	.	.	+
Dicerorhinus hemitoechus	.	.	.	.	+	.	+
Coelodonta antiquitatis	+	O	.	.	.	.	.
Cervus elaphus	+	.	.	.	.	.	+
Megaloceros giganteus	.	.	.	.	.	.	+
Capreolus capreolus	.	.	.	.	.	.	+
Bovidae indet.	.	.	.	.	.	.	+

Table 1. The distribution of the mammal species in the faunas Maastricht-Belvédère 2, 2A, 3A, 3B, 3C, 3, and 4. (+ means determination certain, o means determination cf. or aff.)

land species are well represented (Van Kolfschoten, 1985) and occur together with species such as *Microtus agrestis, M. arvalis* and *Dicerorhinus hemitoechus*, that prefer to live in a more open environment. Species with a habitat which is restricted to a steppe environment and dry continental climatological conditions, are absent in M-B 4. These data document the paleoecological change during the transition from a cold stadial period to a warm-temperate stage. First of all the tundra changes into steppe-like environment, afterwards followed by a more humid environment with forests alternated with some open areas. Comparable environmental changes are known from the Weichselian-Holocene transition (Kretzoi, 1957). Also during the Weichselian the so-called steppe-tundra covered Europe to a great extent (Kowalski, 1977b).

The malacological data from the same layers support our paleo- climatological inferences (Meijer, 1985). Molluscs indicative for a continental climate have been collected from the Units IV-A and IV-B. Higher up in the sequence there is an increase in woodland species from 0% to 48 %, whereas species which prefer a more open vegetation decrease from 58% to 18%. The hygrophile molluscs indicative of a more Atlantic climate are best represented in the upper part of Unit IV-C (Meijer, 1985).

Maastricht – Belvédère 5

The composition of the fauna M-B 5 points to a tundra/steppe environment and a cold and rather dry climate during the period in which the fauna lived.

The fauna differs from M-B 2 and 2A, which indicate more or less similar environmental and climatological conditions, in the presence of *Cricetulus migratorius, Dicrostonyx torquatus, Arvicola terrestris* and *Rangifer tarandus* and the absence of *Neomys* cf. *fodiens, Lemmus lemmus, Microtus arvalis* and *Clethrionomys* sp. These differences might point to a slightly colder climate during the period in which the fauna M-B 5 lived.

I.1.5. Rhenen (Kwintelooijen, Vogelenzang and Leccius de Ridder)

Introduction

In the Central Netherlands there are a number of ice-pushed ridges which were formed during the Saalian glacial. One of these ridges, called the Utrechtse Heuvelrug (running from Amersfoort to Rhenen) forms the south-western border of the glacial basin, which is called the Gelderse Vallei. Near the village of Rhenen there are three sandpits in this ridge: the Kwintelooijen pit, located on the northern inner side of the ridge and the Vogelenzang and Leccius de Ridder pits, both located on the southern outer side of the ridge (see Fig. 6). The Kwintelooijen pit and the Leccius de Ridder pit are still being worked; in the Leccius de Ridder pit the sediments are suction-dredged. The exploitation of Vogelenzang stopped in 1965.

In the pits a number of glaciotectonic thrust sheets were exposed and some of them are still exposed. In these thrust sheets Lower and Middle Pleistocene deposits, yielding mammal fossils, are present. Most of the fossils have been described before (Van Kolfschoten, 1981). In this paper, the mammal fauna described in 1981 is partly revised. Because of the invalid stratigraphic value of most of the larger mammal fossils, information about the new finds is added in the appendix of this paper.

Geological setting and stratigraphy

The geology of the southern part of the ice-pushed ridge Utrechtse Heuvelrug has been studied intensively by Ruegg (1981), Zandstra (1981), De Jong (1981) and Van de Wateren (1981). A summary of the lithostratigraphic sequence is presented in this chapter.

The lithostratigraphic description is based primarily on the sections in the pit Kwintelooijen. The most complete thrust sheets are up to 25 metres thick. Ruegg (1981) distinguishes the following sedimentary units in one of those, from bottom to top: (thicknesses given in parentheses)

Unit 1: pale green to grey very fine sands, locally with thin grey loamy layers (1.3 m.);

Unit 2: bluish grey clay, upward blacker and/or covered with a black humic to peaty layer several cm thick (1.1 m.);

Unit 3: brown silty loam (0.3 m.);

Unit 4: dark brown to greenish-brown moderately fine sands with irregular spheroidal to platy calcareous concretions (1.5 m.);

Unit 5: coarse gravel and gravelly coarse brownish sands; near the base angular cobbles and some boulders, a number of which are fragmented; the contact with Unit 4 is erosive (2.3 m.);

Unit 6: brown coarse sands with pebbles (3.7 m.);

Unit 7: brown coarse sands with fewer pebbles than in Unit 6 (2.0 m.)

Unit 8: brown moderately fine to moderately coarse sands with a few scattered pebbles (2.7 m.);

Unit 9: brown coarse to fine sands, fining upwards gravelly near the base (2.0 m.);

Unit 10: brown gravelly coarse sands and gravels (5.0 m.).

Units 1 to 3 have been assigned to the Kedichem Formation (Fig. 2) (Zandstra, 1981), the clay bed (Unit 2) has been dated to the Waalian Interglacial on the basis of pollen analysis (De Jong, 1981). Unit 4 is poor in volcanic minerals and belongs to the lower part of the Urk Formation correlated with Interglacial IV of the "Cromerian Complex" (Zandstra, 1981). Units 5 to 8 are also part of the Urk Formation. Unit 5, 6 and 7 are rich in augite, in Unit 8 this mineral is replaced by garnet and hornblende. The presence of some Scandinavian crystalline rocks and flints in Units 5 – 8 indicates a Saalian age (Zandstra, 1981). Units 9 and 10 have a glacio-aqueous origin and belong to the Drente Formation.

Many Paleolithic artifacts have been collected from the lower part of Unit 5 (Stapert, 1981). This layer also yielded some unidentifiable larger bone fragments.

The Units 4 – 10 have also been recognized recently in the pit Leccius de Ridder (Ruegg, pers. comm. 1988). This means that the upper units, defined in the pit Kwintelooijen, were previously also exposed in the south-eastern part of the ice-pushed ridge in the Vogelenzang and Leccius de Ridder pits.

In 1966 a section was exposed in the Leccius de Ridder pit showing 4 clay layers or lenses of clay (numbered I-IV by De Jong (1981)) incorporated in the augite-bearing coarse sediments of the Urk Formation (De Jong, 1981). One clay layer (IV) (see Fig. 10) contained small mollusc fragments and a smaller mammal fauna. No pollen was found in this layer. The pollen diagram for clay layer III, consisting of the same type of clay as layers II and IV, indicates the presence of a considerable number of trees, some of which were thermophilous trees such as *Alnus*, *Quercus* and *Corylus*. The spectrum corresponds rather well with the spectra from the Hoogeveen-Interstadial (De Jong, 1981). The pollen spectrum of clay layer I points to an Early Pleistocene age. This means that this layer is not contemporaneous with the coarse deposits of the Urk Formation in which it is incorporated. This may also apply to the clay layers II, III and IV.

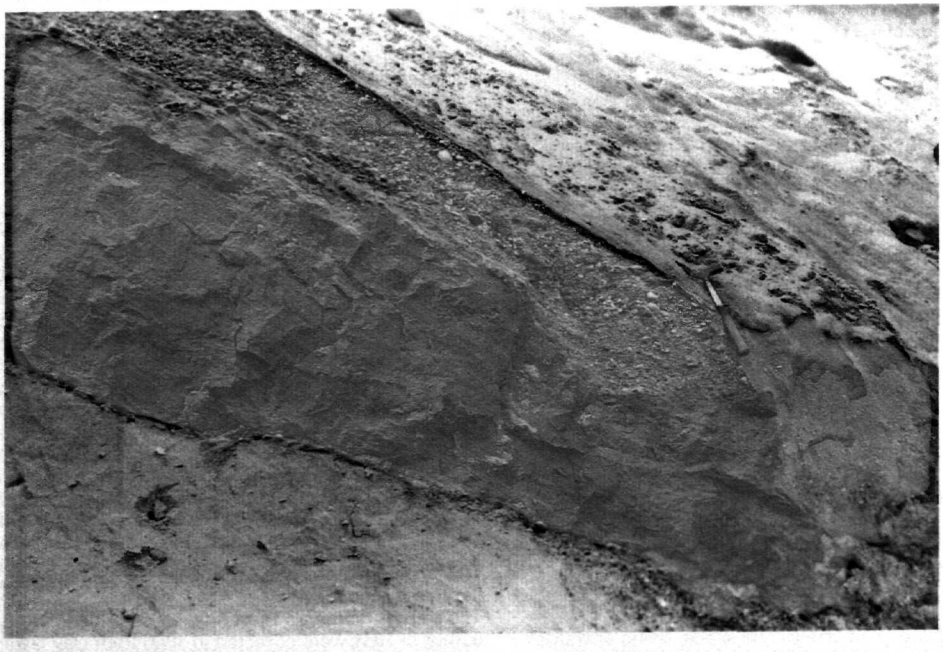
In summary it can be said that the stratigraphical position of Layer IV, the one with the smaller mammal fauna, is not clear on the basis of palynological or other lithological information. Layer IV is assigned to the *Arvicola terrestris* Partial-range-zone on the basis of the smaller mammal fauna. The fauna is correlated to a group of faunas which postdates the lowermost part of this zone. This correlation, in combination with the fact that the layer is ice-pushed, indicates a late Early Saalian age (see also Chapter IV).

The smaller mammals from Rhenen – Leccius de Ridder

The smaller mammals from Rhenen described by the author in 1981 were collected in 1966 from clay layer IV in the Leccius de Ridder pit. The fauna is composed of the following species:



a



b

Fig. 10. Leccius de Ridder, Rhenen (1966): a: view of the section with clay layer IV; b: clay layer IV in more detail.

	number of specimens	
Insectivora		
Neomys sp.	3	3.75%
Talpa europaea	1	1.25%
Desmana moschata	1	1.25%
Rodentia		
Clethrionomys glareolus	22	27.50%
Arvicola terrestris ssp. B	11	13.75%
Microtus agrestis/M. arvalis	15	18.75%
Apodemus sylvaticus	27	33.75%

Remarks

The fauna indicates a wooded environment alternating with open areas and a temperate climate during deposition of the clay.

The fauna indicates a correlation of clay layer IV to the *Arvicola terrestris* Partial-range-zone because of the occurrence of *Arvicola terrestris* ssp. B (see Chapter IV).

The larger mammals from Rhenen (Kwintelooijen, Vogelenzang and Leccius de Ridder)

The larger mammals from the three pits have been found mainly by amateur collectors. In most cases the precise stratigraphic provenance of these finds is not known. It has been claimed by some collectors that the majority of this material derives from coarse, gravelly layers which might correspond with Unit 5. However, according to the present author, this remains uncertain for at least part of the assemblage. A point in case are two specimens (a horn core of *Bison priscus* (Van Kolfschoten, 1981) and an upper molar of *Coelodonta antiquitatis*) which have been collected from units definitely overlying Unit 5. These circumstances, unfortunately, invalidate the stratigraphic value of the large mammal fauna from these pits.

Although it is uncertain from which pit part of the material originates, it appears that the composition of the larger mammal assemblages from the three different pits hardly differs (Van Kolfschoten, 1981). Therefore, they are regarded and treated as one single assemblage.

The fossils collected in the period up till 1981 have been described by Van Kolfschoten (1981). During the past few years a number of new specimens have been collected from sediments in Kwintelooijen and from sediments dredged up in Leccius de Ridder. Except for one specimen, these fossils belong to species already mentioned in Van Kolfschoten (1981) and supplement the information on these species. The extinct beaver *Trogontherium cuvieri* was hitherto unknown from Rhenen, it is represented by a mandible found by Mr. L.A. Lieuwen, Rhenen, in the Kwintelooijen pit. Part of the recently collected fossils will be described and figured separately in an appendix to this article.

List of larger mammal species reported from the three pits

Investigation of the newly discovered finds and revision of the already described material results in the following composite list of species:

Rodentia
- *Trogontherium cuvieri*

Proboscidea
- *Elephas antiquus*
- *Mammuthus primigenius*

Perissodactyla
- *Equus* sp.
- *Equus* cf. *hydruntinus*
- *Dicerorhinus mercki*
- *Dicerorhinus hemitoechus*
- *Coelodonta antiquitatis*

Artiodactyla
- *Sus scrofa*
- *Hippopotamus* sp.
- *Megaloceros giganteus*
- *Cervus elaphus*
- *Ovibos* aff. *moschatus*
- *Bison priscus*

Remarks

This faunal list differs to some extent from the one published in 1981 (Van Kolfschoten, 1981). The names *Elephas namadicus, Equus* spec. a and spec. b., *Hippopotamus* cf. *amphibius* and *Cervus (Megaceros) giganteus* are replaced by *Elephas antiquus, Equus* sp., *Equus* cf. *hydruntinus, Hippopotamus* sp. and *Megaloceros giganteus* respectively. Furthermore, the name *Dicerorhinus mercki* is now preferred to the name *D. kirchbergensis* following Guérin (1980), who regards the name *D. kirchbergensis* as a *nomen oblitum*.

The smaller mammal assemblage has been obtained from a single clay layer whereas the larger mammal fossils derive from various layers. As mentioned above, the majority of the larger mammal material might come from the coarse gravels and sands of Unit 5. The habitats of the larger mammal species differ considerably; one group of species (with *Mammuthus primigenius, Coelodonta antiquitatis* and *Ovibos* aff. *moschatus*) indicates cold, glacial conditions, whereas the other group (with *Elephas antiquus, Dicerorhinus mercki, Sus scrofa* and *Hippopotamus* sp.) indicates temperate conditions. For these reasons the larger mammal assemblage from the three pits near Rhenen (Kwintelooijen, Vogelenzang and Leccius de Ridder) is considered to be composed of species which did not live contemporaneously. The fossils represent at least two different faunas. One fauna, with for instance *Mammuthus primigenius* and *Coelodonta antiquitatis* should be correlated to the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

Trogontherium cuvieri is known from Early and Middle Pleistocene faunas. It became extinct at the end of the Holsteinian (Mayhew, 1978). *Hippopotamus* only occurred during the late Early or early Middle Pleistocene or the Late Pleistocene (see Chapter IV). The occurrence of both species (see Appendix) indicates that part of the fossil material is older than the *Mammuthus primigenius* and *Coelodonta antiqui-*

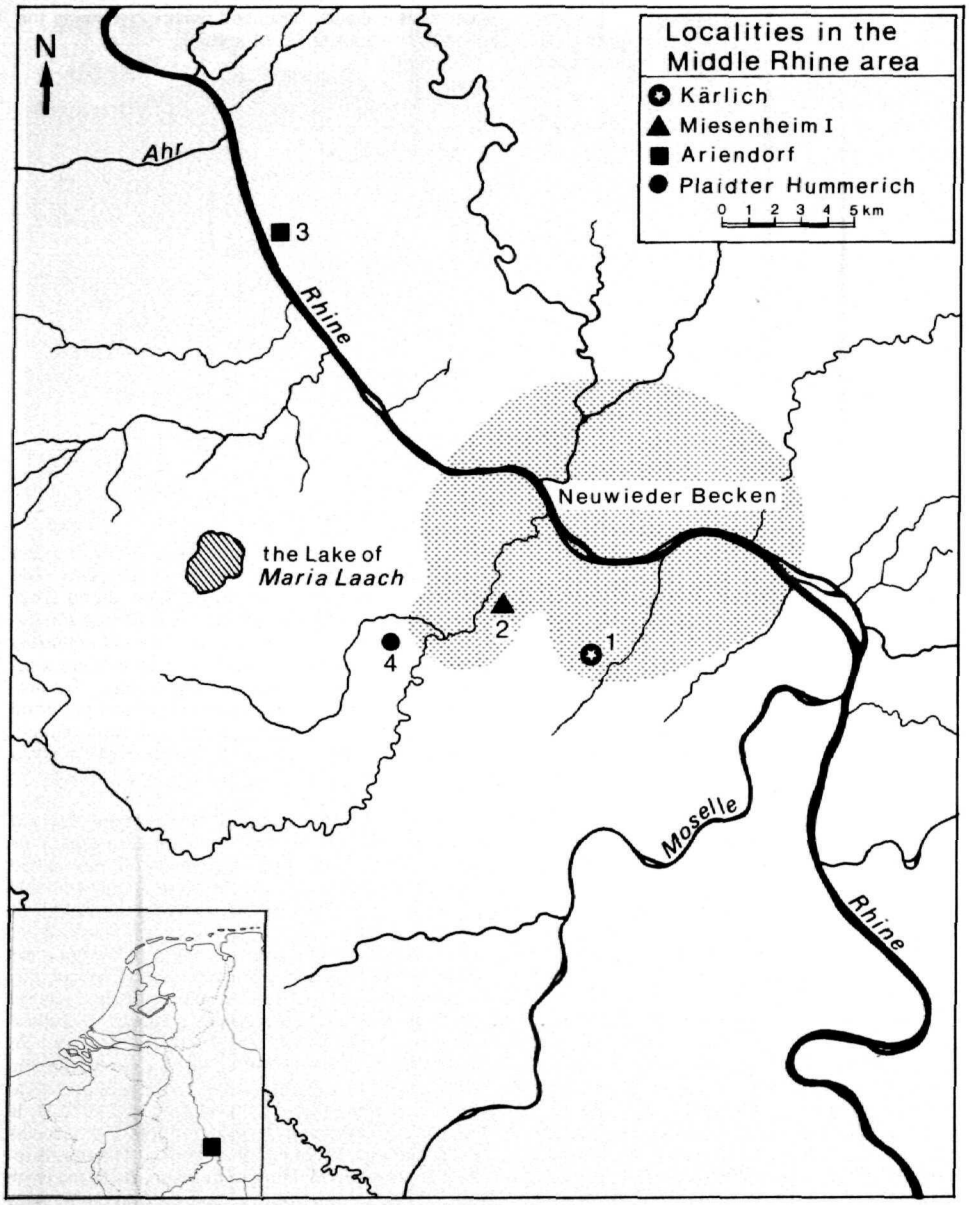


Fig. 11. Geographical position of the localities in the Middle Rhine area (Western Germany).

tatis fossils and might have a late Early or early Middle Pleistocene age. This supports the hypothesis that we are dealing with a mixed faunal assemblage.

I.2. LOCALITIES IN WESTERN GERMANY (THE MIDDLE RHINE AREA INCLUDING THE NEUWIED BASIN)

I.2.1. Introduction

Extensive prospection has led to the discovery of a large number of Paleolithic sites in the Middle Rhine area. The search was triggered off by the excavations undertaken by Prof. G. Bosinski (University of Cologne) in 1968 at the famous Late Paleolithic site of Gönnersdorf. Most of the archeological sites are located in, or just outside, the Neuwied Basin, the central part of the Middle Rhine area (Fig. 11).

The Neuwied Basin originated when the surrounding areas of the "Rheinische Schiefergebirge": the Eifel, Hunsrück and Westerwald rose about 200 metres above the Neuwied Basin. Since its origin the Neuwied Basin has been filled up with Pleistocene sediments: fluviatile sediments, deposited by the river Rhine and its tributaries; loess deposits; and numerous volcanic tuff layers (Fig. 12). The volcanic deposits originated from volcanoes located in the South Eifel region at the northwestern edge of the Neuwied Basin, the so-called "Laacher See" area where many extinct volcanoes and craters occur (Frechen, 1959).

The last eruption, forming the Maria Laach crater, took place at the end of the Weichselian about 9080 years B.C. As a result of this eruption the Neuwied Basin was covered with a layer of pumice several metres thick (Bosinski, 1983).

The local stratigraphy of the Middle Rhine area (see Fig. 12) is based mainly on sections in the Kärlich pit in the Neuwied Basin, in the Ariendorf quarry in the Middle Terrace of the river Rhine and in a quarry in the High Terrace of the Rhine north of Leutesdorf (Brunnacker, 1968, 1971; Brunnacker *et al.*, 1975, 1976). The most complete section of Pleistocene deposits is to be found in the Kärlich clay-pit. Here, Tertiary clay is overlain by about 40 metres of Pleistocene sediments. The base of the latter consists of gravels, which are overlain by loess or loess-like deposits alternating with basalt and pumice. A number of superimposed palaeosols has been identified in the loess-like deposits.

A large number of localities in this area, where excavations for archeological purposes are taking or took place, have yielded mammalian fossils. Faunas from the localities Kärlich, Miesenheim I, Ariendorf and Hummerich will be discussed briefly. Three faunas (Kärlich, Miesenheim I and Plaidter-Hummerich) have been investigated very provisionally, the faunas from Ariendorf have already been studied in detail (Steensma and Van Kolfschoten, in press).

I.2.2. Kärlich

Introduction

The Kärlich pit, a large pit located N.W. of the city of Koblenz, has been quarried since the last century for the highly valuable Tertiary clay deposits. The Quaternary deposits are of late Early Pleistocene to Holocene age and yielded a large number of artefacts and large mammal fossils.

The Kärlich section has been studied by many authors (e.g.Pohlich, 1913; Mordziol, 1913, 1930 and 1952; Remy, 1959; Frechen, 1962; Brunnacker, Streit & Schirmer, 1969). However, the geology and stratigraphy of the Kärlich sequences is still not fully understood. For instance, the correlation between the section exposed in the south-eastern corner of the pit, where the archeological excavations took place, and the northern sections is problematical. In addition the correlation between the Kärlich sections and the general subdivision of the Pleistocene is not clear.

Since 1987 a team of scientists of various disciplines: geology, palynology, paleobotany, malacology, mammal-paleontology, vulcanology, archeology and physics, is re-investigating the Kärlich quarry. The first preliminary paleontological results are reviewed in this paper.

Geological setting and stratigraphy

The Quaternary strata exposed in the Kärlich pit cover Tertiary deposits. The base of the Quaternary sediments consists of gravels deposited by the Rhine followed by gravels of the River Moselle. The section on top on these gravels (Fig. 12) consists of loess or loess-like deposits alternating with basalt and pumice. A number of superimposed paleosols are present in the loess-like deposits. For a more detailed description of the sequence the reader is referred to Brunnacker (1968; 1971) and Brunnacker *et al.* (1969).

The Matuyama/Brunhes boundary with an age of 730,000 years is located in Unit Bb (Brunnacker *et al.*, 1976). Another palaeomagnetic reversal, which might be correlative with the Jaramillo event, has been recognized in the sediments of Unit Ba (Brunnacker *et al.*, 1976).

Urban (1983) presents the results of the palaeobotanical investigations of the limnic sediments at the top of Unit H assigned to the so-called "Kärlich-Interglacial". She concludes that the interglacial has no clear equivalent in Northwestern Europe and that the interglacial must be of intra-Saalian age. Bittmann studied the pollen from the same section and his results (Bittmann, 1988) confirmed the data published by Urban (1983). However, he disagrees with Urban's opinion that the interglacial should be of intra-Saalian age. Bittmann prefers to correlate the Kärlich-Interglacial provisionally with the "Cromerian complex" because it differs palynologically in many respects from the Holsteinian and later interglacials whereas it corresponds rather well to the Cromerian s.l. Interglacials of Bilshausen and Voigtstedt.

The results of various studies to determine the absolute age of some layers, are contradictory and confusing. Van den Bogaard and Schmincke (1988) have dated, with the 40Ar/39Ar laser-dating method, the Wehrer Pumice I (683 $\pm$ 8 ka), the overlying "Wehrer

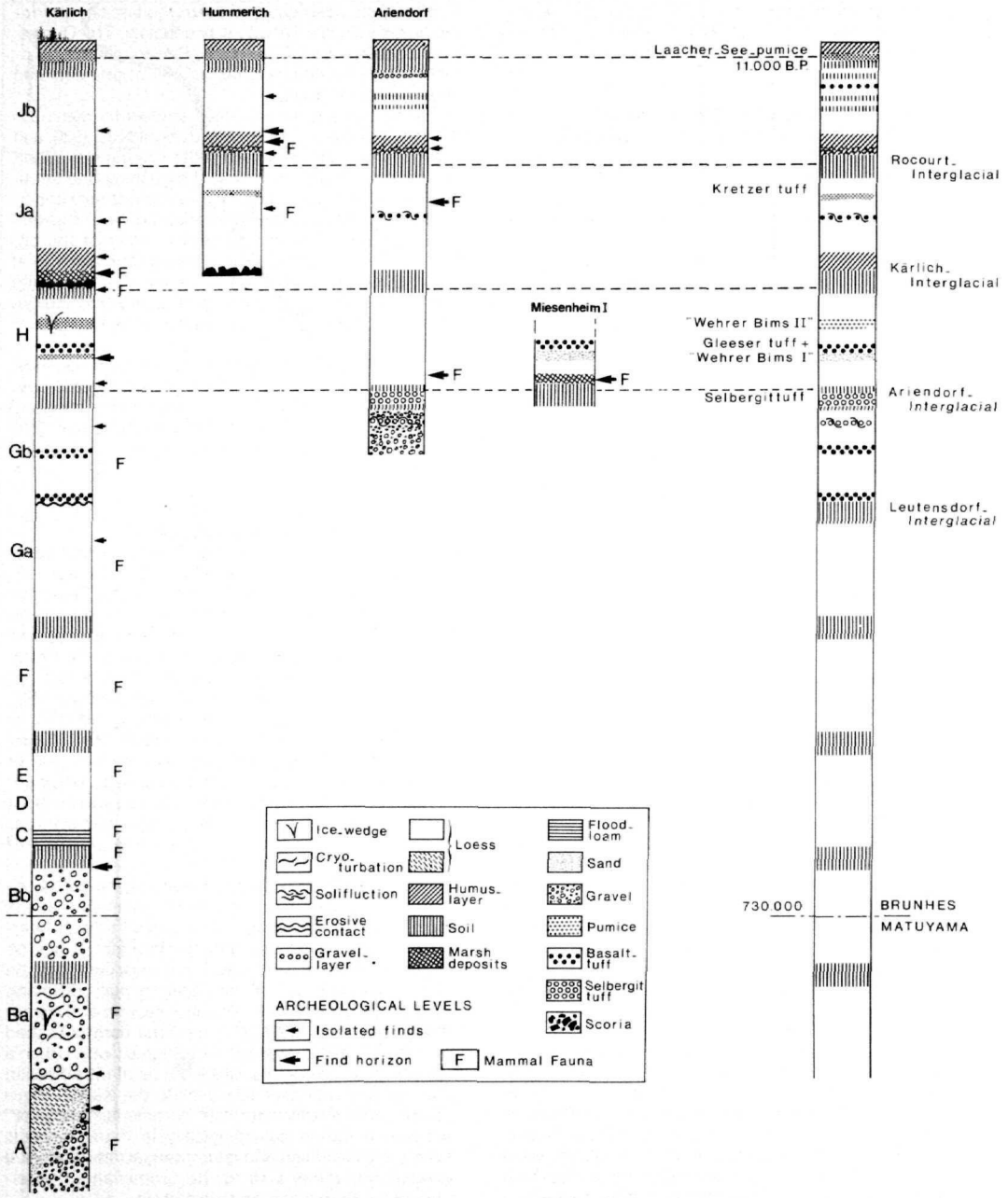


Fig. 12. Schematic figure showing the sections exposed at the localities Kärlich, Plaidter - Hummerich, Ariendorf and Miesenheim I in relation to the local stratigraphical zonation (the right collumn) (after Bosinski, *et al.*, 1986; with minor modifications).

Pumice II" (467 ± 8 ka) and the scoria of Unit H (the so-called "Kärlicher Brockentuff") (440 ± 18 ka).

Windheuser *et al.* (1982) have published ages for the "Wehrer Pumice" and the scoria of Unit H of 283 ± 90 ka and 150 ± 40 ka respectively.

Zöller *et al.* (in press) give TL dates of loess sediments just underlying the scoria of Unit H (232 ± 28 ka; 222 ± 25 ka) and above the scoria (152 ± 15 ka) (Zöller *et al.*, in press).

The correlation between the succession exposed in the Kärlich pit and the terraces of the Lower Rhine District as presented in table 2 is based on Brunnacker *et al.* (1976). Zagwijn (1985) correlates the terrace deposits with the Dutch lithostratigraphical units on the basis of palynological, heavy mineral analysis and lithostratigraphy. He correlates Middle Terrace I with the Lingsfort Beds in the Southern Netherlands, which contain high percentages of brown hornblende. These beds form the lowermost part of the Urk Formation and might be contemporaneous with the so-called Roswinkel and Weerdinge Beds which underlie deposits assigned to the Beilen Mineral Zone (Zandstra, 1981; Zagwijn, 1985). The Beilen Mineral Zone, palynologically dated as Interglacial IV of the "Cromerian Complex", is intercalated in deposits with a high percentage of pyroxenes, mainly augite. The Beilen Mineral Zone is characterised by a high percentage of green hornblende.

The deposits from the Leutesdorf Interglacial and those of the upper part of Unit Ga contain (as the above mentioned Lingsfort Beds) a high percentage of brown hornblende (Brunnacker et al., 1974). This indicates an age older than Interglacial IV of the "Cromerian Complex" for the Leutesdorf Interglacial and for Unit Ga if the above correlations are correct.

The uppermost beds of Middle Terrace IV are correlated with the lower part of the Kreftenheije Formation which dates from the late Saalian (Zagwijn, 1985).

lithostratigraphical units of the Kärlich sequence	Terraces of the Lower Rhine District
Unit Jb	Lower Terrace
Unit Ja	Middle Terrace IV
Unit H	Middle Terrace IIIb
Unit Gb	Middle Terrace IIb + IIIa
Unit Ga	Middle Terrace I + IIa
Unit F	Main Terrace IV

Table 2. The correlation between the lithostratigraphical units of the Kärlich sequence and the terraces of the Lower Rhine District (after Brunnacker *et al.*, 1976).

In summary it can be said that the paleomagnetic data indicate that the Pleistocene sequence of Kärlich has been deposited since the late Early Pleistocene; this is confirmed by the mammal paleontological data. Indirect lithostratigraphical data indicate that Unit Ga predates interglacial IV of the Cromerian complex, and that Unit Ja probably dates from the Late Saalian. Unit E yielded a fauna which is correlated to the Late "Biharian".

Unit Gb is, on the basis of the smaller mammal fauna, assigned to the *Arvicola terrestris cantiana-Sorex (Drepanosorex)* Concurrent-range-subzone, which is correlated to Interglacial IV of the "Cromerian complex" and part of the Elsterian (see Chapter IV). This correlation indicates that the absolute age of the Wehrer Pumice I (683 ± 8 ka.)(Van den Bogaard and Schminke, 1988), as well as the conclusion of Bittman (1988), who correlates the Kärlich Interglacial to the "Cromerian complex" seem to be incorrect.

The faunas from Kärlich

The Kärlich section has yielded a large amount of fossils collected from the Tertiary deposits as well as from the Pleistocene sediments (see Table 3 and 4). Wehrli (1943) mentioned an incisor of a hippopotamus from the Kärlich Main Terrace gravels which must be equivalent of Unit A according to Brunnacker (1968). Nobis (1974) has described some horse remains from Units E or F and H; Rothausen (1970) has described fossil antler fragments of *Praemegaceros* (= *Megaloceros*) cf. *verticornis* from Unit F (or perhaps from Unit E). Most of the larger mammal fossils are in the private collection of Mr. K. Würges (Mülheim-Kärlich) who found the majority of the material.

Larger mammal remains of *Elephas antiquus*, *Equus* sp., *Cervus elaphus*, *Sus scrofa* and a large bovid (cf. *Bos primigenius*) were found during the archeological excavations which took place during 1981, 1982 and 1987 in a layer in the upper part of Unit H, just above the scoria of Unit H (Bosinski *et al.*, 1980, 1986; Turner, 1989). The larger mammal fossils are being studied and described by Turner (1989).

Brunnacker (1968) mentioned a small collection of smaller mammal remains deriving from Unit F. This collection has been studied by Heller and dated as post-Cromerian in the sense of Heller (1969). The composition of this collection is unknown to the author.

Prof. Schirmer (from Düsseldorf) has sampled some material from the paleosol at the top of Unit B and from Unit E (see table 4). The other information presented in table 4 is obtained by the author by processing large sediment samples from the different units.

Remarks on the smaller mammal faunas (see Table 4)
The *Ungaromys* from Unit Bb is only represented by one specimen. The collection from Unit E (collected by Prof. Schirmer) is dominated by *Microtus* molars. The *Microtus* m1 molars with a so-called *Pitymys* rhombus, broadly confluent T4 and T5, and pointed salient angles, are referred to *Microtus* ("*Pitymys*") *arvalidens* or to *M.* ("*Pitymys*") *gregaloides* (see Chapter IV). Based on the knowledge of the stratigraphical range of *M. agrestis* and because of the absence of upper molars (M1 and M2) with a *M. agrestis* morphology, the *Microtus* molars with a *M. arvalis/agrestis* morphology from the Units E, Ga and Gb are referred to *M. arvalis*. The fauna from Unit H is stratigraphically younger and the presence of *M. agrestis* should not be excluded. The *Microtus* molars

Unit Ja	Carnivora *Elephas antiquus* Rhinoceros *Equus* sp. large Bovid
Unit H	(top of Unit H collected in the course of the archeological excavations)
	Elephas antiquus *Equus* sp. *Sus scrofa* *Cervus elaphus* large Bovid (cf. *Bos primigenius*)
Unit H	*Lepus/Oryctolagus* *Elephas antiquus* *Mammuthus* sp. (cf. *M. trogontherii*) *Equus* sp. *Cervus elaphus* medium sized Deer/Bovid large Bovid (*Bos/Bison*)
Unit Gb	*Mammuthus* sp. *Dicerorhinus* sp. *Equus* sp. (cf. *E. marxi*) *Megaloceros verticornis* *Cervus elaphus* *Dama* sp. (cf. *Dama dama*) large Bovid
Unit Ga	*Equus* sp. (caballine) *Cervus elaphus*
Unit F	*Mammuthus* sp. (*M. meridionalis/M. trogontherii* *Equus* sp. (*?E. süssenbornensis*) *Cervus elaphus* *Megaloceros* cf. *verticornis*
Unit D – E	*Mammuthus* sp. (cf. *M. trogontherii*)
Unit C	*Cervus* cf. *elaphus* large Bovid
Unit Bb	large Bovid (cf. *Praeovibos priscus*)
Unit Ba	*Mammuthus trogontherii* *M. trogontherii/M. meridionalis*
Unit A	*Hippopotamus major*

Table 3. Distribution of the larger mammal species found in the Kärlich pit. The information for this preliminary list is obtained from literature and from co-operative studies of E. Turner and the author.

are therefore assigned to *M. arvalis/agrestis*. *Mimomys* is represented by a larger and a smaller species; there is only one specimen of *Dicrostonyx*. The composition of the fauna from Unit E indicates that Unit E should be assigned to the "Biharian" (see Chapter IV).

The fauna from Unit Gb is dominated by *Pliomys* sp. and *Microtus*; both occur abundantly. Also the large collection (> 800 specimens) from Unit Gb is characterized by a predominance of *Pliomys* and *Microtus*. The other species are represented by a small number (1 – 15) of specimens. Remarkable is the occurrence of *Arvicola terrestris cantiana*. Unit Gb is placed in the *Arvicola terrestris cantiana-Sorex (Drepanosorex)* sp. Concurrent-range-subzone (see Chapter IV).

The smaller mammal fauna from Unit H, with about 20 identifiable specimens, was collected from a level just below the Kärlicher Brockentuff. Most of the material, except for the single mandible fragment of *Talpa europaea* and some *Microtus* molars, is derived from the upper 50 cm. of the section of Unit H.

I.2.3. Miesenheim I

Introduction

The locality Miesenheim I is situated on the east bank of the Nette River, a tributary of the Rhine (Fig. 11), on a small spur east of Miesenheim village. The first fossil bone fragments were found in 1982 (after basalt and pumice extraction had taken place) and this discovery resulted in a number of archeological excavations in the period 1982 – 1986 and the discovery of artefacts in Unit F. The first results have been published by Boscheinen *et al.* (1984) and Bosinski *et al.* (1988).

Unit H	Insectivora *Talpa europaea* *Sorex* cf. *araneus* Rodentia *Spermophilus* sp. *Clethrionomys* cf. *glareolus* *Microtus arvalis/agrestis* *Apodemus* sp.
Unit Gb	Chiroptera Insectivora *Talpa europaea* *Sorex* cf. *araneus* *Sorex* cf. (*D.*) *savini* Lagomorpha Lagomorpha indet. Rodentia *Eliomys* sp. *Cricetulus* sp. *Cricetus* sp. *Lemmus lemmus* *Pliomys* sp. *Arvicola terrestris cantiana* *Microtus ("Pitymys") arvalidens* *Microtus arvalis* *Microtus* sp. *Apodemus* sp. Carnivora Cf. *Mustela nivalis*
Unit Ga	Insectivora *Talpa europaea* *Sorex* cf. *araneus* Rodentia *Pliomys* sp. *Microtus arvalis*
Unit F	Rodentia *Microtus arvalis* *Microtus* sp.
Unit E	Rodentia *Dicrostonyx* sp. *Mimomys savini* *Mimomys* sp. (small) *Microtus ("Pitymys") gregaloides* *Microtus arvalis*
Unit Bb	Rodentia *Ungaromys* sp.

Table 4. Distribution of the smaller mammal species collected in the Kärlich pit.

Geological setting and stratigraphy

The section of Miesenheim I consists of 7 superimposed lithostratigraphical units (Brunnacker in Boscheinen *et al.*, 1984 and Turner, 1989) (the thicknesses are given in parentheses).

- The lowermost unit (Unit I) consists of alternating lenses of fine sand and loamier, sandy sediment.
- Unit H (0.2 – 0.3 m.) consists of calcareous loamy sediments. The transition from Unit H to Unit G is gradual.
- Unit G (0.1 – 0.5 m.) is divided into a lower and an upper part. The lower part consists of a homogeneous, calcareous colluvium. The upper part consists of a less calcareous, loamier sediment.
- Unit F is divided into three parts. Fi (0.2 – 0.3 m.): a horizon transitional between Unit F and G; Fii (about 0.1 m.): an irregular clay – like horizon described by Brunnacker as a marsh deposit; Fiii (0.1 – 0.2 m.): a more loamy deposit which forms the transition from F to C.
- Unit C (0.1 – 1.0 m.); a loamy colluvium.
- Unit B (0.1 – 0.2 m.); a level of gravel including pebbles up to 10 cm. According to Brunnacker this is a fluviatile deposit of the Nette River.
- Unit A (0.1 – 0.6 m.); a reworked loess.

At first Units D and E were also distinguished; they are composed of grey clay layers and light blue coloured clay lenses. Later on these units were considered to be part of Unit Fiii.

The sedimentary succession was originally overlain by a thin pumice bed and a thicker basalt deposit which correspond to the volcanic layers in Unit H of the Kärlich sequence and are macroscopically identified as the "Wehrer Pumice" and the "Gleeser Basalt" respectively. These layers in their turn were overlain by loess deposits and the Laacher Pumice.

The section described above covers loess deposits which contain pyroxenes, deriving from volcanic eruptions dated after the Leutesdorf Interglacial (Brunnacker in: Boscheinen *et al.*, 1984). Palynological data from Unit F indicate deposition of this unit at the end of an interglacial, provisionally correlated on the basis of its geological setting, with the so-called Ariendorf – Interglacial. However, so far the palynological data are too poor to correlate this warm phase with any of the Pleistocene interglacials of the Dutch Standard division (Urban in: Boscheinen *et al.*, 1984).

The sediments which yielded the fauna Miesenheim I are assigned to the *Arvicola terrestris cantiana -Sorex (Drepanosorex)* Concurrent-range-subzone and on the basis of this correlated to Interglacial IV of the "Cromerian complex" (see Chapter IV).

The mammal fauna from Miesenheim I

Mammal fossils have been recovered from the transitional layer between Unit H and Unit G, from the upper part of Unit G, from Unit F (Fi – Fiii) and Unit C.

The smaller mammal fauna

A rich, well-preserved smaller mammal fauna has been collected from Units C to G. The following species have been recognized after a preliminary investigation (see Fig. 13):

Insectivora
- *Talpa europaea*
- *Talpa minor*
- *Desmana* sp.
- *Sorex runtonensis*
- *Sorex minutus*
- *Sorex (Drepanosorex) savini*
- *Neomys* cf. *newtoni*

Rodentia
- *Trogontherium cuvieri*
- *Castor fiber*
- *Eliomys quercinus*
- *Muscardinus avellanarius*
- *Sicista* sp.
- *Cricetus* sp.
- *Allocricetus bursae*
- *Lemmus lemmus*
- *Pliomys episcopalis*
- *Clethrionomys glareolus*
- *Arvicola terrestris cantiana*
- *Microtus ("Pitymys") arvalidens*
- *Microtus arvalis*
- *Microtus agrestis*
- *Microtus oeconomus*
- *Microtus gregalis*
- *Apodemus sylvaticus*
- *Apodemus* aff. *maastrichtiensis*

There are slight differences between the compositions of the smaller mammal assemblages from the various layers. The glirids *Eliomys quercinus* and *Muscardinus avellanarius* occur mainly in the lowermost fossiliferous level (Unit G). In the upper horizons there is a decrease of *Clethrionomys glareolus* and an increase of *Microtus* species.

Remarks on the smaller mammal fauna

Insectivora

Insectivores are well represented. *Sorex runtonensis* and *Neomys* cf. *newtoni* are the most common species; *Desmana* sp. is rare. Moles are represented by two species differing markedly in size: the extinct small *Talpa minor* and the much larger living *Talpa europaea*, the common mole. In the Miesenheim I fauna there are three *Sorex* species which differ in size. *Sorex minutus* the smaller representative, the medium-sized *Sorex runtonensis* and *Sorex (Drepanosorex) savini*, the largest one.

Rodentia

Trogontherium cuvieri and *Castor fiber* are well represented by dental as well as by skeletal material. One of the most common species in the Miesenheim fauna is *Arvicola cantiana*. The molars of *A. terrestris cantiana* (Fig. 28) show the so-called *Mimomys*- differentiation of the enamel thickness. Rare in the fauna are: *Eliomys quercinus, Muscardinus avellanarius, Sicista* sp., *Allocricetus bursae, Lemmus lemmus, Pliomys episcopalis* and *Microtus agrestis*. So far *Microtus agrestis* is indicated only by one M2 with the diag-

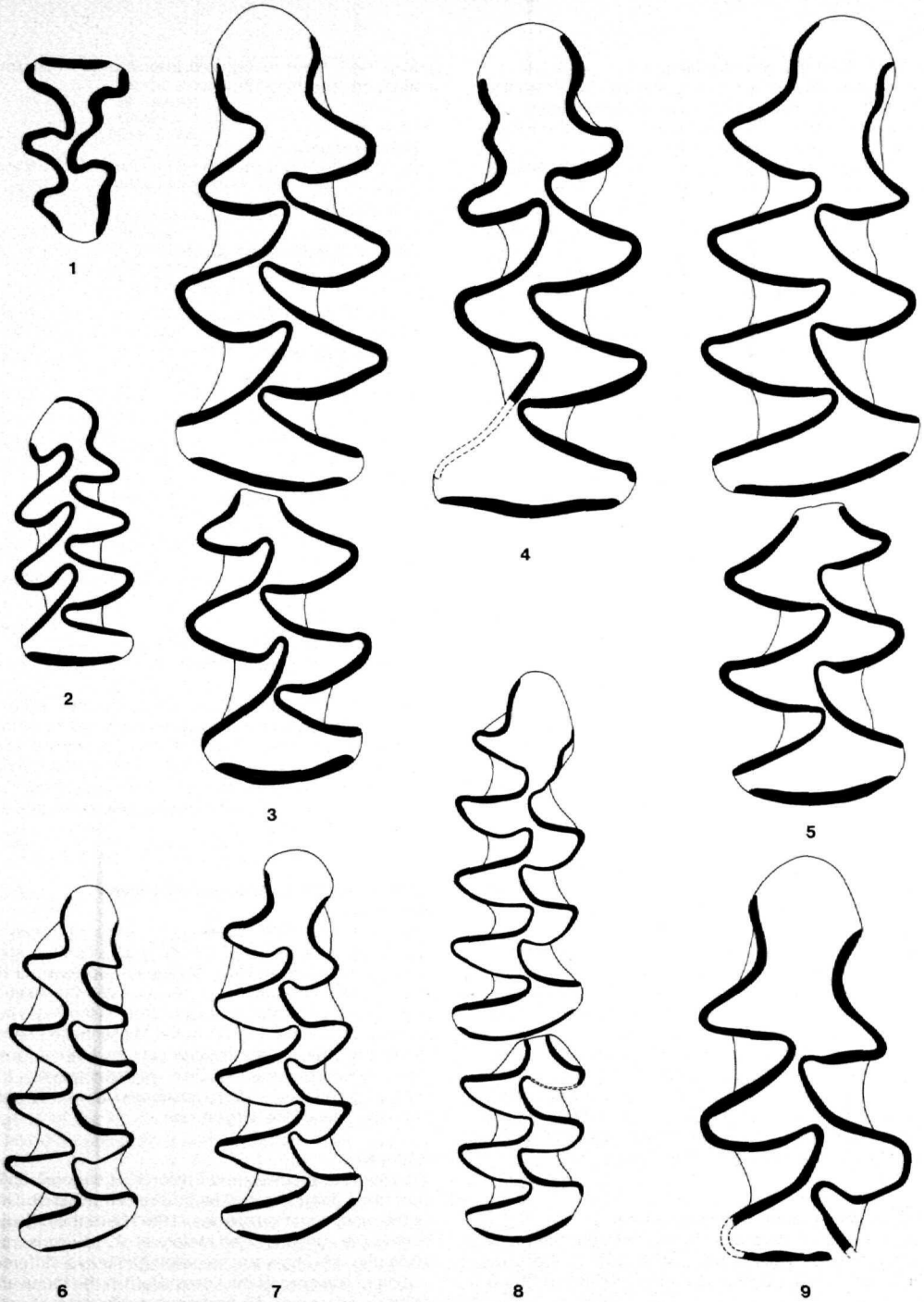


Fig. 13. Miesenheim I: 1: *Pliomys episcopalis*: M3 sin.: 2: *Clethrionomys glareolus*: m1 sin.: 3-5 and 9: *Arvicola terrestris cantiana*: 3: m1 and m2 sin.; 4: m1 sin.; 5: m1 and m2 dext.; 9; m1 dext.: 6: *Microtus ("Pitymys") arvalidens*: m1 dext.: 7: *Microtus arvalis* or *M. agrestis*: m1 dext.: 8: *Microtus gregalis*: m1 and m2 dext.

nostic *M. agrestis* morphology (i.e. having the extra postero-lingual salient angle). *Apodemus* aff. *maastrichtiensis* has also been recognized in the fauna Miesenheim I and occurs together with the wood mouse *A. sylvaticus*.

The fauna represents an association of the *Arvicola terrestris cantiana – Sorex (Drepanosorex)* sp. Concurrent-range-subzone (see Chapter IV).

The larger mammal fauna*
(* after Turner, 1989)

Carnivora
Canis lupus mosbachensis
Ursus cf. *deningeri*
Mustela (Putorius) putorius
Mustela nivalis
Meles sp.
Proboscidea
Mammuthus cf. *trogontherii*
Perissodactyla
Equus sp.
Dicerorhinus etruscus cf. *brachycephalus*
Artiodactyla
Cervus elaphus
Capreolus capreolus
Bos sp. or *Bison* sp.

Paleo-environmental and paleo-climatological interpretations of the fauna-association

The environment as indicated by the smaller mammals seems to have consisted of forests and open, probably somewhat drier land away from the river. The presence of the dormice *Eliomys quercinus* and *Muscardinus avellanarius* leads us to conclude that the climatic conditions during deposition of the sediment were very much like those of today.

The larger mammalian fauna also points to a locally mixed biotope. *Equus* sp. and *Dicerorhinus etruscus* cf. *brachycephalus* preferred an open environment, roe deer and red deer are associated with woodland.

Remarkable is the occurrence of *Lemmus lemmus*. Its present distribution is restricted to the arctic areas. However, *Lemmus lemmus* occurs in Poland in Early and Middle Pleistocene faunas which do not suggest an arctic environment but indicate a temperate climate with the presence of forest and steppe elements (Kowalski, 1977a). *Lemmus lemmus* also occurs in the fauna from Petersbuch together with species which indicate warm temperate climatic conditions and a partially wooded environment (Von Koenigswald, 1970). According to Kowalski (1977a) *Lemmus lemmus* has been restricted to the arctic zone only since the Late Pleistocene.

The mammalian fauna support the paleo-ecological conclusions of the pollen analysis. The pollen spectra are available for Unit F only. They indicate the end of a warm phase during the time of deposition (Urban in: Boscheinen *et al.*, 1984).

I.2.4. Ariendorf

Introduction

About 30 kilometres north of the Neuwied Basin in the middle terrace of the Rhine near the village of Ariendorf is a large gravel quarry: the Karl Schneider quarry, where a section of Pleistocene sediments is exposed. The section (see Fig. 12) has been described by several authors (e.g. Brunnacker *et al.*, 1975; Bibus, 1980).

The gravels at the base are covered with sand and loess deposits alternating with tuff layers. Artefacts and mammal fossils have been discovered in the layers above the so-called Selbergit-tuff. There are three different artefact-bearing levels. The lowermost one is located at the base of the sand-loess bed, the other horizons are in the upper part of the middle loess bed and at the base of the upper one. The first results of the archeological excavations took place in the period 1981 – 1983 are published by Bosinski *et al.* (1983).

Geological setting and stratigraphy

The lower part of the section consists of about 30 metres of gravels deposited by the Rhine. The sediments contain a high percentage of pyroxenes, which are derived from the eastern Eifel volcanic deposits (Brunnacker et al., 1975). The gravels are covered with a layer of the so-called Selbergit-tuff. Overlying the tuff there is a gravel layer, a loam deposit and a layer of eroded Selbergit-tuff covered with a gravelly sand horizon, which is up to 50 cm thick. Superimposed on this horizon there are a sand-loess and two loess beds separated by interglacial paleosols. At the base of the uppermost loess bed is so-called Metternicher-tuff layer. On top of the loess beds are Holocene deposits. The mammal fossils are collected from the base of the lower sand-loess and the overlying loess bed.

For a more detailed description of the sequence the reader is referred to Brunnacker *et al.* (1975) and Bosinski *et al.* (1983).

The high percentage of pyroxenes in the lowermost Rhine gravels indicate that these gravels were deposited after the Leutesdorf – Interglacial. Sediments superimposed directly on the gravels have been deposited in the so-called Ariendorf-Interglacial (Brunnacker in: Boscheinen *et al.*, 1984).

The Selbergit-tuff has a K/Ar age of 350 – 420 ka (Frechen & Lippolt, 1965). Lippolt *et al.* (1986) have published a 40Ar/39Ar age for the upper Selbergit-tuff layer of 420 ± 30 ka whereas Van den Bogaard and Schmincke (1988) give 40Ar/39Ar laser-ages of 710 ± 20 ka and 451 ± 6 and 442 ± 3 ka respectively for the lowermost and the upper Selbergit-tuff layers. Zöller *et al.* (in press) present TL sediment dates of the three loess-beds. According to these authors the lowermost sand – loess has ages of 300 ± 34, 244 ± 25 and 235 ± 42 ka; the overlying loess deposit has an age of 199 ± 18 ka and the upper loess bed an age of 30.8 ± 3.1 ka.

It is concluded that the Ariendorf section dates from the Middle and Late Pleistocene. The mammal fossils from the lowermost level are correlated to the lowermost part of the *Arvicola terrestris* Partial-range-zone, which itself is correlated to the Early Saalian (see Chapter IV). The younger faunal assemblage predates the Rocourt (= Eemian) Interglacial (see fig. 12) and is correlated to the second group of faunas referred to the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

These correlations are in agreement with the absolute ages, except for the 710 ± 20 ka..

The faunas from Ariendorf

The smaller mammals have been described by Steensma and Van Kolfschoten (in press), the larger mammals by Poplin (in Brunnacker *et al.*, 1975) and by Turner (in Bosinski *et al.*, 1983; and Turner, 1989).

Fauna Ariendorf 1

Provenance: The base of the sand-loess bed

The smaller mammal assemblage

Insectivora	min. no. of individuals
Talpa cf. *europaea*	1
Sorex cf. *minutus*	1
Rodentia	
Spermophilus cf.*undulatus*	4
Cricetus cricetus cf. *praeglacialis*	1
Dicrostonyx torquatus	4
Lemmus lemmus	6
Arvicola terrestris ssp. A	1
Microtus arvalis and/or *M. agrestis*	14
Microtus gregalis	10
Microtus oeconomus	3

Remarks

Microtus arvalis, M. agrestis and *M. gregalis* are the most common species in the small mammal fauna of Ariendorf 1. The lemmings *Dicrostonyx torquatus* and *Lemmus lemmus*, and the ground squirrel *Spermophilus* cf. *undulatus* are common. The other species are rare.

The fauna represents an association of the lower part of the *Arvicola terrestris* Partial-range-zone.

The larger mammal assemblage (After Turner, 1989)
Carnivora
Canis lupus
Canis sp.
Ursus sp.
Felis sp.
Proboscidea
Mammuthus sp.
Perissodactyla
Equus sp.
Coelodonta antiquitatis
Artiodactyla
Cervus elaphus
Bos sp./*Bison* sp.

Fauna Ariendorf 2

Provenance: The upper part of the middle loess bed

The smaller mammal assemblage

Rodentia
Arvicola terrestris ssp. B

Remarks

Arvicola terrestris, represented by two molars, is the only smaller mammal species in Ariendorf 2.

The occurrence of *A. terrestris* indicates that the interval which yielded fauna Ariendorf 2 should be placed in the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

The larger mammal assemblage (After Turner, 1989)
Carnivora
Canis lupus
Proboscidea
Mammuthus sp.
Perissodactyla
Equus sp.
Coelodonta antiquitatis
Artiodactyla
Cervus elaphus elaphus
Bison priscus

Paleo-environmental and paleo-climatological interpretation of the fauna-associations

The presence of tundra and steppe elements such as *Spermophilus* cf. *undulatus, Dicrostonyx torquatus, Lemmus lemmus* and *Microtus gregalis* and the absence of typical forest-dwellers such as *Apodemus sylvaticus* and *Clethrionomys glareolus* in the smaller mammal fauna Ariendorf 1 indicate a tundra/steppe environment and a cool climate during the deposition of the lowermost mammal- and artefact-bearing level in the Early Saalian. The composition of the larger mammal association confirms this interpretation.

The small mammals of the fauna-association Ariendorf 2 are only represented by the water vole *Arvicola terrestris*, which has a wide geographical distribution. The larger mammal assemblages of Ariendorf 1 and 2 correspond fairly well, which suggests similar environmental and climatological conditions during the deposition of both levels.

I.2.5. Plaidter-Hummerich

Introduction

The Plaidter-Hummerich is one of the extinct volcanoes located in the South Eifel region. The volcano originated during the Middle Pleistocene and according to Schmincke & Mertes (1979) has an age of about 240,000 years (K/Ar dating). In the course of time the crater has filled up with loess, pumice and volcanic material from the edge of the crater itself (Bosinski *et al.*, 1983 and 1986).

Recent archeological investigations have shown that the craters of the extinct volcanoes were regularly in-

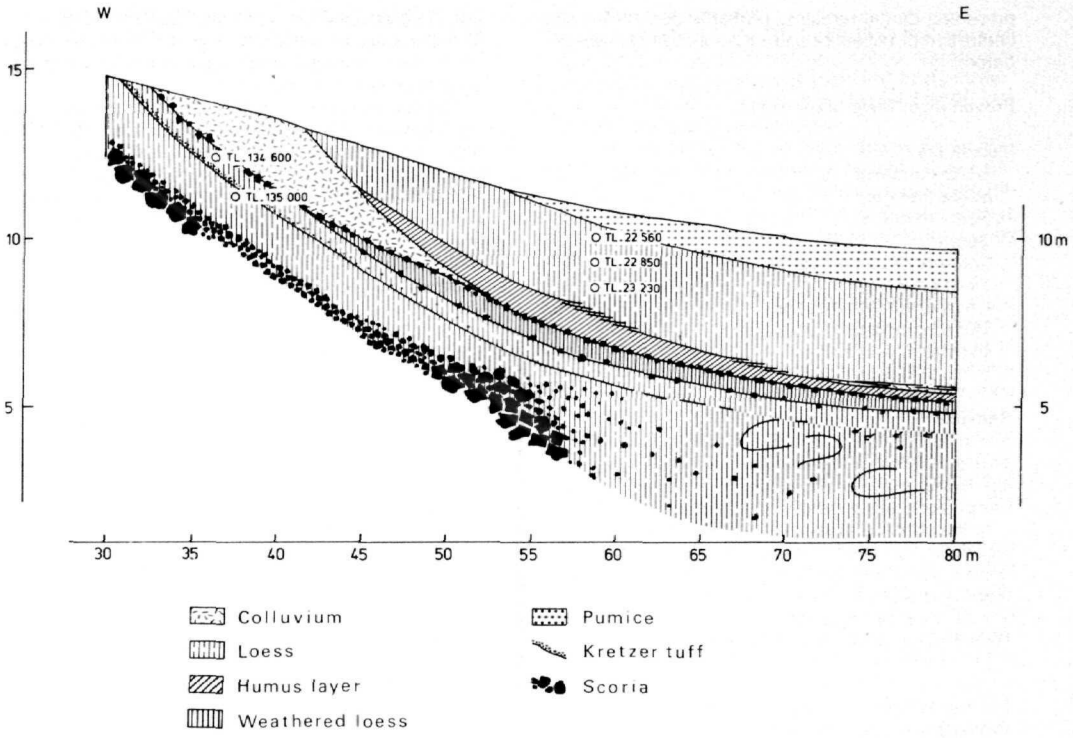


Fig. 14. Schematic diagram showing the stratigraphy of the deposits in the crater at Plaidter - Hummerich (after Bosinski *et al.*, 1986).

habited by prehistoric man. Much of the archeological material excavated at Plaidter-Hummerich has been found in situ in the loess beds deposited in the crater hollow. The first results of the archeological excavations have been published by Bosinski *et al.*, 1983 and 1986.

Geological setting and stratigraphy

The base of the section in the crater consists of a loess horizon lying on top of lava. In the middle of the crater this horizon is up to 8 metres thick. A still undescribed pumice referred to as Kretzer-tuff subdivides the lower loess deposits. This loess horizon is separated from the overlying second loess horizon by a weathered loess layer and a dark humic layer which is correlated with the Eemian Rocourt Paleosol (Bosinski *et al.*, 1986). The upper loess horizon is covered by the Laacher pumice and a Holocene humic horizon.

Singhvi *et al.* (1986) have published loess TL ages of 135 and 134.6 ka for the lower loess bed and 23.23, 22.85 and 22.56 ka for the upper loess layer (see Fig. 14)

On the basis of the occurrence of two loess beds separated by a clear paleosol, correlated to the Eemian Rocourt Paleosol, and supported by the TL-dates, it is concluded that the crater has filled up with Saalian and Weichselian deposits.

The composition of the smaller mammal fauna from the lower loess bed indicates that the interval should be assigned to the *Arvicola terrestris* Partial-range-zone. The fauna is correlated to the second group of faunas with a late Early – Late Saalian age (see Chapter IV).

The fauna from Plaidter-Hummerich

The dark humic horizon and the red-brown paleosol, located between the two loess horizons, have yielded many mammal fossils. The remains of the smaller mammals from this part of the section have not yet been studied. The larger mammal assemblages have been studied and preliminarily described by Turner (in Bosinski et al., 1983; Turner, 1989).

The smaller mammal fauna I

The smaller mammal assemblage discussed briefly in this paper was derived from a small lenticular layer with fossils in the lowermost loess layer close to the edge of the crater. The lens (about 0.5 square metre and 10 cm. thick) yielded about 800 to 1000 well-

preserved dental remains, probably due to the concentration of pellets of diurnal or nocturnal avian predators.

Provenance: lower loess bed

Insectivora
Talpa europaea
Sorex araneus
Sorex minutus
Rodentia
Spermophilus undulatus
Sicista subtilus
Arvicola terrestris ssp. B
Microtus arvalis
Microtus oeconomus

Remarks
The most common species in this fauna is *Microtus arvalis*. There is a high percentage of young individuals. Upper molars (M2 and M1) with the *M. agrestis* morphology are absent in this fauna.

In the absence of species indicating the presence of woods and in the absence of lemmings, the species mentioned in the faunal list point to a steppe environment and a rather warm, dry climate.

Fauna I is an association of the *Arvicola terrestris* Partial-range-zone (see Chapter IV).

Plaidter-Hummerich larger mammal assemblage
Provenance: from the humic horizon

Carnivora
Crocuta crocuta
Panthera leo spelaea
Perissodactyla
Equus sp. (large horse)
Equus hydruntinus
Coelodonta antiquitatis
Artiodactyla
Cervus elaphus
Dama dama
Capreolus capreolus
Bos primigenius

Fossils of marmot are also present in the humic horizon but they are probably much younger than the larger mammal fossils. The marmots are thought to have burrowed down into the section.

II. SYSTEMATIC DESCRIPTIONS

II.1. INTRODUCTION
The mammal fossils with a well known stratigraphical provenance from the locality Neede supplemented with a number of recently collected specimens from the localities Maastricht-Belvédère will be described in this chapter. The collected *Arvicola* molars are mentioned briefly in this chapter. The taxonomy and evolution of *Arvicola* will be discussed in detail in the next chapter.

II.2. TERMINOLOGY AND MEASUREMENTS
The elements of the upper jaw are indicated by an upper case character, the elements of the lower jaw by a lower case character.

The dental elements and lower jaw of the Soricidae are measured and described after Reumer (1984). The terminology and measurements of the dental elements of the Arvicolidae are after Van der Meulen (1973) and those of the Muridae after Van der Weerd (1976). The remains of the Elephantidae are described and measured after Maglio (1973), those of the Equidae after Eisenmann, (1979), those of the Rhinocerotidae after Guérin (1980). The terminology used in the description of the Cervidae and Bovidae and the method of measuring are after Heintz (1970).

The measurements of the smaller mammal dentitions have been made using a Reflex Microscope which can measure three dimensions and which is linked through the RS 232 to an IBM personal computer. All measurements are given in millimetres.

Abbreviations
There are a number of standard abbreviations such as: N = number of observations; min. = minimum, smallest measurement; max. = maximum, largest measurement; dext. = dextral; sin. = sinistral; SE = standard error; SD = standard deviation. Furthermore the following abbreviations are used to indicate where the material is stored:

- I.V.A.U. = Institute of Earth Sciences, Utrecht University
- R.G.M. = National Museum of Geology and Mineralogy at Leiden
- N.H.M.E. = Museum of Natural History at Enschede
- N.D.D. = Museum of Natural History "Natura Docet" at Denekamp
- RM = Rotterdam-Maasvlakte (Collection: N.C. Kerkhoff, Schiedam)

II.3. INSECTIVORA

Soricidae Gray, 1821
***Sorex* cf. *araneus* Linnaeus, 1758**
(Common shrew)

Material: antemolar sup. dext., antemolar sup. sin., 2 M1 sin., i sin., m1 sin., mandibular fragment dext.

Provenance: Neede (The Neede Clay)

Measurements (in mm.):
M1 (Ne 101) : PE = 1.07, LL = 1.38, BL = 1.36, AW = –, PW = 1.57
M1 (Ne 102) : BL = 1.22
m1 (Ne 106) : TRW = 0.71, TAW = 0.83, L = 1.53

Description and remarks
The presence or absence of pigmentation of the teeth is an important diagnostic character for the genera of the family of the Soricidae. Unfortunately the soricid

material from Neede does not show any trace of the pigmentation. Therefore, the determination is based purely on morphological characters and on size.

The lower incisor is tricuspulate. The morphology and the measurements of the incisor and the molars correspond well to those of the fossils from Wageningen – Fransche Kamp which are referred to *Sorex araneus* (Van Kolfschoten, in press). Because we are dealing with a small number of specimens we prefer a 'confer' determination for the Neede material.

II.4. RODENTIA

Castoridae
Trogontherium cuvieri Fischer, 1809

Material:
mandible dext. with i1, p4 and m1 (N.H.M.E. no. 2553)
mandible dext. with p4, m1 and m2 (N.H.M.E. no. 2554)

Provenance: Neede (The Neede Clay)

Measurements:

i:	length: 12.6 – mm.,	width: 11.5 – mm.
p4:	length: 13.0-13.0 mm.,	width: 10.5-10.0 mm.
m1:	lenght: 7.4- 7.8 mm.,	width: 9.0- 9.5 mm.
m2:	lenght: - 8.1 mm.,	width: - 9.3 mm.

Description and remarks
The two mandibles (Figs. 15.1 and 15.2) are very well preserved; the two p4 both show the occurrence of an accessory antero- internal fold. For further information the reader is referred to Hooijer (1959) who described the mandibles in detail.

The dimensions of the p4 from Neede are smaller than the p4 from Rhenen (Kwinteloojen). They compare more with the dimensions of specimens from Bilzingsleben and Mauer and fall within the large range of variation of the fossils of *Trogontherium cuvieri* from e.g. Mosbach (see Table 5).

Mayhew (1978) revised *Trogontherium* species on the basis of material from a large number of localities and showed that there are two trends in the evolution of *Trogontherium* during the Early and Middle Pleistocene. Firstly there is a significant progressive change in the length-width ratio of the incisor dimensions through time. This change is independent of size. Therefore, the changing length-width ratio is considered to be of biostratigraphical value. The second trend is the posterior extension of the M3 and the anterior extension of the p4.

The length/width ratio of the incisor from Neede (Table 6) is low, indicating that the mandible is rather advanced. The two p4 from Neede show the presence of an accessory antero-internal fold, mentioned by Mayhew (1978) as being an advanced characteristic. This characteristic occurs occasionally in the

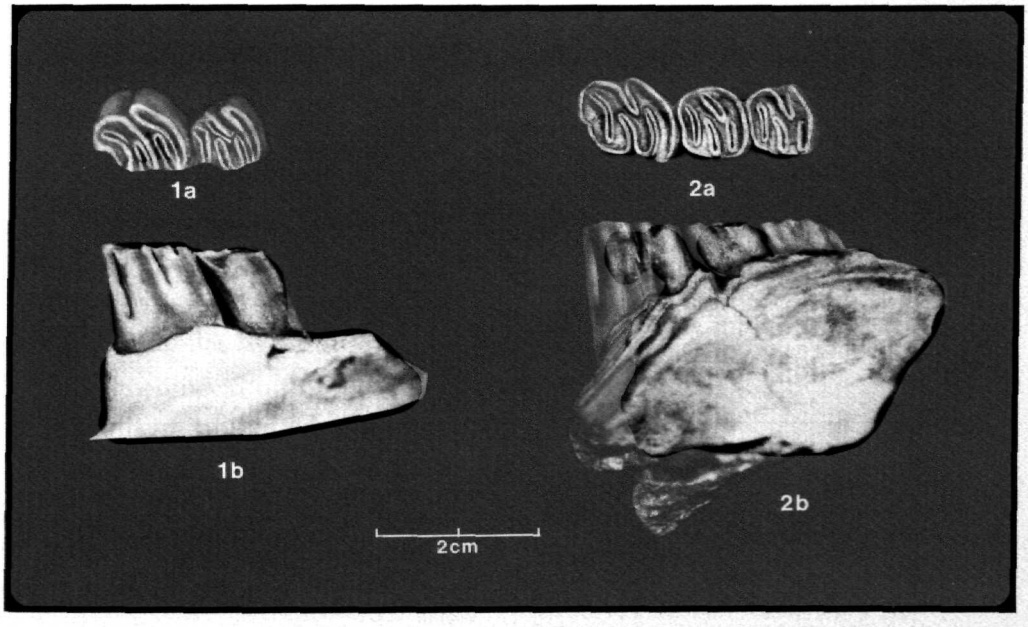


Fig. 15. Neede: 1 and 2: *Trogontherium cuvieri*: 1: mandibula dext. with p4 and m1 (coll. no. 2553): a: occlusal view; b: lingual view; 2: mandibula dext. with p4, m1 and m2 (coll. no. 2554): a: occlusal view; b: lingual view.

	N	length min.	length mean	length max.	width min.	width mean	width max.
Neede (N.H.M.E. 2553)			13.0			10.5	
(N.H.M.E. 2554)			13.0			10.0	
Rhenen			14.5			11.2	
Maasvlakte (RM 112)			14.2			10.6	
Bilzingsleben*	6	12.5	14.6	17.0	9.5	9.7	10.0
Mauer*	2	13.0	14.0	15.0	10.4	10.5	10.6
Mosbach*	20	7.8	-	18.6	8.8	-	11.2
Tegelen*	17	9.5	-	14.4	8.2	-	10.2

Table 5. The dimensions of the p4 of *Trogontherium cuvieri* from various localities. (* = information obtained from Mai (1979).

material of *Trogontherium cuvieri boisvilletti* from Tegelen and more frequently in the Mosbach collection. The p4 from the Maasvlakte, with a late Early Pleistocene age (Vervoort-Kerkhoff & Van Kolfschoten, 1988), also shows the presence of the anterior extension.

Arvicolidae Gray, 1821
***Clethrionomys* cf. *glareolus* (Schreber, 1780)**

Material: 18 enamel fragments

Provenance: Neede (The Neede Clay)

Measurements: -

Description and remarks
The enamel fragments from Neede mainly represent rooted molars. The enamel is relatively thick, the salient angles are rounded at their tips and the molars most probably had crown-cementum in the re-entrant folds.

There is not a single complete molar; only buccal or lingual parts have been preserved. The morphology and the size of the fragments correspond to the molars of the living bank vole *Clethrionomys glareolus* with which they were directly compared.

Arvicola terrestris cantiana

Material:
3 M1 dext., 2 M1 sin., 2 M2 dext., M2 sin., M3 dext., M3 sin., m1 dext., m1 sin., 3 m1/m2 dext., m1/m2 sin., m3 dext. (Fig. 16. 1-2)

Provenance: Neede (The Neede Clay)

Measurements:

	N	RANGE	MEAN	SE	SD
M1 length	3	2.99-3.20	3.063	0.056	0.097
M1 width	3	1.65-1.71	1.687	0.015	0.026
M2 length	2	2.09-2.26	2.175	0.060	0.085
M2 width	1	-	1.440	-	-
M3 length	2	2.31-2.32	2.315	0.004	0.005
M3 width	2	1.24-1.27	1.255	0.011	0.015

Description and remarks
The molars show a so-called *Mimomys* enamel differentiation (SDQ- values: 124 - 169; mean: 146.58; N: 12; see Chapter III) which allows the material to be determined as *Arvicola terrestris cantiana* The molars have about the same size as the molars of *A. terrestris* ssp. A from Maastricht-Belvédère 3 and 4.

Microtini indet.

Material: about 10 lamellar fragments

	length	width	length/width ratio min.	length/width ratio mean	length/width ratio max.	N
Neede	12.6	11.5		1.096		
Maasvlakte (RM 103)	12.3	15.6		1.268		
(RM 116)	11.3	14.2		1.257		
Mosbach*			1.088	1.161	1.315	28
West Runton*			1.162	1.263	1.320	4
Tegelen*			1.172	1.271	1.421	29

Table 6. Length, width and length/width ratio of the lower incisors of *Trogontherium cuvieri* from a number of localities. The information about the fossils from Mosbach, West Runton and Tegelen is obtained from Mayhew (1978) and Mai (1979).

Provenance: Neede (The Neede Clay)

Measurements: -

Description and remarks
A number of lamellar fragments of rootless molars, which are a little smaller than those of *Arvicola terrestris cantiana* and have thinner enamel, indicates the presence of Microtini, which include e.g. *Microtus* and *Pitymys*. However, the material is too incomplete to permit even a generic determination.

mus maastrichtiensis but does not share the morphological characteristics of this species in that the slopes of its cusps are not so vertical and the angle formed by the chevrons is smaller (see Van Kolfschoten, 1985). It is too short to be assigned to *A. sylvaticus*. Furthermore the m1 of *A. sylvaticus* usually has a well developed antero-central cusp. The morphology and the size of the m2 are about the same as those of the smallest m2 of *A. sylvaticus* from Maastricht-Belvédère faunas 3 and 4.

The molars differ from the lower molars of *Mus musculus* in having well developed labial accessory

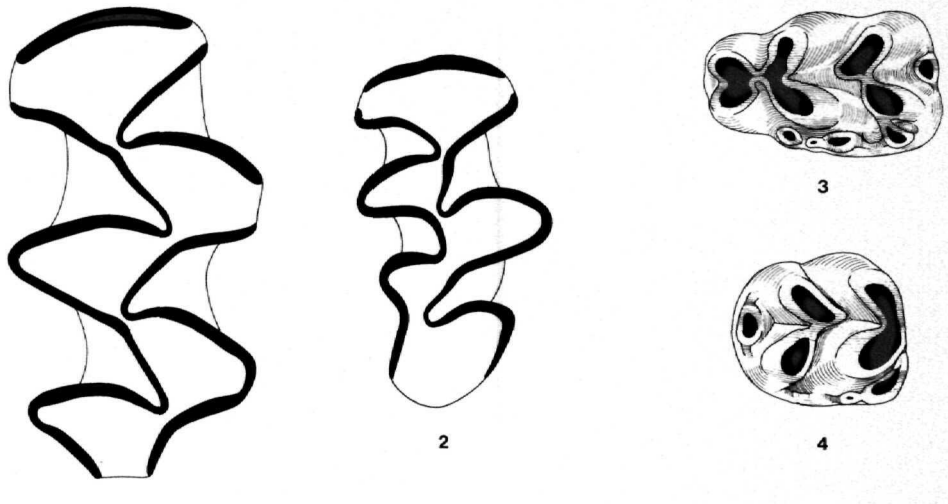


Fig. 16. Neede: 1 and 2: *Arvicola terrestris cantiana*: 1: M1 dext. (Ne 111); 2: M3 dext. (Ne 119); 3 and 4: *Apodemus* sp.: 3: m1 sin. (Ne 071); 4: m2 dext. (Ne 072).

Muridae
***Apodemus* sp.**
(Figs. 16.3 and 16.4)

Material: m1 sin., m2 dext.

Provenance: Neede (The Neede Clay)

Measurements:
m1: length 1,57 mm., width 0.99 mm.
m2: length 1.14 mm., width 1.03 mm.

Description and remarks
The antero-central cusp of the m1 is so small that it is hardly noticeable. The labial accessory cusps are well developed. The anterior cusps are connected with protoconid and metaconid. The angle between the two posterior parts of the chevrons in both molars is narrow. The antero-labial cusp of the m2 is well developed.

The m1 has the same length as the m1 of *Apodemus* cusps (Heinrich and Maul, 1983). The molars of *Micromys minutus* are much smaller (the length of the m1 varies between 1.23 and 1.36 mm (mean: 1.28 mm; N = 33) (Heinrich and Maul, 1983).

Because of the peculiar combination of characters and the small size of our sample we cannot assign these molars from Neede to a particular species.

II.5. PROBOSCIDEA

Elephantidae
***Elephas antiquus* Falconer and Cautley, 1845**
(Straight-tusked elephant)

Synonyms (incomplete):

Elephas antiquus Falc. in: Rutten, 1909, p. 19
Elephas antiquus Falconer in: Roding, 1953, p. 293
Elephas namadicus Falconer and Cautley, 1845 (partly) in: Maglio, 1973, p. 40
Elephas namadicus (Falconer and Cautley, 1845) in: Van Kolfschoten, 1981, p. 229

Palaeoloxodon antiquus (Falconer) in: Stuart, 1982, p. 44
Palaeoloxodon antiquus (Falconer) in: Guenther, 1984, p. 395
Elephas antiquus Falconer and Cautley, 1845 in:
Van Kolfschoten, 1985, p. 61.

Note:
Some authors (Guérin (1980), Guenther (1984), Stuart (1982) and Sutcliffe (1985) prefer to use the name *Palaeoloxodon antiquus* instead of *Elephas antiquus*. According to Maglio (1973) the diagnosis given for *Palaeoloxodon* is inadequate and cannot be maintained. The opinion of Maglio, who stated that the material should be assigned to *Elephas*, is followed by for instance Beden, 1976 and the present author. The genus *Elephas* is very diverse, but is united on cranial characteristics in which it contrasts sharply with the genus *Loxodonta* (Maglio, 1973).

Osborn (1942) referred two species to the genus *Elephas* (*Palaeoloxodon*): *E.* (*P.*) *antiquus* a European elephant and the Asiatic *E.* (*P.*) *namadicus*. Because of the similarities between the two species Maglio (1973) regards *Elephas antiquus* as a synonym of *E. namadicus*. However, many authors (including Beden, 1976) do not follow Maglio's opinion.

Aguirre (1969) states that the earliest forms of both species are difficult to distinguish. The molars of younger specimens differ clearly for instance in hypsodonty. *E. antiquus* developed high crowned, long and narrow molars with rather thin plates (Aguirre, 1969).

Material: molar fragments

Provenance: Maastricht-Belvédère 4 (Unit IV-C I, site G)

Measurements:-

Description and remarks
The fragments are very small and show the presence of strongly folded rather thick (about 2 mm.) enamel. In this character they resemble the molars of *Elephas antiquus*. The fragments are from unworn (pre) molars.

The presence of Elephantidae in fauna M-B 4 was already indicated by an ulna fragment (Van Kolfschoten, 1985).

II.6. PERISSODACTYLA

Equidae
Equus sp.

Material: metatarsus III dext. (incomplete) (Fig. 17.1) (Collection N.D.D.)

Provenance: Neede (The Neede Clay; the metatarsus was found in clay deposits, as is indicated by the clay attached to the specimen.)

Measurements:

estimated length:	275	mm
diaphysal width:	27.5	mm
antero-posterior diameter of the diaphysis:	32	mm
width of the articular facet for the *ectocuneiform*:	*ca.* 44	*mm*
supra-articular distal width:	46	mm

Description and remarks
The metatarsus is broken and severely eroded, the distal epiphysis is almost missing. The metatarsus must have belonged to an adult individual; this is indicated by the growing together of the diaphysis and the distal epiphysis. The slenderness of the metatarsus is remarkable. It is much more slender than the metatarsus known from Rhenen (see Table 7).

Slender metacarpals and metatarsals determined as *Equus hydruntinus* are known from Late Pleistocene deposits of the Brown Ridge area of the North Sea (Hooyer, 1984 and 1985). Dental material of *E. hydruntinus* is present in the old collection from Maastricht-Belvédère (Van Kolfschoten, 1985). Middle Pleistocene material of *E. hydruntinus* is known from the Neuwied Basin (Western Germany) and from Rhenen (see above).

During several different time intervals of the Pleistocene two types of horses, a slender and a more robust one, co-occurred in Northwestern Europe. The one from Neede belongs to the group of slender types. The antero-posterior diameter of the diaphysis of the specimen from Neede exceeds the range of the measurements of the metatarsals of *Equus hydruntinus* (26.5 - 30. 5 mm.) derived from literature and published by Hooyer, 1985. The metatarsus from Neede is, therefore, not assigned to that species.

Equus sp.

Material: P3 dext. and p3/4 dext.
(Coll. I.V.A.U.)(Figs. 18.2 and 18.3)

Provenance: Maastricht-Belvédère Unit III-A; Fauna 2

Measurements:
P4: length 31.4 mm., width 30.5 mm.,
length protocone 15.0 mm.
p4: length 30 mm., width 17.6 mm.

Description and remarks
The P3 is characterized by a long, well-developed protocone, a well-developed "plicabaline" and concave interstylar faces. The enamel is thin and undulated. The p4 shows some features which are regarded to be caballine features (Bouchud, 1972) such as: thin undulated enamel; a well-developed external groove ("ptychostylid"); external concave faces of protoconid and hypoconid. However, the shape of the double knot and the lingual V shaped sinus are stenonine characteristics.

The co-occurrence of caballine and stenonine characters in single molars is also present in molars of *Equus* cf. *steinheimensis* from La Fage (Bouchud, 1972). There is much correspondence in morphology and size between the premolar from Maastricht-Bel-

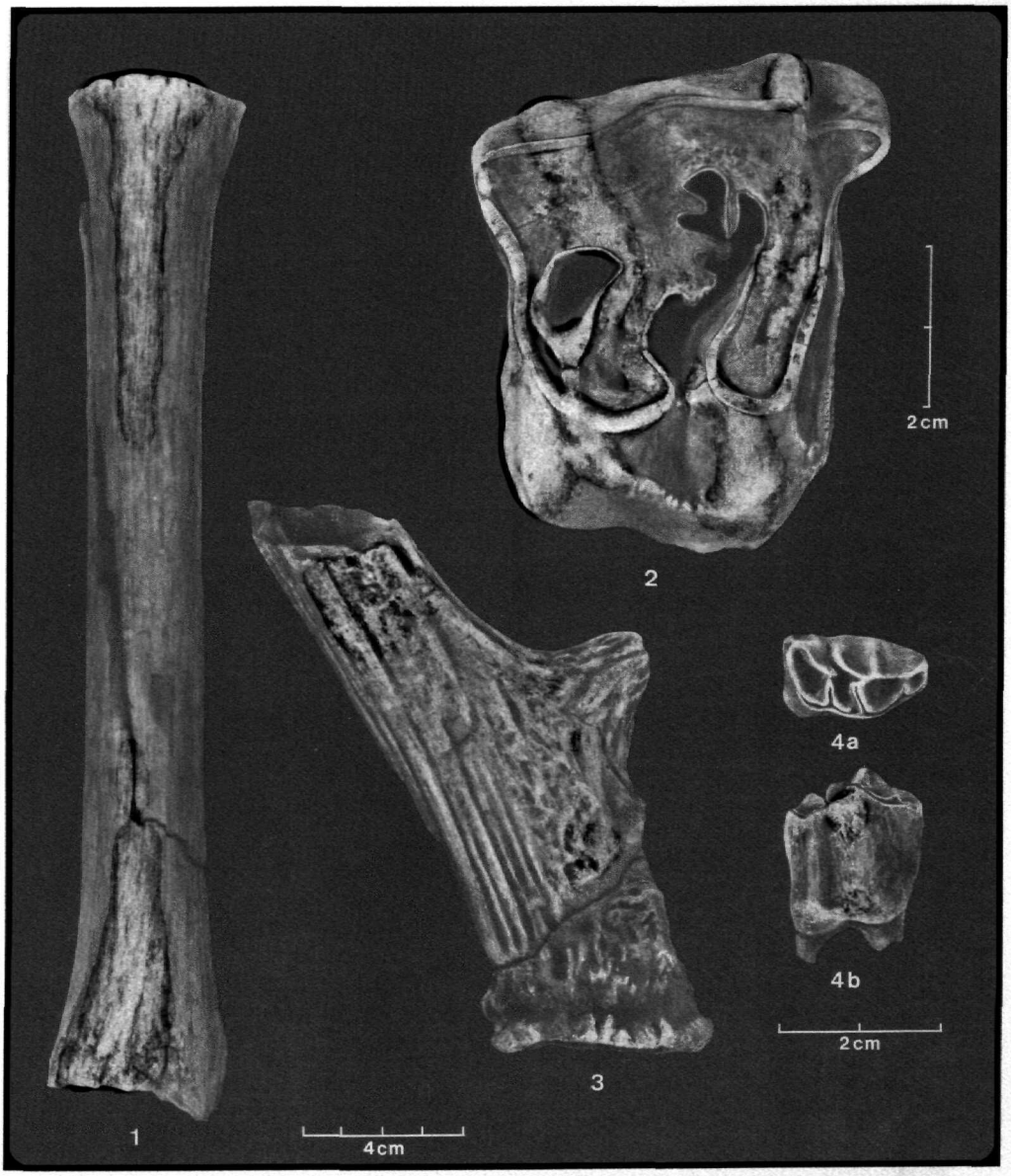


Fig. 17. Neede: 1: *Equus* sp.: metatarsus dext.; 2: *Dicerorhinus mercki*: P4 or M1 dext.: occlusal view; 3 - 4: *Cervus elaphus*: 3: antlerfragment (coll. RGM no. 85094); 4: p4 dext. (coll. RGM no. 61970) a: occlusal view; b: labial view.

védère and the premolars from La Fage. (measurements of the molars from La Fage (Bouchud, 1972): p3: 31.0 x 17.8 mm.; p4: 31.0 x 18.0 mm.). However, the upper premolar does not show the reduction of the protocone which is typical for *Equus steinheimensis* (Reichenau, 1915). Therefore, and because we are dealing with only two specimens, the author prefers to assign the molars to *Equus* sp.

***Equus* sp.**

Material: metatarsus dext. (Fig. 18.1)

Provenance: Maastricht-Belvédère Unit III-B

Measurements: see Table 7

	Equus sp.				*Equus steinheimensis*		
M	Neede	M-B 3	Rhenen RV 107	Heppenl. 7590		Steinheim	
					N	range	mean
1	27.5	40.4	40.0	41.5	8	37.9 - 41.6	39.01
2	32	33.2	34.8	38.5	8	34.2 - 41.2	37.83
3	–	57.6	–	61.0	6	53.0 - 61.0	57.17
4	–	50	–	53.0	6	43.9 - 49.5	46.02
5	44	58	–	54.0	7	48.4 - 57.0	51.63
6	–	13.0	–	12.5	4	13.4 - 17.3	15.23

Table 7. Measurements of the metatarsus of *Equus* sp. from Neede, Maastricht-Belvédère 3 and Rhenen and of *Equus steinheimensis* from Heppenloch and Steinheim (authors observations). The measurements are: 1: diaphysal width; 2: diaphysal antero-posterior diameter; 3: maximum proximal width; 4: maximum antero- posterior diameter; 5: width of the articular facet for the ectocuneiform; 6: diameter of the articular facet for the cuboid.

Description and remarks
The metatarsus represents a large and robust species. The dimensions of the metatarsus correspond fairly well with the dimensions of the metatarsus from Rhenen and fall within or just outside the ranges of the dimensions of metatarsus from Heppenloch and Steinheim assigned to *Equus steinheimensis* by Adam (1975) and Reichenau (1915) respectively. The diaphysal width and the maximum proximal width of the M-B specimen correspond also with the dimensions of the metatarsus of *Equus mosbachensis* from Mosbach (38.4 - 42; 55 - 61) but are slightly smaller than the dimensions of *Equus germanicus* from several localities (33 - 39; 49.5 - 57) (Reichenau, 1915).

Rhinocerotidae
***Dicerorhinus mercki* (Jäger, 1839)**

Material: P4 or M1 dext. (Coll.I.V.A.U.) (Fig. 17.2)

Provenance: Neede (The Neede Clay)

Measurements:

length	53.5 mm.
width	67 mm.
height of the crown	> 62 mm.

Remarks
Rutten (1909) gives a detailed description of the element which he determined as an M1. If its dimensions are compared with those of P4 and M1 of *D. mercki* (given by Guérin, 1980) it appears that the element is either a P4 or an M1. On the basis of the length/width ratio it is more likely that we are dealing with a P4 (Table 8).

The ectoloph is only slightly undulated and at a height of 2.5 cm above the base of the crown it has two very shallow grooves. In this characteristic it differs from the P4 of *D. hemitoechus* from Rhenen, which has four, more distinct grooves (Van Kolfschoten, 1981). Most of the ectolophs of the M1 of *D. hemitoechus* are also more deeply undulated than those of *D. merkci* (Guérin, 1980). Therefore I do not agree with Loose (1975), who assigned the tooth to *D. hemitoechus* without comment.

***Dicerorhinus hemitoechus* (Falconer, 1868)**
(Steppe rhinoceros)

Material: P2 - M3 dext., P2, M1 and M2 sin., skull-fragments, post-cranial bones of at least two individuals; a rather complete skeleton and an ulna dext. of a second one.

Provenance: Maastricht-Belvédère 3C (Unit IV-B)

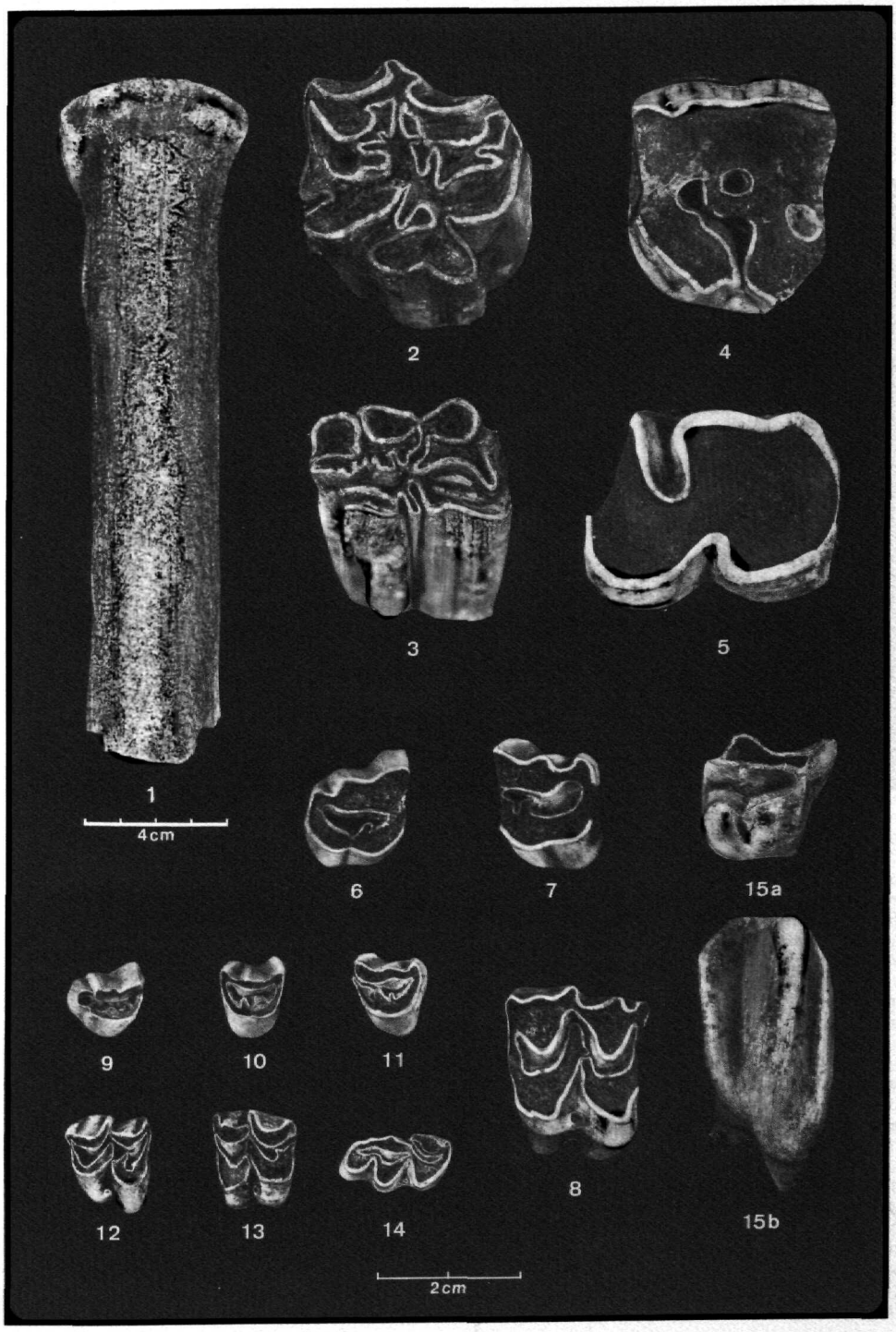
Measurements:

	LENGTH	WIDTH
P2 dext.	33.0 mm.	38.4 mm.
P2 sin.	32.6 mm.	40.5 mm.
P3 dext.	40.5 mm.	48.6 mm.
P4 dext.	44.0 mm.	55.0 mm
M1 dext.	50.0 mm.	64.0 mm.
M1 sin.	50.6 mm.	65.5 mm.
M2 dext.	57.6 mm.	62.2 mm.
M2 sin.	57.5 mm.	65.2 mm.
M3 dext.	63.0 mm.	59.0 mm.

Description and remarks
The enamel of the (pre)molars (Fig. 19) is finely rugose, looks a little leathery and is locally covered with much cement. The profiles of the ectolophs show relatively strong undulations, typical for the upper (pre)molars of *D. hemitoechus* (Guérin, 1980). The (pre)molars, except for the P2, have a well-developed crochet; the anticrochet is absent (P2 - M1) or small (M2 and M3). Only the M2 dext. and the M3 have a closed medifossette. An internal cingulum is, if present, small and discontinuous.

The morphological characteristics of the (pre)molars and their dimensions correspond well with those of *D. hemitoechus* from various localities as described by

Fig. 18. Maastricht-Belvédère: M-B 3: 1: *Equus* sp.: metatarsus dext.: M-B 2: 2 - 3: *Equus* sp.: upper premolar dext.; 3: lower premolar dext.: M-B 4: 4 - 5: *Dicerorhinus hemitoechus*: 4: DP2 sin.; 5: m1/2 dext.: 6 - 8: *Cervus elaphus*: 6: P3 sin.; 7: P4 dext.; 8: M1 dext.: 9 - 14: *Capreolus capreolus*: 9: P2 sin.; 10: P4 sin.; 11: P4 dext.; 12: M1/2 dext.; 13: M1/2 sin.; 14: m3 dext.: 15: Bovidae indet.: P2 sin.: a: occlusal view; b: buccal view.


1
4cm
2
3
4
5
6
7
15a
9
10
11
8
15b
12
13
14
2cm

	P4			M1		
	N	RANGE	MEAN	N	RANGE	MEAN
length	26	43.5-58	(51.06)	12	48.5-63.5	(57.33)
width	31	54 -69.5	(62.71)	21	55 -68	(62.21)
height	2	50 -77	(65.50)	3	61 -64	(62.17)

Table 8. Measurements of P4 and M1 of *Dicerorhinus mercki* from several European localities (after Guérin, 1980).

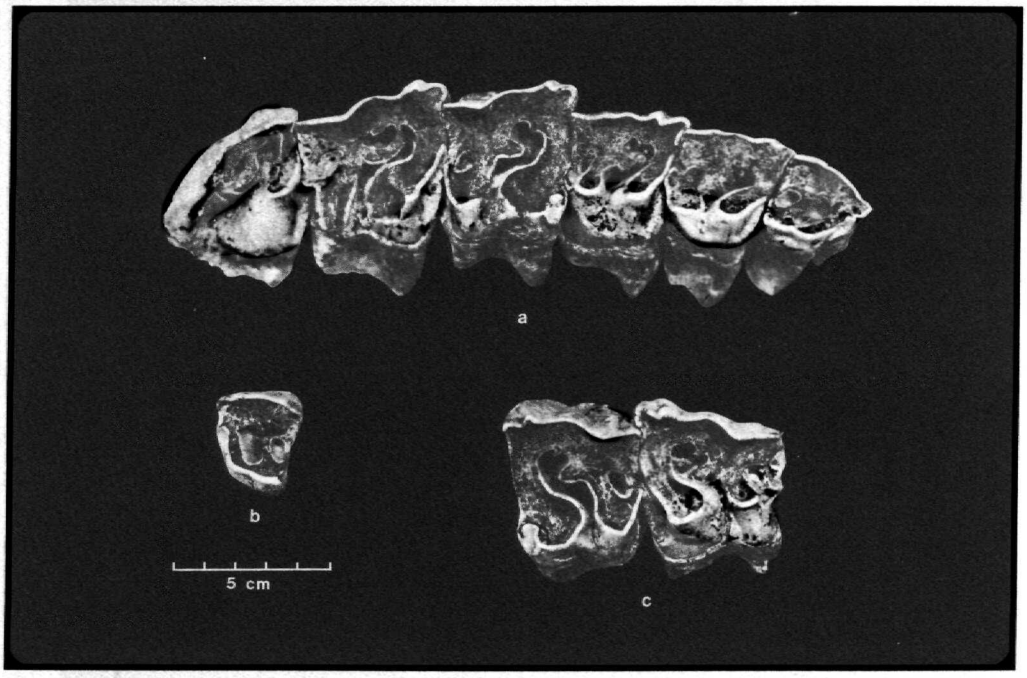


Fig. 19. *Dicerorhinus hemitoechus* (Maastricht-Belvédère fauna 3C): a: P2 - M3 dext.; b: P2 sin.; c: M1 and M2 sin.

Guérin (1980) and with the characteristics of the P4 from Rhenen (van Kolfschoten, 1981) (see also Table 9). The (pre)molars are not assigned to *Coelodonta antiquitatis* because the molars of that species have mainly a closed medifossette and rather rough enamel. The molars of *Dicerorhinus mercki* are in general larger (Table 9) and have less undulated ectolophs (Guérin, 1980).

A review of the skeletal material present is given by Van Kolfschoten, 1988. The bones have not been studied in detail yet. They will be described in another paper.

Dicerorhinus hemitoechus

Material: DP2 sin.,DP3/4 dext., 3 upper milk-molar fragments, 3 upper (pre)molar fragments, m1/2 dext., 2 lower molar fragments, sacrum fragment, radius fragment

Provenance: Maastricht-Belvédère 4 (Unit IV-C I, site G)

Measurements:
DP2 length >28.9 mm., width 34.0 mm.
m1/2 length 36.0 mm., width 29.0 mm.

Description and remarks
The DP2 (Fig. 18.4) and the lower molar are both very worn. The milk-molar has smooth very thin enamel, the enamel of the lower molar is much thicker. The profiles of the ectolophs of the milk- molars are undulated like those of *D. hemitoechus* from Lunel-Viel and more undulated than the profiles of milk-molars of *D. mercki* (Guérin, 1980).

The size of the DP2 falls within the range of the measurements of DP2 of *D. hemitoechus* (length (N = 16): range 33 - 38, mean 35,38; width (N = 22): range 30 - 38,5; mean 34.41) from several localities (Guérin, 1980).

Besides these specimens there are a number of

	D. mercki	*D. hemitoechus*		
	Neede	Rhenen		Maastricht-Belvédère 3C
	P4/M1	P4	P4	M1
Length	53.5	45.6	44.0	50.0 - 50.6
Width	67.0	62.0	55.0	64.0 - 65.5

Table 9. The dimensions of the (pre)molars of *Dicerorhinus mercki* from Neede and of *D. hemitoechus* from Rhenen and Maastricht-Belvédère Fauna 3C.

fragments of milk-molars and (pre)molars and fragmented bone material of a rhinoceros. Milk-molars of this species are also known from site C. (see Van Kolfschoten, 1985).

The complete and fragmentary milk-molars and the fragments of unworn (pre)molars indicate that we are dealing with young individuals. However, at least one specimen, the much worn m1/2 (Fig. 18.5), shows the presence of a very old individual.

II.7. ARTIODACTYLA

Cervidae
Cervus elaphus Linnaeus, 1758
(Red deer)

Material: 18 antler fragments, p4 dext., 3 vertebrae lumbalis, scapula sin., humerus dext., 2 humerus sin., navicocuboid sin., metacarpus dext., metacarpus sin., 2 tibia sin., 3 astragalus dext., 2 astragalus sin., 2 calcaneum dext., 3 metatarsus sin., first phalange.

(material in the collections of: R.G.M. (most of the material), I.V.A.U., N.H.M.E., N.D.D., the village of Neede and Mr. A. Buter, Borne)

Provenance: Neede (The Neede Clay)

Measurements:

p4: length	18.2 mm.
width (at the base of the crown)	11.2 mm.
height of the crown	17.5 mm.
metacarpus: proximal width	45 mm.
proximal antero-posterior diameter	31 mm.
tibia: distal width	43 - 49 mm.
distal antero-posterior diameter	36 - 41 mm.
astragalus: length	53 - 55 mm.
proximal width	31.4 - 32.5 mm.
distal width	30.9 - 35.5 mm.
calcaneum: width	29 - 34 mm.
antero-posterior diameter	33 - 37 mm.
metatarsus: proximal width	40 mm.
proximal antero-posterior diameter	43 mm.
diaphysal width	22.5 mm.
antero-posterior diameter of the diaphyse	23 - 29 mm.
first phalange: length	61 mm.
proximal width	21.5 mm.
prox. antero-posterior diameter	26 mm.
distal width	20 mm.
dist. antero-posterior diameter	16 mm.

Description and remarks
The vertebrae, astragali, one calcaneum and the first phalange are the only more or less complete bones, the others are very fragmentary. The material is in various states of preservation, which may indicate that some fossils derive from other lithological levels than those from the Neede Clay. One of the astragali clearly shows gnawing traces.

The antler fossils consist of a few proximal fragments (Fig. 17.3), beam fragments and terminal tines, all with a more or less rugged surface. The proximal parts have a brown tine and a bez tine within a small distance of the burr. This is characteristic for the more developed antlers of the red deer *Cervus elaphus*. Unfortunately the material is too incomplete for us to decide whether the antler belonged to the subspecies *C. e. acoronatus* or *C. e. elaphus*. The top of the antlers of strong adult individuals of *C. e. acoronatus* comprises a simple two-point transverse fork, very occasionally with a small accessory point between and in the plane of the two main points (Lister, 1985). The fully grown antlers of *C. e. elaphus* are characterised by a main pointed three dimensional "crown". They are known from amongst others the fauna Ariendorf 2.

The p4 (Fig. 17.4) is nearly unworn and has the same morphology and size as the p4 of the living red deer with which it was directly compared. Its dimensions are comparable with those of a p4 from La Fage with a length of 17.9 mm. and a width of 9.7 mm. (Crégut-Bonnoure & Guérin, 1982).

Cervus elaphus

Material: antler, P3 sin., P4 dext., M1 dext., i2 sin., metatarsus dext. (Fig. 18. 6-8)

Provenance: Maastricht-Belvédère 4 (Unit IV-C I, site G)

Measurements:

P3	length 16.4 mm., width 15.0 mm.
P4	length 14.5 mm., width 18.8 mm.
M1	length 21.0 mm., width 22.0 mm.

Description and remarks
The almost complete antler is badly preserved. The shed antler has a brow and a trez tine and two termi-

nal tines, indicating that it is not fully grown. Therefore we cannot tell whether it is a simple antler of *C. elaphus acoronatus* or one of *C. elaphus elephas*.

The state of wear of the upper (pre)molars indicates that they derive from one individual. They are the same size as those of the extant red deer with which they have been compared. The metatarsus is incomplete; only a fragment of the proximal part is present.

***Capreolus capreolus* Linnaeus, 1758**
(Roe deer)

Material: DP3 dext., P2 sin., P4 dext., P4 sin., M1/2 dext., M1/2 sin., m3 dext., lower molar fragment (Fig. 18: 9 - 14)

Provenance: Maastricht-Belvédère 4 (Unit IV-C I, site G)

Measurements:
P2 length 10.4 mm., width 9.4 mm.
P4 length 9.1 mm., width 11.3 - 11.5 mm.
M1/2 length 11.9 mm., width 14.7 - 14.9 mm.
m3 length 15.0 mm., width 8.3 mm.

Description and remarks
The (pre)molars (except for the m3) are only slightly worn, the state of wear indicates that they probably derived from the same young individual. The very worn m3 represents an old fully grown individual. The dimensions of the elements are similar to those of the living roe deer.

Bovidae
Bovidae indet.
(large bovid)

Material: P2 sin. (Fig. 18: 15 a-b)

Provenance: Maastricht-Belvédère 4 (Unit IV-C i, site G)

Measurements: length 20.1 mm., width 16.7 mm., height of the crown larger than 36 mm.

Description and remarks
The premolar is characterized by a very high crown which is much higher than the crowns of the molars of *Cervus elaphus* from the same locality and the same site. The assignment to the Bovidae is based on this character. The dimensions of the premolar indicate that we are dealing with a large bovid (*Bos/Bison*). A more specific determination cannot be made.

III. TAXONOMY AND EVOLUTION OF *ARVICOLA* LACÉPÉDE, 1799

The genus *Arvicola* will be discussed in detail because of its generally accepted biostratigraphic significance for the Middle and Late Pleistocene.

Modern species and subspecies
The genus *Arvicola* is represented in the present European fauna by two species, *A. terrestris* and *A. sapidus*. *Arvicola terrestris* has a karyotype 2n = 36 whereas the karyotype for *A. sapidus* is 2n = 40. Furthermore the two species differ in the shape of the nasal bones. (Reichstein, 1982).

The morphology of the molars of *A. terrestris* and *A. sapidus* is almost identical. The molars are rootless and have crown- cementum in their re-entrant folds. The occlusal surface of the m1 shows a posterior lobe, three closed triangles and an anteroconid complex (Fig. 20).

A. sapidus ranges from Portugal through Spain and southern France eastwards to the Italian border. *A. sapidus* is subdivided into two subspecies; *A. s. sapidus* occurring in the southern part of the area of distribution and *A. s. tenebricus* is living in the northern part. *A. sapidus* is much larger than *A. terrestris* from the same area (Röttger, 1986).

Arvicola terrestris has an extremely wide, Palaearctic, distribution. The species is present in almost the whole of Europe; it extends through Siberia to the Pacific Ocean in the east and as far as Iran in the south (Nadachowski, 1982). The species shows a large variability and is subdivided into a large number of subspecies. Reichstein (1982) presents a list of the subspecies which occur in Europe.

Northern Europe (i.e. Scandinavia and Denmark) is inhabited by *A. t. terrestris*, a subspecies which is predominantly surface dwelling during the summer and which is characterized by a relatively dolichocephalic skull. *Arvicola t. exitus* occurs in the alpine region and westwards in western central and southern France. This subspecies is adapted to a burrowing way of life and has a short tail and short legs (Kratochvil, 1983). *A. t. exitus* differs from *A. t. terrestris* in the smaller curvature of the incisors. Those of *A. t. terrestris* are more orthodont (see Reichstein, 1982).

A. t. scherman resembles *A. t. exitus* although most of the populations of *A. t. scherman* are predominantly surface dwelling. The subspecies occurs in the northern part of Western Europe, in a territory north of the Alps and in the whole Carpathian area. Populations of this subspecies are intermingled with immigrants of eastern origin and are therefore rather variable (Kratochvil, 1983). The body dimensions of *A. t. scherman* decrease in two directions; from north to south and from lower altitudes to higher altitudes in Central Europe and the Carpathians (Kratochvil, 1983). *A. t. persicus* occurs in Turkey and Iran and has a semi-aquatic habit.

There is a large variation in the size between the individuals of the different populations of *Arvicola* (Reichstein, 1982; Röttger, 1986). The largest representatives of *A. terrestris* are *A. t. amphibius* which inhabit Great Britain. They are almost as large as the *A. sapidus* from Spain. The smallest specimens, occurring in Liechtenstein and assigned to *A. terrestris exitus*, are about 20% smaller than those from Great Britain.

Fossil species

The fossil representatives of the genus *Arvicola* have been assigned to a large number of different species. The earliest representatives of *Arvicola* are generally supposed to be the direct descendants of *Mimomys savini*. The dentition of the latter differs from that of the former only in the presence of roots. The morphologies of the occlusal surface of m1 of the oldest representatives of *Arvicola*, and of *Mimomys savini*, are very similar. The differences of the occlusal patterns led Hinton (1926) to distinguish a number of morphotypes upon which he based the species: *Mimomys savini, M. intermedius, M. majori, M. cantianus, Arvicola bactonensis, A. greenii, A. praeceptor* and *A. mosbachensis*.

Fejfar (in Von Koenigswald, 1970) re-examined the holotype of *Mimomys cantianus* and found no trace of root – formation. This form must, therefore, be included in the genus *Arvicola*. Kretzoi (1965) indicated that *M. intermedius (= M. milleri), M. majori* and *M. savini* should be regarded as a single species: to be called *M. savini*.

The different morphotypes in *Arvicola*, distinguished by Hinton (1926), occur together in assemblages from localities such as Petersbuch (Von Koenigswald, 1970) and Miesenheim I (this paper). Therefore, all primitive representatives of *Arvicola* such as *A. bactonensis, A. greenii, A. praeceptor* and *A. mosbachensis* are included in *A. cantiana*, because the name *Arvicola cantiana* (Hinton, 1926) has priority (Sutcliffe and Kowalski, 1976).

Storch (1973) described *Arvicola antiquus* from Late Pleistocene deposits of Brillenhöhle (Western Germany). He distinguished this species on the basis of a number of characters in which his material differs from the living *A. terrestris*, i.e. the pro-odontism of the incisors, the shape of the nasal bones, large variation in the morphology of the m1, large dimensions of the the condyle of the mandible.

However, the living *A. terrestris* shows a large variation in the curvature of the incisors and in size, and *A. t. stankovici* from Siberia (like *A. antiquus*) has nasal bones whose shape resembles that of *A. sapidus* (Reichstein, 1982). Therefore the differences described by Storch seem to be insufficient to distinguish a third *Arvicola* species, but sufficient for a subspecies.

Carls (1986) defined a new species, *Arvicola hunasensis* from the late Middle Pleistocene deposits at Hunas (Western Germany). The molars of this species are characterized by equally thick enamel on both sides of the dentine fields, i.e. a morphology intermediate between *A. cantiana* and *A. terrestris* (see below). Molars which do not show a clear differentiation in the enamel thickness have been hitherto assigned to *A. cantiana/terrestris* by for instance Von Koenigswald (1973), Sutcliffe and Kowalski (1976), and Van Kolfschoten (1985, 1986).

Evaluation of the dental characters used in the systematics and evolution of *Arvicola*

Almost all fossil species have been defined on dental characters: thickness of the enamel of one or more molars, morphology of m1 and M3, and size of the molars (m1 in particular). All these characters have also been used to demonstrate evolution in *Arvicola*.

Enamel thickness

The occlusal surface of the molars of *Arvicola* shows a number of dentine fields. The outer sides of these fields are covered with enamel. The salient angles of the lower molars consist of a concave anterior enamel edge and a convex posterior enamel edge. In the upper molars this situation is reversed.

During the longitudinal movement of mastication the anterior concave edges of the lower molars and the posterior concave edges of the upper molars occlude first and are therefore called the leading edges. The convex edges of both lower and upper molars are called the trailing edges (Von Koenigswald, 1982).

Three different microstructural types have been distinguished in the enamel of the molars of the Arvicolidae (Von Koenigswald, 1980): radial, tangential and lamellar enamel. The leading edges consist of two layers: an inner layer of lamellar enamel which comprises more than 50% of the total thickness of the edge, and an outer layer of radial enamel. The convex trailing edges also consist of two different layers. The inner layer is composed of radial enamel and the outer one of tangential enamel.

In the living *Arvicola t. terrestris* and most of the other recent subspecies, the trailing edges are thinner than the leading edges and are easily worn, since they cannot withstand the chewing forces. The trailing edges, being lower than the leading edges, do not work as cutting edges. Molars with reduced trailing edges have the so-called *Microtus* enamel thickness differentiation (in short *Microtus* differentiation).

The molars of most of the *Mimomys* species have the so-called *Mimomys* enamel differentiation. The enamel of the trailing edges is markedly thicker than that of the leading edges. The tangential enamel of the trailing edges lacks strengthening elements in the third dimension. So it is assumed by Von Koenigswald (1982) that the poor quality of the enamel is compensated by an increase in quantity.

Until recently it was generally accepted that the main evolutionary trend in the lineage *Arvicola cantiana – Arvicola terrestris* is the change in the thickness of the enamel, from *Mimomys* to *Microtus* differentiation (a.o.: Von Koenigswald, 1973; Heinrich, 1978, 1982; Sutcliffe and Kowalski, 1976).

In the succession of Middle and Late Pleistocene faunas, which is based on criteria other than *Arvicola* evolution, one can observe the reduction of the trailing edges (Von Koenigswald, 1973). All molars of *Mimomys savini*, the supposed ancestor of *Arvicola terrestris*, have a *Mimomys* enamel differentiation just like the molars assigned to *Arvicola cantiana* from e.g. Mauer, Hundsheim, Swanscombe, Petersbuch

and Heppenloch (Von Koenigswald, 1973).

Arvicola molars without a distinct enamel differentiation are known from the faunas from Tornewton Cave (Glutton Stratum) and Erkenbrachtsweiler (Von Koenigswald, 1973). These faunas are regarded as younger than the faunas from Petersbuch and Heppenloch because of e.g. the absence of *Talpa minor*, which still occurs in the faunas from Petersbuch and Heppenloch. The stratigraphically youngest and recent *Arvicola*-molars from Central and Western Europe have a *Microtus* enamel differentiation.

The evolution of *Arvicola*, as is indicated by Von Koenigswald (1973) for fossils of Central European faunas, can also be traced in the British faunas (Sutcliffe and Kowalski, 1976). Jánossy (1976) noticed the same evolution in the Hungarian faunas.

Heinrich (1982) measured the thickness of the enamel in the first lower molars of *Arvicola* from a large number of localities in Central Europe. He demonstrated the same evolutionary trend: reduction of the trailing edges and an increase in the thickness of the leading edges.

To quantify the differences in the enamel thicknesses Heinrich (1978) proposed to calculate the enamel thickness quotient (SDQ in the terminology of Heinrich, 1982). He measured the enamel thickness on both sides of the saliant angles of the m1 (see Fig. 20.4), dividing the value of the trailing edge by the one of the leading edge and multiplying the quotient by 100. The SDQ of one molar is the mean of the SDQ-values of all salient angles.

The present author calculated the SDQ values of all elements of *Arvicola* from the Miesenheim I assemblage (the largest sample available) in order to compare the results for m1 with those for the other elements (Fig. 20 and 21). It appears that there are no significant differences between the obtained ratios and that measuring all elements is useful to increase the statistical sample.

Röttger (1986, 1987), who studied the geographical and interspecific variation of recent populations of *Arvicola*, calculated SDQ values (Table 10) following the method of Heinrich (1978). However, she measured only the fourth lingual salient angle of the lower m1 and the second buccal salient angle at the upper M3. Her results will be discussed below.

The SDQ values of all the *Arvicola* molars from the localities discussed in this paper have been calculated (Fig. 22). The *Arvicola* molars from Ariendorf 1 and 2 are badly preserved and difficult to measure. The succession of the faunas in the diagram is first of all based on stratigraphical data. The material from Neede has a Holsteinian Age, the fauna Ariendorf 1 has a post-Holsteinian Age because of the occurrence of *Coelodonta antiquitatis* which appeared in Europe after the Holsteinian (see Chapter 4). The faunas M-B 3-4 also post-date the appearance of *Coelodonta antiquitatis* because this species is known from the same locality, from a stratigraphically lower level. The fauna from Rhenen is collected from ice-pushed sediments, so it has a pre-Eemian Age just like the faunas Ariendorf 2 and Plaidter-Hummerich I. The fauna M-B 5 is obtained from a unit above a paleosol which is correlated with the Eemian "Sol de Rocourt".

There is a significant difference, at the 95 % confidence level, between the SDQ values of the *A. t. cantiana* population from Miesenheim I and the *A. terrestris* ssp. A population of M-B 4 and between the values of the superimposed assemblages M-B 4 and 5 and between those of the superimposed faunas Ariendorf 1 and 2. The SDQ values of the populations from Rhenen, Ariendorf 2, Plaidter Hummerich I and Maastricht-Belvédère 5 assigned to *A. terrestris* ssp. B do not differ significantly.

Table 11 shows the SDQ values of the *Arvicola* molars of the faunas discussed in this paper and of the populations from Central Europe as presented by Heinrich (1987). Both successions show the same trend. The older populations are characterized by high SDQ values whereas the younger populations have lower values. The SDQ values of the older *Arvicola* populations from the areas discussed in this paper are higher than those of the older Central European populations. These differences suggest that our populations should be older than the Central European ones. However, the mean SDQ values of the molars from Neede and Miesenheim I are even higher than those of the molars of *Mimomys savini*, the ancestor of *Arvicola*. It is therefore very unlikely that the observed differences are due to differences in age. At the moment I am unable to explain the differences.

In our succession Eemian faunas are missing whereas late Saalian data are lacking in Heinrich's succession. We know very little about Dutch faunas dating to the Eemian. It is remarkable that Eemian faunas from Central Europe have higher SDQ values than the populations from Rhenen, Ariendorf 2 and Plaidter-Hummerich I with a pre-Eemian Age (see Chapter I). There are many Eemian faunas known from the British Isles which show the occurrence of *Arvicola* molars with a *Mimomys* enamel differentiation during the Ipswichian (= Eemian) (Stuart, 1982; Lister & Stuart in: Coxon *et al.*, 1980). This confirms the data presented by Heinrich (1982, 1987), and my conclusion is that the trend in enamel differentiation is not a simple progressive one, of decreasing SDQ values, but one with an important fluctuation.

There is a decrease in SDQ values from about 120 to about 80 during the Saalian. At the beginning of the Eemian there is a significant increase in the SDQ values of the *Arvicola* populations in N.W. and Central Europe. In my opinion, this is due to the immigration of a population with molars with higher SDQ values. This hypothesis is based on the work of Röttger (1986, 1987) who studied extant *Arvicola* populations from Europe, Turkey and Iran to investigate the interspecific variation in the molars. Her results (Table 10) show that there is a large variation in the differentiation of the enamel thickness in the extant *Arvicola* subspecies. The Western European populations show the so-called *Microtus* differentiation whereas the populations from Iran show the *Mimomys* enamel diffe-

Subspecies and geographical provenance	SDQ-values m1	M3	N
A. terrestris amphibius (Great Britain: Shropshire)	72.5	70.7	19
A. terrestris terrestris (West Germany: northern part)	74.3	74.6	35
A. terrestris sherman (West Germany: Bonn)	78.1	76.9	54
A. terrestris sherman (West Germany: Trier)	75.7	76.1	11
A. terrestris sherman (France: eastern part)	65.7	71.9	16
A. terrestris exitus (Switzerland: Interlaken)	68.8	69.4	33
A. terrestris exitus (Liechtenstein)	71.6	75.2	8
A. terrestris sherman (Hungary: Fehértó)	93.8	94.3	4
A. terrestris italicus (Northern Italy: Turin)	94.2	93.0	13
A. terrestris musignani (Southern Italy: Camigliatello)	98.4	106.0	7
A. terrestris persicus (Turkey: Tatvan)	124.6	131.9	5
A. terrestris persicus (Iran)	134.4	148.1	3
A. terrestris monticola (Northern Spain: Reinosa)	73.3	68.1	12
A. sapidus sapidus (Western Spain: Salamanca)	119.7	119.0	31
A. sapidus sapidus Northern Spain: Villarréal de Alava)	120.8	120.6	4

Table 10. The SDQ-values of the m1 and M3 of the molars of recent populations of *Arvicola terrestris* ssp. and *Arvicola sapidus* ssp. from various areas (after Röttger, 1987; with minor modifications).

rentiation (Fig. 23). The values for Hungary and Italy are intermediate.

Röttger's results indicate not only the occurrence of "advanced" populations in N.W. Europe and "primitive" populations in S. E. Europe. Her SDQ values seem to indicate also a biogeographical gradient. Furthermore she found out the that subspecies of *A. terrestris* with a *Mimomys* enamel differentiation for instance *A. t. persicus* live semi-aquatically whereas subspecies with a *Microtus* enamel differentiation are semi-aquatic or fully terrestrial. This might indicate that the *Microtus* enamel differentiation can be regarded as an adaptation by the terrestrial forms to the use of more abrasive nutrition (Röttger, 1987).

Röttger's results show also that we should not define a distinct species on the basis of its degree of differentiation of the enamel. Nadachowski (1982) stated that it is better to base the systematics of the genus *Arvicola* on other characters as well, for instance on the variation in the frequency of morphotypes.

The morphology of m1 and M3

Carls (1986) studied the morphology of the *Arvicola* molars from 15 Middle and Late Pleistocene faunas and of the living *Arvicola terrestris* and *A. sapidus*. All populations studied by her show a large variation in the morphology of the anterior loop of the m1. She distinguished 8 morphotypes on the basis of e.g. the presence or absence of a *Mimomys* ridge (an extra edge on the anterior margin of the third buccal salient angle) and the development of the different anterior re-entrant angles. According to Carls (1986) there are, in the coarse of time, changes in the relative frequency of certain morphotypes. Molars with a *Mimomys* ridge occur most frequently (but not more than 20 %) in the Middle Pleistocene faunas such as Petersbuch and Hunas. They still occur, but in very low percentages, in populations of the living *Arvicola terrestris*. Molars with a so-called intermedius morphotype, characterized by very shallow anterior re-entrant angles, are restricted to the Middle Pleistocene populations from Hunas; they do not occur in the population from

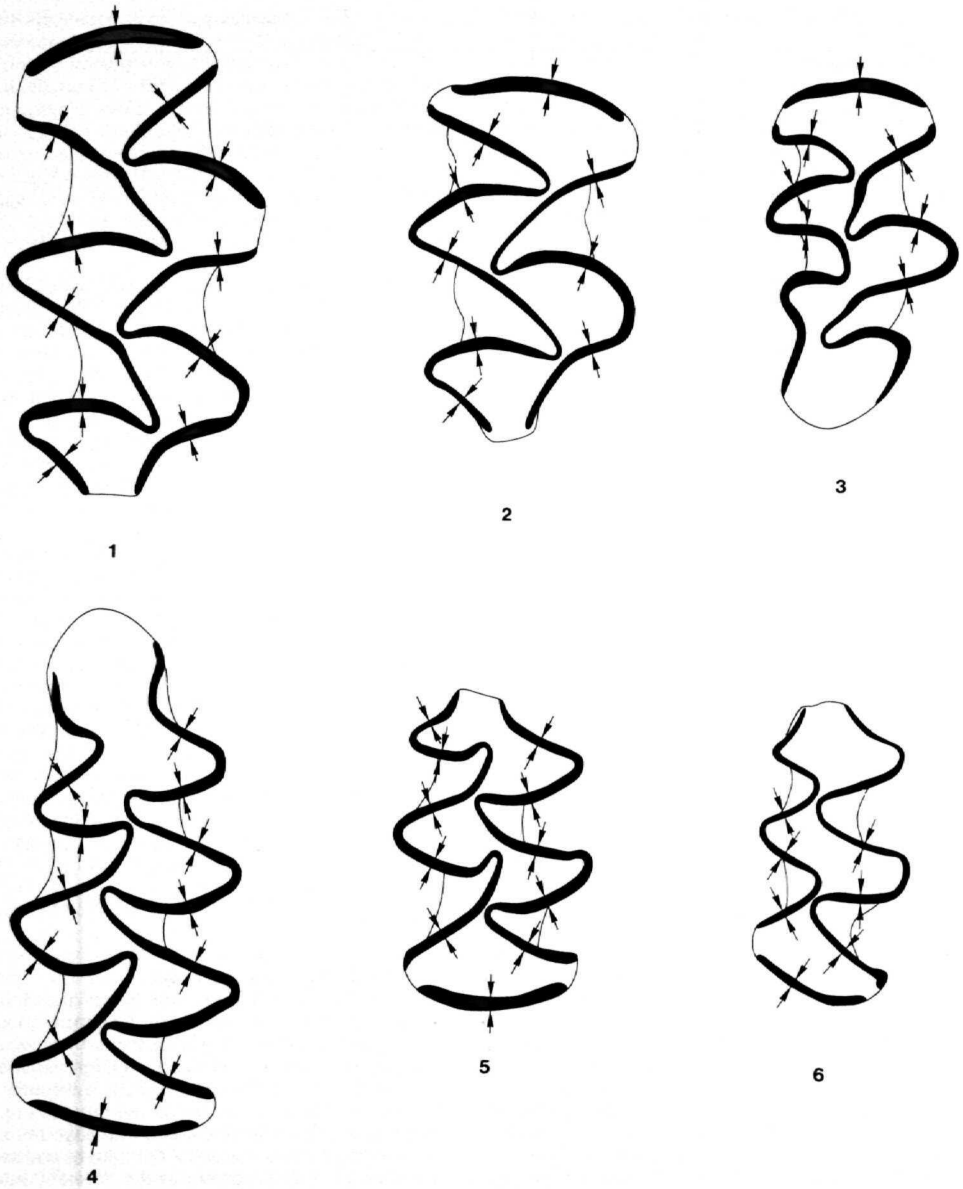


Fig. 20. The places where the thickness of the enamel band of the upper (1 - 3) and lower (4 - 6) *Arvicola* molars are measured in order to calculate the enamel thickness quotient of the molars. 1: M1; 2: M2; 3: M3; 4: m1; 5: m2; 6: m3.

Petersbuch. The other morphotypes occur in various frequencies in nearly all the populations studied by Carls (1986).

In the population from Miesenheim I there is much variation in the morphology of the anterior loop of the m1. Most of the molars have a symmetrical anterior cap with rather deep re-entrant angles (Fig. 13.9). In two out of twenty-eight specimens the anterior re-entrant angles are very shallow (intermedius type). Seven out of twenty-eight molars have an asymmetrical anterior loop with differences in the development

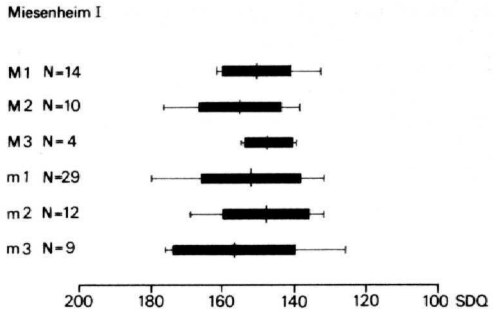


Fig. 21. The range, standard deviation and mean of the enamel thickness quotient (SDQ values) of the molars of *Arvicola terrestris cantiana* from Miesenheim I.

of the salient angles (Fig. 13.3); In five of them the lingual re-entrant angle is deeper than the buccal one. Five molars show the presence of a small so-called "*Mimomys*-ridge" (Fig. 13.4).

Except for one m1 all seven molars from Maastricht-Belvédère fauna 3 and 4 have rather deep anterior re-entrant angles. The other has shallow re-entrant angles. The anterior re-entrant angles of the four m1 from Wageningen – Fransche Kamp are well developed, the buccal one is a little deeper than the lingual one.

Three molars from Rhenen have deep anterior re-entrant angles, one molar has shallow re-entrant angles. A very young individual shows a rudimentary *Mimomys*-ridge. Also the seven molars from Plaidter-Hummerich I show some variation in the development of the anterior re-entrant angles. Most of the re-entrant angles are rather deep.

Two of the molars from Maastricht-Belvédère fauna 5 have a symmetrical anterior loop with deep re-entrant angles. One has a shallow buccal re-entrant angle and a deep lingual one. The single molar from Ariendorf 2 has a symmetrical anterior cap with shallow re-entrant angles.

It appears that the differences in the frequency of the morphotypes present in the discussed populations are only minor. The most primitive types such as those with a *Mimomys*-ridge and those with an anterior loop with shallow re-entrant angles are indeed most frequent in Miesenheim I, one of the oldest assemblages. The absence or the presence of a low percentage of primitive morphotypes in the other populations can be caused by the low number of individuals, but it is possible that we are dealing with a decrease in the percentage of primitive morphotypes, as postulated by Carls (1986).

Carls (1986) also studied the morphology of the M3 of *Arvicola* from the different populations. She noticed a large variation in the morphology of the living *Arvicola terrestris* M3 as well as in that of the M3 of *Arvicola* from fossil populations, although the fossil record does not show evolutionary changes (Carls, 1986). Our material does not show an evolution in the morphology of the M3 either.

Nadachowski (1982) described the changes in the frequency distribution of the different m1 amd M3 morphotypes during the Late Quaternary (Weichselian (Lower Pleniglacial) – Holocene). He noted that there are no significant changes in the frequency of the distinct morphotypes of the m1 during that particular period. The Holocene and Late Glacial M3's do show some differences. M3's with a complicated pattern occur more frequently in the Late Pleistocene populations than in the Holocene ones. Nadachowski attributed these changes to the immigration from Asia of large water voles with less complicated patterns in the M3 , at the beginning of the Holocene.

Apparently M3 morphology is not a useful tool in the taxonomy of *Arvicola terrestris* subspecies.

The size of the molars

According to Stuart (1982), there is a trend towards increased size in the m1 of *Arvicola*. The modern *A. terrestris* molars from England are some 30 % larger than those of the Cromerian *Mimomys savini*. Carls (1986) too states that there is an increase in size during the Middle and Late Pleistocene. She also noticed a trend towards increased relative length of the anteroconid complex of the Late Pleistocene m1, indicated by the increase of the A/L ratio. However, the trend is not always progressive: the A/L ratio of the m1 of the living *A. terrestris* is smaller than the values of the Late Pleistocene specimens (Carls, 1986).

The lengths of the different *Arvicola* molars from our localities do not show significant changes except for the m1 (Table 12). There is an increase in length between the m1 from Miesenheim I and those from Maastricht-Belvédère 4. The small number of molars from the other localities do not differ significantly.

The increase in the length might partly be the result of the length increase in the anterior loop. This is indicated by the A/L ratio (Fig. 24), a value for the relative length of the anterior loop.

In summary it can be said that on the basis of what is known from literature and based on our own results, there appears to be an increase in the length of the m1 of *A. terrestris* after its appearance. The earliest populations contain m1 with a length of 3.21 – 3.71 mm which corresponds with the dimensions of the latest *Mimomys savini* populations (Heinrich, 1987). The m1 of younger Central and N. W. European *A. terrestris* populations show temporarily fluctuating lengths between 3.6 and 4.4 mm. (Stuart, 1982; Carls, 1986; Heinrich, 1987; this paper).

Conclusions

The large variation in the SDQ values of the modern *Arvicola* populations and the minor differences in other dental characters (morphology of m1 and M3, dimensions) lead to the conclusion that all the fossil NW and Central European assemblages of the genus *Arvicola*, should be considered as belonging to a subspecies of *A. terrestris*.

			POPULATIONS FROM CENTRAL EUROPE		POPULATIONS FROM THE NETHERLANDS AND THE MIDDLE RHINE AREA	
HOLOCENE			*Arvicola*		*Arvicola*	
PLEISTOCENE	LATE PLEISTOCENE	Weichselian	Euerwanger Bühl H	83.03 (74 - 94)		
			Krockstein/Rübeland	89.08 (72 - 102)		
			Kemathenhöhle	89.23 (82 - 100)		
			Dzerava Skala	92.04 (72 - 108)		
			Roter Berg/Saalfeld	97.25 (87 - 110)		
			Burgtonna 2	98.44 (76 - 117)		
					Maastricht-Belvédère 5	88.67 (75 - 99)
		Eemian	Untertürkheim	100.81 (89 - 133)		
			Adlerberg/Nördlingen	100.83 (91 - 109)		
			Taubach	105.15 (97 - 115)		
			Schönfeld	106.02 (96 - 117)		
	MIDDLE PLEISTOCENE	Saalian			Plaidter-Hummerich I	82.17 (66 - 94)
					Ariendorf 2	76.50 (74 - 79)
					Rhenen	84.22 (73 - 97)
					Wageningen-F. Kamp II	114.38 (111 - 120)
			Weimar-Ehringsdorf UT	112.30 (102 - 126)	Maastricht-Belvédère 4	102.04 (86 - 113)
					Maastricht-Belvédère 3	102.66 (94 - 114)
					Ariendorf 1	118.50 (112 - 128)
		Holsteinian	Dobrkovice 2	123.21 (113 - 139)	Needе	146.58 (124 - 169)
			Bilzingsleben	132.52 (121 - 145)		
		Elsterian	Mosbach	133,54		
					Miesenheim I	152.03 (126 - 180)
			Hundsheim	135.15		
		"Cromerian Complex"	*Mimomys*			
			Prezletice	132.98		
			Voigtstedt	139.09		
			Koneprusy	141.69		

Table 11. Comparison between the mean SDQ values of the *Arvicola* molars from localities discussed in this paper and values of molars of *Mimomys* and *Arvicola* of populations from Central Europe as presented by Heinrich, 1987.

The Middle Pleistocene representatives of the genus *Arvicola* are now assigned to *Arvicola terrestris cantiana*. This subspecies is mainly characterized by a *Mimomys* enamel differentiation of the molars, and furthermore, by the occurrence of a relatively high percentage of "primitive" m1 morphotypes, and by a relatively small size. Little is known about the morphological variation of *A. terrestris persicus*. Based on the data published by Röttger (1987) it is concluded that *A. terrestris persicus* is larger than *A. terrestris cantiana*.

The definition of *A. terrestris cantiana* differs from the one by Heinrich (1982) who proposed to use the name *A. cantiana* for molars with a *Mimomys* enamel differentiation (SDQ >100) and to assign molars with a *Microtus* differentiation (SDQ <100) to *A. terrestris*.

For biostratigraphical purposes it is useful (at least for N.W. Europe, see Chapter IV) to assign the intermediate populations with SDQ values between 120 and 95 to a distinct subspecies of *A. terrestris: A. terrestris* ssp. A (= *A. terrestris hunasensis* defined by Carls (1986) in her still unpublished thesis).

The nature of the relationship of the fossil assemblages (from our localities) showing *Microtus* enamel differentiation (SDQ < 95) to one of the present subspecies is unknown at the moment. The material is, therefore, provisionally assigned to *Arvicola terrestris* ssp. B.

The limit between *A. terrestris* A and B is drawn at the value of 95 because even with values close to 95 it can be seen that we are dealing with a *Microtus* differentiation because the trailing edges lack strengthening elements in the third dimension (Von

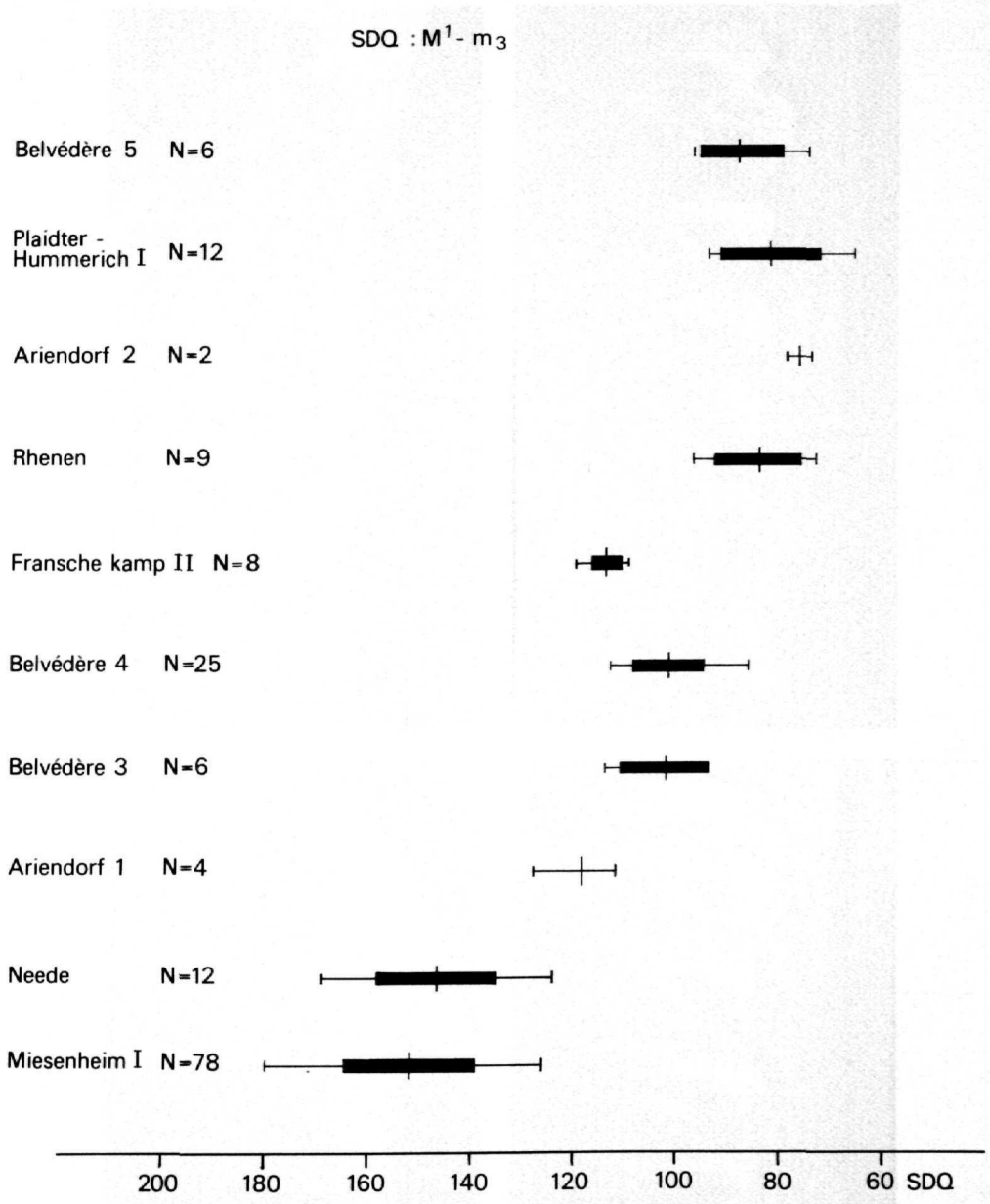


Fig. 22. The range, standard deviation and mean of the enamel thickness quotient (SDQ values) of the *Arvicola* molars from the discussed assemblages.

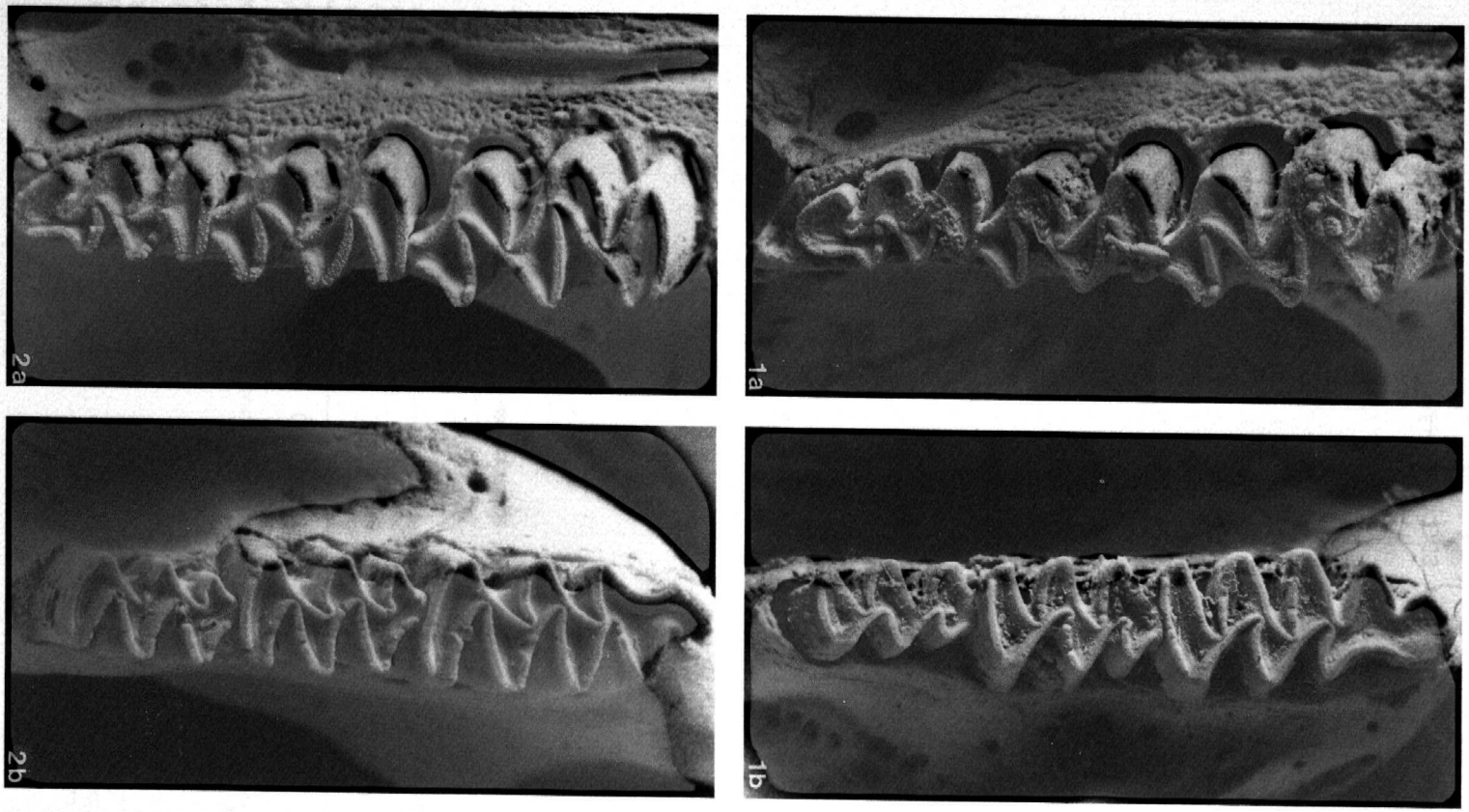


Fig. 23. The upper and lower dentition of *Arvicola terrestris persicus* from Turkey (nr. 1) (Coll. Koenig Museum, Bonn; nr. 68.284) and Iran (nr. 2) (Coll. Senckenberg Museum, Frankfurt; nr. 35407). (Photos made by Mr. G. Oleschinski, Bonn)

	N	Range	Mean	SD
Maastricht-Belvédère 5	1	–	3.80	–
Plaidter Hummerich I	5	3.56 - 3.97	3.796	0.180
Rhenen	2	3.45 - 3.65	3.550	0.141
W.- Fransche Kamp II	1	–	3.68	–
Maastricht-Belvédère 4	5	3.60 - 3.90	3.738	0.116
Miesenheim I	18	3.21 - 3.71	3.495	0.143

Table 12. Lenght of the m1 of *Arvicola* from the localities discussed in this paper.

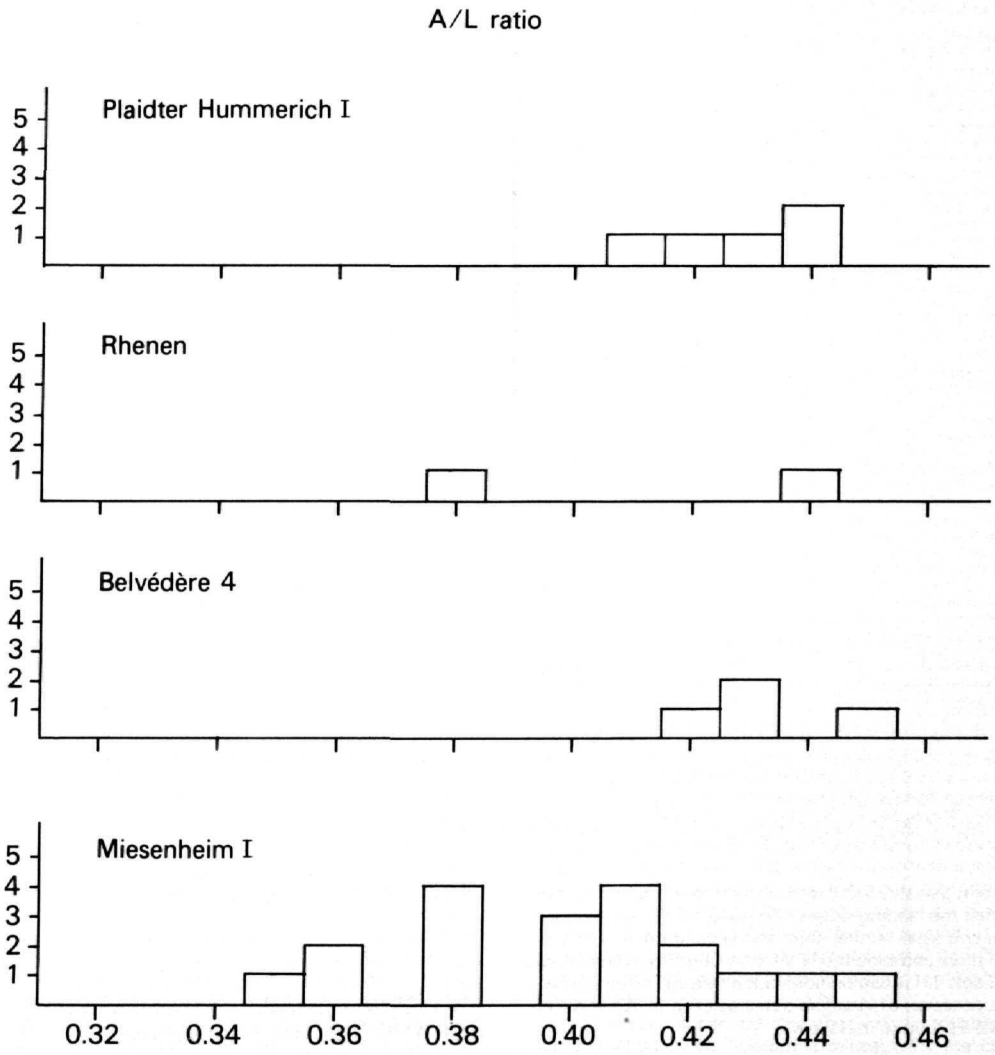


Fig. 24. The A/L ratio of the *Arvicola* m1 from the faunas Miesenheim I, Maastricht-Belvédère 4, Rhenen and Plaidter-Hummerich I.

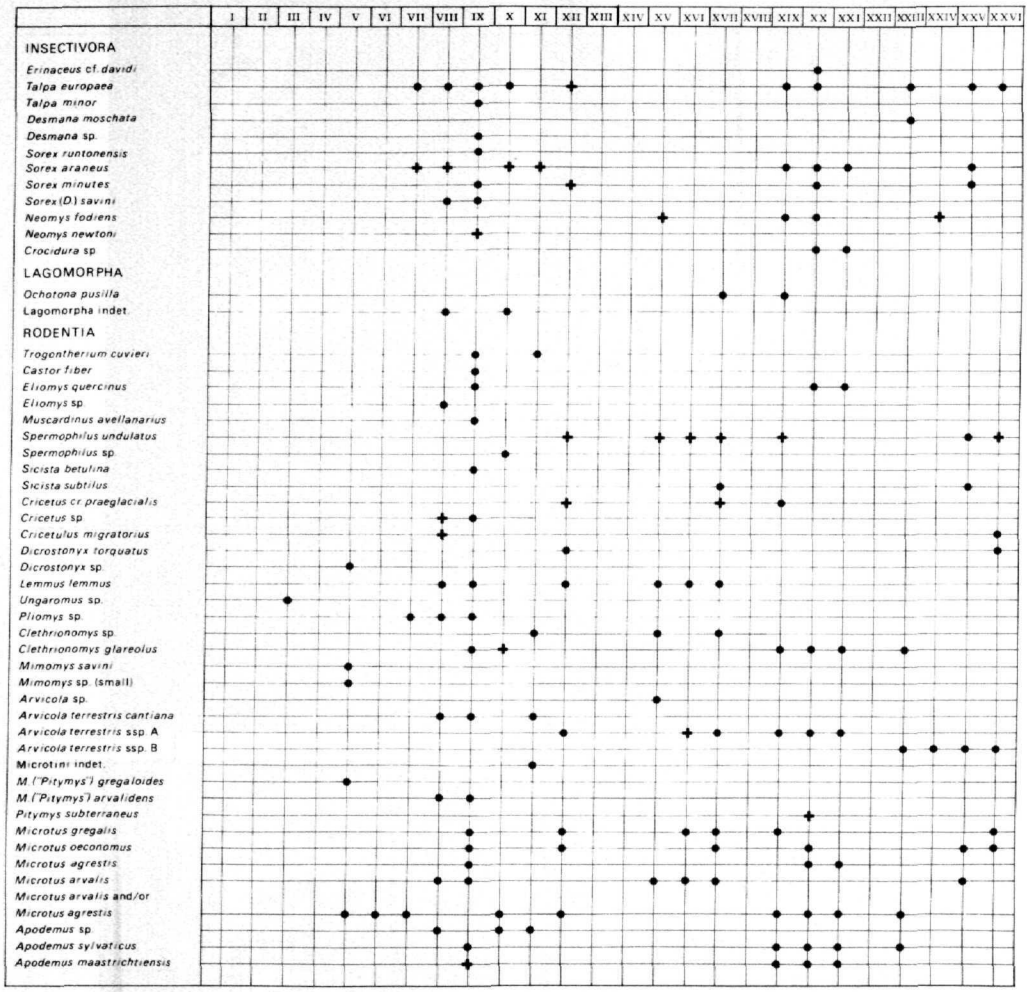


Fig. 25. The distribution of the mammal species in the studied faunas. I = Kärlich A; II = Kärlich Ba; III = Kärlich Bb; IV = Kärlich C; V = Kärlich D-E; VI = Kärlich F; VII = Kärlich Ga; VIII = Kärlich Gb; IX = Miesenheim I; X = Kärlich H; XI = Neede; XII = Ariendorf 1; XIII = Wageningen-Fransche Kamp I; XIV = M-B 2; XV = M-B 2A; XVI = M-B 3A; XVII = M-B 3B; XVIII = M-B 3C; XIX = M-B 3; XX = M-B 4; XXI = Wageningen-Fransche Kamp II; XXII = Kärlich Ja; XXIII = Rhenen; XXIV = Ariendorf 2; XXV = Plaidter-Hummerich I; XXVI = M-B 5. (o means determination certain, + means determination cf. or aff.)

Koenigswald, 1980) and erode, therefore, much more than the leading edges even when the trailing edge is only a little thinner than the leading edges.

If we combine the N.W. and Central European data (Table 11) it can be concluded that the stratigraphical succession of *Arvicola* subspecies in N.W. and Central Europa is as follows:

A. terrestris ssp. B
|
A. terrestris ssp. A
|
A. terrestris ssp. B
|

A. terrestris ssp. A
|
A. terrestris cantiana
|

IV. STRATIGRAPHICAL SUCCESSION OF THE DISCUSSED FAUNAS

IV.1. INTRODUCTION

The distribution of the species that occur in the localities discussed in the previous chapters is shown in Fig 25. Only those species have been entered for which

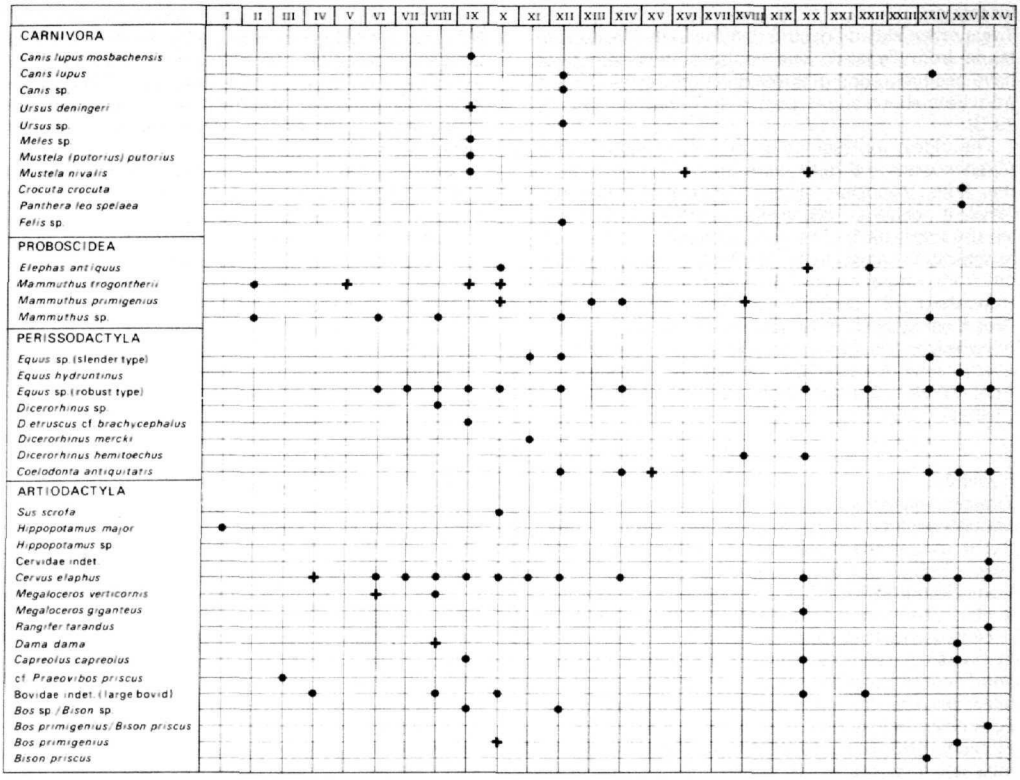


Fig. 25. Continuation.

we have proper data regarding the lithostratigraphical provenance.

IV.2. STRATIGRAPHICAL RANGES OF SPECIES WHICH ARE RELEVANT FOR THE BIOSTRATIGRAPHY OF THE MIDDLE PLEISTOCENE

Introduction

The data about the stratigraphical range of the species are based mainly on information obtained from literature. This means that one should bear in mind that this method is hampered by the fact that the taxonomy of some groups such as the Middle Pleistocene Insectivora is not well understood and should be revised. The taxonomy of the caballine horses is also is very complicated. The stratigraphical ranges of the different species of the three distinguished lineages (Eisenmann, *et al.*, 1985) are not well known yet. Furthermore, the determination of material from some of the older collections needs revision. Therefore, for many species it is very difficult to determine their exact stratigraphical range.

Numerous species represented in the discussed faunas (*Talpa europaea, Sorex minutus, Crocidura* sp., *Castor fiber, Eliomys quercinus, Muscardinus avellanarius, Cricetus cricetus, Dicrostonyx torquatus, Lemmus lemmus, Clethrionomys glareolus, Microtus arvalis, Apodemus sylvaticus, Ursus deningeri, Elephas antiquus, Dicerorhinus mercki, Sus scrofa, Capreolus capreolus, Bison schoetensacki, B. priscus, Bos primigenius*) have a rather long stratigraphical range and occurred already in N. W. Europe in the Early and/or Early Middle Pleistocene.

The stratigraphical ranges of a number of species: *Erinaceus davidi, E. europaea, Apodemus maastrichtiensis, Mustela nivalis, M. putorius, Equus hydruntinus* and *Rangifer tarandus* is so far not well known because the Middle Pleistocene record is too poor.

Another group of species (*Ochotona pusilla, Spermophilus undulatus, Sicista subtilus, S. betulina, Cricetulus migratorius (= Allocricetus bursea)* and *Ovibos moschatus*) occurred rarely during the Middle Pleistocene.

In summary it can be said that only a restricted number of mammal species is relevant for the creation of a biostratigraphical subdivision of the Middle Pleistocene. The stratigraphical ranges of these species (see Fig. 26) will be discussed in the next paragraph.

Insectivora

Talpa minor already occurred in the Early Pleistocene fauna from Tegelen. The youngest representatives have been recorded in the Middle Pleistocene faunas from Petersbuch and Heppenloch (Von Koenigswald, 1973).

The oldest representative of the subgenus *Sorex (Drepanosorex), S. (D.) praearaneus*, is known from the Late Villányian (Early Pleistocene) (Reumer, 1985). It occurs for instance in the fauna from Tegelen (Reumer, 1984). The youngest species *Sorex (D.) austriacus* is known from the Middle Pleistocene faunas from Vergranne and Montoussé (Jammot, 1976), Hundsheim, Sudmer-Berg-2, Tarkö and Erpfingen (Von Koenigswald, 1973; Reumer, 1985). *S. (D.) savini*, which is thought to be a little older than *S. (D.) austriacus* (Reumer, 1985), occurs e.g. in the faunas from West Runton and Westbury-Sub-Mendip (Bishop, 1982).

Rodentia

Trogontherium cuvieri occurred in the Early and Middle Pleistocene European faunas (Mayhew, 1978). It is known in the fauna from Tegelen (Early Pleistocene: Tiglian). Its last occurrence is in the faunas from Bilzingsleben (G.D.R.) and Neede (The Netherlands); they have a Holsteinian Age.

Ungaromys is present in many Early Pleistocene faunas such as in the faunas from Tegelen, Betfia 2 and Deutsch-Altenburg (Rabeder, 1981). One of the latest occurrences known until recently is in the Late Early Pleistocene fauna from Mt Peglia; (Van der Meulen, 1973) but its presence at Kärlich in Unit Bb indicates that the genus survived until at least the Middle Pleistocene.

Pliomys occurred in the European faunas already during the Early Pleistocene. *P. episcopalis* appeared in the *Allophaiomys pliocaenicus* Range-zone of the Early Biharian (Van der Meulen, 1973). *Pliomys episcopalis* survived in Italy until the Holsteinian; in northern parts of Europe it became extinct earlier (Sutcliffe and Kowalski, 1976). *Pliomys lenki* appeared during the late Early Pleistocene and occurred all over Europe until the late Elsterian. From the early Saalian until the early Weichselian it inhabited only South West Europe (Bartolomei, *et al.*, 1975).

The transition from *Mimomys* to *Arvicola* took place during the Middle Pleistocene. According to Heinrich (1987) the latter genus appeared at the beginning of the Holsteinian. Von Koenigswald (1973) correlates the oldest *Arvicola* faunas with the Elsterian whereas Bishop (1982) suggests that *Arvicola* might already have occurred at the end of the "Cromerian complex".

Revision of the *A. terrestris* material from a number of Dutch localities indicated the appearance of *A. terrestris cantiana* during the late Cromerian. The stratigraphically oldest fossils of *Arvicola t. cantiana* are known from the Noordbergum 13 and 14 boreholes. Noordbergum 13 yielded from a depth of between 46 - 65 metres two incomplete molars of *A. t. cantiana*. Schreuder (1943) determined the fragments as M1 dext and M1 sin of *Arvicola bactonensis (= A. t. cantiana)*. However, the M1 sin is vertically curved and should be assigned to an m2 dext. The enamel differentiation (SDQ value of 144) corresponds well with those of the *Arvicola* molars from Neede and Miesenheim I.

Noordbergum 14 also yielded mammal fossils. Schreuder (1943) describes and figures a complete M1 dext of *Arvicola bactonensis* (= A. t. cantiana). According to Schreuder the molar is from an adult animal and shows a distinct enamel differentiation at its base.

The *A. t. cantiana* molars from Noordbergum 13 and 14 were collected from the marine deposits of the Urk Formation (Meijer, pers. comm., 1987). The fossils are derived from a level which is located below the layers of "pottery clay" assigned to the Elsterian Peelo Formation (Doppert *et al*, 1975). The marine deposits from Noordbergum 13 and 14 from which the mammal fossils are obtained are dated by pollen analysis as Cromerian Interglacial IV deposits.

The Late Cromerian occurrence of *A. terrestris cantiana* is also known from the English localities Ostend and Westbury-Sub-Mendip (Bishop, 1982; Stuart, 1982) and recently also from the locality Boxgrove (Roberts, 1986; Roberts, pers. comm., 1988). The view that *Arvicola* firstly appeared during the Elsterian or even later is based mainly on the occurrence of *Mimomys savini*, the ancestor of *Arvicola t. cantiana*, in the fauna from West Runton, the type locality of the British Cromerian. The Upper Fresh Waterbeds of West Runton, which are overlain by the Anglian (= Elsterian) till, were supposed to have a Late Cromerian Age. This age determination was supported by the palynological correlation to Interglacial IV of the "Cromerian complex" of the type section of West Runton (West, 1980).

This may imply that both *Mimomys savini* and *Arvicola t. cantiana* would occur in the same interglacial, and a drastic faunistic change took place in this interglacial. This is, in my opinion, very unlikely because the differences between the faunas (e.g. the differences in the Soricidae) from Westbury-Sub-Mendip and the fauna from West Runton (own observations) are too large to correlate both faunas with the same stage (see Bishop, 1982). Therefore, the author proposes to correlate the fauna from West Runton with an earlier interglacial of the "Cromerian complex" (Interglacial II or III). Malacological data seem to suggest a correlation between Interglacial II of the Dutch "Cromerian complex" and the type locality of the English Cromerian s.s. (Meijer, pers. comm., 1988).

A. t. cantiana is also known from the locality Neede, from sediments which are palynologically dated as Holsteinian. *A. terrestris* ssp. A is known from the Early Saalian and Eemian faunas; *A. terrestris* ssp. B from Early - Late Saalian and Weichselian faunas (see Chapter III).

The taxonomy of those arvicolids with m1 with a so-called *Pitymys* rhombus, is complex and not uniform. Most authors (Chaline, 1972; Van der Meulen, 1973;

Rabeder, 1981) refer these species to the subgenus *Microtus* (*Pitymys*). However, in this group of arvicolids one can observe two different types of molars; one group with pointed salient angles (a type which is characteristic for the Early- and early Middle Pleistocene "*Pitymys*" molars (*Microtus ("Pitymys") arvalidens* and *M. ("Pitymys") gregaloides*), and one with more rounded salient angles (a type one can observe in the m1 of the living *Pitymys subterraneus*). The second type appears in N.W. Europe during the late Middle Pleistocene. It is known from faunas such as Maastricht-Belvédère 4 (the specimens are referred to *P.* cf. *subterraneus*)(Van Kolfschoten, 1985) and the french faunas Nestier, Lazaret and L' Hortus (material referred to *M. (P.) duodecimcostatus* by Chaline (1972)). This group might be related to the *Pitymys* species from North America, where species with comparable morphotypes occur much earlier than in Europe (Van der Meulen, 1978) and not to the Early Pleistocene representatives with the pointed salient angles, which are part of the *Microtus* lineage. This would imply that, in spite of the *Pitymys* rhombus in the m1, there is no close relationship between the group of Early- and early Middle Pleistocene "*Pitymys*" and the younger representatives of the genus *Pitymys*. The older group is referred to, in this article, as *Microtus ("Pitymys")* as the late Middle Pleistocene molars with a *Pitymys* rhombus and rounded salient angles, are referred to the genus *Pitymys*.

The tundra or narrow-skulled vole *Microtus gregalis* occurs nowadays in the tundra in the north and in the wooded steppes of central Asia. It is present in a large number of European faunas dating from the last glaciation. Chaline (1972, 1973) reported the presence of *M. gregalis* in the fauna from La Fage dating from the penultimate glaciation. It is also present in the fauna from Miesenheim I with a late Cromerian Age.

According to Chaline (1972) *Microtus oeconomus (=M. ratticeps)*, which still inhabits Europe, appeared during the Saalian stage. However Stuart (1982) mentioned the occurrence of *M. oeconomus* in the fauna from West Runton with a Cromerian Age. Sutcliffe and Kowalski (1976) referred the material from West Runton to the closely related but smaller *M. ratticepoides*.

Microtus agrestis is nowadays widely distributed in Europe. Fossil remains of this species indicate that it appeared in Western Europe at the beginning of the Saalian, the penultimate glaciation (Sutcliffe and Kowalski, 1976). However, according to Chaline (1972) *M. agrestis* appeared during the Elsterian. Nadachowski (1985) described *Microtus* ex gr. *agrestis* from the Biharian fauna from Kozi Grzbiet (Poland) co-occurring with *Mimomys savini*. *Microtus agrestis* occurs in the pre-Elsterian faunas from Miesenheim I (this paper) and Boxgrove (Currant, pers. comm., 1988). In the younger faunas Maastricht-Belvédère 3 and 4 it occurs more frequently.

Carnivora

The extant wolf, *Canis lupus* has occurred in Europe since the "Cromerian complex". It is known from West Runton (Stuart, 1982). However, according to Bonifay (1971), who regards *Canis lupus mosbachensis* as a synonym of *C. etruscus*, *Canis lupus* appeared during the Holsteinian whereas *Canis etruscus* is restricted to the Elsterian and older periods.

Proboscidea

Elephas antiquus has been recorded from a large number of Middle Pleistocene interglacial faunas such as the faunas from Mauer, Bilzingsleben, Swanscombe and Weimar-Ehringsdorf. The species also occurs frequently in the Eemian faunas of Western Europe (Stuart, 1982).

Mammuthus primigenius, which frequently occurred in Western Europe during the last two cold stages, evolved from *M. trogontherii (=M. armeniacus)* at the end of the Elsterian or somewhat later. It became extinct in N.W. Europe at the end of the Weichselian (Coope and Lister, 1987).

Perissodactyla

Dicerorhinus hemitoechus most probably evolved from *D. etruscus*, which occurred in Europe during the Early and early Middle Pleistocene. The oldest representatives of *D. hemitoechus* are known from the Elsterian period (Guérin, 1980). It also became extinct during the Weichselian stage.

Coelodonta antiquitatis migrated from Asia to Europe during the Early Saalian and has occurred frequently in the "cold" faunas of the Saalian and Weichselian stages (Guérin, 1980). The species also occurs in the poor faunas from Bornhausen, Neuekrug and Bad Frankenhausen which are correlated by Kahlke (1975) with the Elsterian. However, the stratigraphical position of these faunas is discussable (Guérin & Crégut, 1979). *Coelodonta antiquitatis* became extinct at the end of the Weichselian. The locality Gönnersdorf (Western Germany) yielded fossils of *Coelodonta antiquitatis* and entgravings showing the woolly rhinoceros. The finds from Gönnersdorf have a Radiocarbon age of 12.500 $\pm$ 300 years (Bosinski, 1979).

Artiodactyla

Hippopotamus invaded Europe during the Late Early Pleistocene. Records of *Hippopotamus major (=H. antiquus)* are known from, for instance, Untermassfeld (G.D.R.) (Kahlke, 1987) and the Forest Bed formation in Great Britain (Faure, 1985; Stuart, 1982). Its occurrence is restricted to the Late Early and Early Middle Pleistocene. According to Faure (1985) when *Hippopotamus incognitus* first occurred in Europe it was contemporaneous with *H. major* although they are never found together in the same fauna. *H. incognitus* is known from Early Middle Pleistocene faunas like those from the localities Mosbach and Le Vallonet (Faure, 1985). So far *Hippopotamus* is unknown from Holsteinian and Saalian deposits in Western Europe. It is absent in the faunas from Bilzingsleben, Swanscombe, Neede, Weimar-Ehringsdorf, La Fage a.o. *H. incognitus* occurred frequently in Eemian deposits in Great Britain, Western Germany and The Netherlands

(Faure, 1985; Van Kolfschoten and Vervoort-Kerkhoff, 1985).

The known first appearance of *Cervus elaphus* is during the "Cromerian complex". It is recorded in the faunas from West Runton and Voigtstedt. The species has survived up to the present day (Lister, 1985). Cromerian and Elsterian representatives of this species have an "acoronate" antler; they are assigned to the ssp. *C. e. acoronatus*. The earliest occurrences of coronate red deer, *C. e. elaphus*, have been recorded in the Hoxnian (=Holsteinian) fauna from Clacton channel (Lister, 1985).

The known stratigraphical range of *Megaloceros giganteus* is from the Holsteinian (perhaps Late Elsterian) to Late Weichselian (11,000 bp.) (Lister, 1985).

IV.3. EXISTING BIOZONATIONS

The climatological changes in the higher latitudes during the Pleistocene period have caused many changes in the European mammal fauna. The composition of the fauna has changed due to evolution, extinction and migration of species. On the basis of these faunal changes a number of mammal biozonations have been established by different authors. However, a number of these zonations are not defined according to the guide to stratigraphic nomenclature published by Hedberg (1976). Furthermore, the terminology used by some authors is confusing.

The biozonation presented by Guérin (1980) is based on the Neogene Mediterranean mammal zonation (MN zones) proposed by Mein (1975). Guérin partly revises the MN zonation and extends it to include the Pleistocene period. For Middle and Late Pleistocene faunas he defines six different MN zones. Each zone is defined simultaneously by the evolutionary stage of several different species, on the assemblage of certain (sub)species and on the appearance of species. The data for such a definition are gathered from a number of different, correlated localities. This illustrates the artificial character of the MN zones.

Chaline studied the rodent fauna succession in France and distinguished two major parts in the Pleistocene period; the *Mimomys* faunal complex and the *Microtus* faunal complex (Chaline, 1976). The former complex is divided into three "complexes" (Septimanien, Arondellien and Briellien), the latter into four (Monterien, Etstévien, Aldénien and Régourdien). Each of these "faunal complexes", which can be regarded as, and are used as, biozones, is subdivided into many so-called "climatozones". These climatozones are characterized by a fauna association. However, these associations are also dependent on the latitude, the geographical position and the geomorphological context of the locality. Therefore, these climatozones have a mostly local applicability.
Von Koenigswald (1973) grouped the German smaller mammal faunas. He distinguishes four faunal types from the "Cromerian complex" to the Eemian Interglacial. The "*Mimomys savini* Fauna" comprises faunas that contain *M. savini*. *A. terrestris cantiana* occurs in the "*Arvicola* Fauna Type 1 and 2". The "*Arvicola* Fauna Type 1" (*Arvicola-Pliomys*-Fauna) is characterized by the co-occurrence of *A. t. cantiana* and *Pliomys*. *Pliomys* is common in faunas of "*Arvicola* Fauna Type 1", and is characteristically absent or rare in faunas of the "*Arvicola* Fauna Type 2". The "*Arvicola* Fauna Type 3" is characterized by the absence of *Talpa minor* and the presence of the more evolved *A. terrestris*. Populations with a type of *Arvicola*, which is regarded as transitional between *A. t. cantiana* and the modern Western European subspecies of *A. terrestris* occur in both "*Arvicola* Fauna Type 2 and 3".

The Hungarian smaller mammal zonation, which is based mainly on the work of Kretzoi (see e.g. Kretzoi, 1965; Kretzoi and Pécsi, 1979; Van der Meulen, 1973), is used as a standard for the Early and Middle Pleistocene of Europe. In this subdivision three "stages" were recognized for the Pleistocene period; Villányian, Biharian and Peribaltian. The Villányian faunas can be recognized by the dominance of *Mimomys*, the Biharian faunas by a *Microtus* dominance. In the Biharian "Stage" one has distinguished two substages: Lower and Upper Biharian. The disappearance of *Mimomys* marks the transition from the Lower to the Upper Biharian (Kretzoi and Pécsi, 1979). The latter authors correlate the Peribaltian to the Holsteinian - Weichselian time interval without producing paleontological evidence. The Peribaltian consists of two substages: Oldenburgian and Utrechtian. The former corresponds to the Needian (=Holsteinian) and Drenthian (=Saalian), the latter to the Eemian and Weichselian (Kretzoi and Pécsi, 1979). However, the Peribaltian Stage and the Substages are not defined on the basis of biostratigraphical changes. Only a few authors like Kretzoi and Pécsi, (1979) use this terminology.

Jánossy (1976) revised the Late Middle Pleistocene vertebrate faunas from Hungary. On the basis of the evolutionary stage of *Arvicola* and the composition of the faunas he distinguished a number of biozones, which he called "phases": "Tarkö Phase" (with a "Tarkö Zone" (Lower Biharian)) and a "Vértesszölös Zone" (Upper Biharian), "Uppony Phase" (Upper Biharian), " Castellum Phase", "Solymár Phase", "Varbó/Süttö Phase" and "Istállóskö/Tokod/Subalyuk Phase" (Jánossy, 1976). Van der Meulen (1973) already commented on the use of phases and their definition.

Fejfar and Heinrich (1981) proposed a biostratigraphical subdivision of the Quaternary period on the basis of the Arvicolidae succession. They also used the "Stage" names Villányian and Biharian but in another sense than Kretzoi and Pécsi (1979) did. Their Biharian "Stage" corresponds to a part of the Lower Biharian as defined by Kretzoi (Kretzoi and Pécsi, 1979). It can be recognized by the co-occurrence of *Microtus* and *Mimomys*. The Toringian "Stage" can be recognized by *Arvicola* - *Microtus* assemblages. The type-locality of the Toringian "Stage" is Burgtonna (G.D.R.) (Fejfar & Heinrich, 1981).

Fejfar and Heinrich (1981) distinguished two biozones in the Toringian "Stage"; *Arvicola cantiana* Zone (= Steinheimian) and *Arvicola terrestris* Zone (= Post Steinheimian). On the basis of our results it appears that this subdivision is not valid, at least not for N.W. Europe. The reason for this will be discussed in the following pages.

It should be noted in this discussion that the aforementioned "stages" (Villányian, Biharian and Toringian) are not true chronostratigraphic units, according to the rules of the International Stratigraphic Guide (Hedberg, 1976). They are in fact biozones based on a concept of evolutionary stages, their boundaries remaining undefined by boundary-stratotypes, as required by the rules. For this reason the term "stage", as used by many authors in the field of mammal biostratigraphy, have been placed between hyphens, in this study, in those cases were they do not fulfil the requirements of Hedberg (1976).

IV.4. BIOZONATION OF THE LATE MIDDLE PLEISTOCENE

Introduction

Fejfar and Heinrich (1981) introduced the Toringian "Stage" as the period which can be recognized by *Arvicola* - *Microtus* assemblages and divided the stage into two biozones: an *Arvicola cantiana* Zone and an *Arvicola terrestris* Zone. The limit between these zones depends upon the separation of the two species, which has been arbitrarily set at an SDQ value of 100. This zonation starts from the assumption that the evolution in the lineage *A. cantiana* - *A. terrestris* is progressive and does not show important fluctuations.

However, it has been shown before that we are not dealing with distinct species but with subspecies, and that the mean SDQ values of the succesive subspecies in N.W. Europe do not display a simple decreasing trend (see Table 11). Therefore, another subdivision valid for N.W. Europe will be proposed.

The *Arvicola* faunas discussed in this paper can be divided into two groups: one group with *Arvicola terrestris cantiana* co-occurring with so-called relict species (such as *Talpa minor*, *Trogontherium cuvieri*) and another group with *Arvicola terrestris* ssp. A and B co-occurring with a modern smaller mammal fauna.

These two groups are characteristic for the two distinguished zones: *Arvicola terrestris cantiana* Range-zone and the *Arvicola terrestris* Partial-range-zone.

Arvicola terrestris cantiana Range-zone

Diagnosis: Total range zone characterized by the occurrence of *Arvicola terrestris cantiana* (for the definition of the subspecies see Chapter III).

Remarks

The *Arvicola terrestris cantiana* Range-zone is equivalent to the lower part of the *A. cantiana* Zone of Fejfar and Heinrich (1981) (see Fig. 26). The *Arvicola terrestris cantiana* Range-zone comprises a large number of faunas which differ in composition. Therefore, it is proposed to divide the *Arvicola terrestris cantiana* Range-zone into two subzones: the *Arvicola terrestris cantiana-Sorex (Drepanosorex)* sp. Concurrent-range-subzone and the *Arvicola terrestris cantiana* Partial-range-subzone.

Arvicola terrestris cantiana-Sorex (Drepanosorex) sp. Concurrent-range-subzone

Diagnosis: Concurrent-range-subzone characterized by the co-occurrence of the zonal markers with *Pliomys* sp.

Remarks

The subzone is also characterized by the first appearance of *Microtus gregalis* and *Microtus agrestis*. This subzone is more or less equivalent to "*Arvicola* Fauna type 1" of Von Koenigswald (1973). It comprises faunas such as Miesenheim I, Kärlich Gb, Boxgrove, Westbury-Sub-Mendip, Sprimont (Belle Roche), Mauer, Erpfingen 1 and 3, Hundsheim, Petersbuch, Sudmer Berg 2, Tarkö and the upper Mosbach faunas.

This subzone can be correlated with at least part of the Estévien faunal Complex which is characterized by the first appearance of *Arvicola* and the co-occurrance of *Arvicola* and *Pliomys episcopalis* (Chaline, 1976).

The subzone also corresponds to at least part of the Tarkö Zone, the oldest part of the Tarkö Phase (Jánossy, 1976). The fauna from Petersbuch is also assigned to this subzone because of the occurrence of *Sorex (D.)* cf. *margaritodon* and a medium-sized *Sorex* sp. with relatively small dimensions. In these respects it corresponds better to faunas assigned to this subzone than to the younger faunas. There may be paleo-ecological reasons for the absence of *Pliomys* in the fauna from Petersbuch (see Kretzoi, 1965). *Pliomys* is for instance also rare in the fauna from Miesenheim I.

Arvicola terrestris cantiana Partial-range-subzone

Diagnosis: Partial-range-subzone characterized by the occurrence of *Arvicola terrestris cantiana* and the absence of *Sorex (Drepanosorex)* sp. and *Pliomys* sp.

Remarks

This subzone is characterized by the occurrence of the zonal marker and the last occurrence of *Talpa minor*, and *Trogontherium cuvieri*.

The subzone comprises faunas such as Heppenloch and Swanscombe (Von Koenigswald, 1973), Bilzingsleben (Heinrich, 1982) and the fauna from Neede (this paper).

This subzone is more or less equivalent with part of

Fig. 26. Range-chart of a number of species present in the discussed faunas, a tentative biozonation of the late Middle and Late Pleistocene deposits of N.W. Europe and the correlation between the zonation and the chronostratigraphic subdivision of the Pleistocene.

"*Arvicola* Fauna type 2" of Von Koenigswald (1973). Hungarian faunas assigned to the Vértesszölös Zone differ from the faunas of the Tarkö Zone by the absence of *Sorex (Drepanosorex)* and *Beremendia* (Jánossy, 1976). The disappearance of some relict species also marks the transition from the Elstévien to the Aldénien Complexes (Chaline, 1976). It is not clear whether these three transitions are contemporanous. The transition between the Tarkö Zone to the Vértesszölös Zone and the Estévien/Aldénien transition may correspond to the transition from our *Arvicola terrestris cantiana - Sorex (Drepanosorex)* sp. Concurrent-range-subzone to the *Arvicola terrestris cantiana* Partial-range-subzone.

Arvicola terrestris Partial-range-zone

Diagnosis: Partial-range-zone characterized by the occurrence of *Arvicola terrestris* ssp. A and B (for the definition of the subspecies: see Chapter III).

Remarks

This zone is also characterized by the absence of Early Middle Pleistocene relicts such as *Talpa minor*, and *Trogontherium cuvieri*. *Mammuthus primigenius* and *Coelodonta antiquitatis* appear for the first time in the European faunas at the base of the *Arvicola terrestris* Partial-range-zone.

This zone corresponds to the upper part of the *Arvicola cantiana* Zone and the *Arvicola terrestris* Zone of Fejfar and Heinrich (1981). The correlation between the faunas from La Fage (France) and Maastricht-Belvédère 3-4 indicates the correspondence of part of the *Arvicola terrestris* Partial-range-zone with at least part of the Aldénien Complex (see Chaline, 1976).

The first appearance of *Coelodonta antiquitatis* marks the beginning of MN Zone 24 of the subdivision proposed by Guérin (1980). This indicates that the lower part of the *Arvicola terrestris* Partial-range-zone corresponds to Guérin's Zone 24.

This zone comprises a large number of faunas which strongly resemble each other. The faunas can be divided into one group characterized by the occurrence of *A. terrestris* ssp. A and one group with *A. terrestris* ssp. B. These two groups cannot be the base for a subdivision of this partial range zone because each group contains (almost) indistinguishable faunas from two separate periods. The earliest faunas with *A. terrestris* ssp. A are almost identical to the younger faunas with the same subspecies. They only differ in the absence or presence of *Hippopotamus* (Fig. 26). Purely on the basis of geological data (for instance because of the occurrence of a fauna in sediments which has been pushed by the Saalian inland-ice) we know that these faunas were not contemporaneous.

With the present state of knowledge we cannot distinguish the two groups of faunas with *A. terrestris* ssp. B at all on the basis of the faunal composition. So we are not able to give a definition of a subzone which is unique for one of the *A. terrestris* ssp. B group of faunas.

The oldest group, characterized by the occurrence of *A. terrestris* ssp. A, comprises faunas such as Weimar-Ehringsdorf, Hunas, La Fage, Lazaret, the fauna from the lower loess deposits of Achenheim, Mesvin IV, Ariendorf 1, Wageningen - Fransche Kamp and Maastricht-Belvédère 2-4.

The oldest *A. terrestris* ssp. B group of faunas comprises faunas such as the smaller mammal fauna from Rhenen, Ariendorf 2, Plaidter-Hummerich I (this paper) and faunas such as Biach St. Vaast (Chaline, 1978) and Uppony I/1-2. The third group of faunas is characterized by the occurrence of *A. terrestris* ssp. A and furthermore by that of *Hippopotamus*. As far as we know, *Hippopotamus* was absent in the N.W. and Central European faunas during the Holsteinian Interglacial and the early Saalian interstadials. But in the Eemian it inhabited N.W. Europe (*Hippopotamus* is known from many English and Dutch localities) (Van Kolfschoten and Vervoort-Kerkhoff, 1985; Van Kolfschoten and Vervoort-Kerkhoff, in prep.). *Dama dama* occurred also in The Netherlands during the Eemian (Van Kolfschoten, in prep.). Its occurrence during the Holsteinian and the early Saalian interstadials has not been indicated yet but this is known from the English fossil record (Stuart, 1982; Currant, pers. comm., 1988).

None of the faunas discussed in this paper can be assigned to this group. The group comprises faunas such as Swanton Morley, Barrington, Tornewton Cave glutton stratum, Schönfeld and Taubach (Stuart, 1982; Heinrich, 1987). These faunas can be correlated with faunas with *Arvicola* populations characterized by molars without a distinct enamel differentiation, assigned to the Castellum and Solymár Phase (Jánossy, 1976). These faunas are thought to be younger than the fauna Uppony I/1-2 in spite of the presence of a more "primitive" *A. terrestris* (Jánossy, 1976). Heinrich (1982) rejects Jánossy's arguments and correlates Uppony I/1-2 with a younger phase of the Pleistocene period on the base of the evolutionary stage of the *Arvicola* molars.

The last group of *A. terrestris* faunas with *A. terrestris* ssp. B comprises faunas such as Maastricht-Belvédère fauna 5, the faunas from Kesselt, Zoolithen Höhle, Weinberghöhlen and Fuchsenloch C, D and many other late-glacial faunas.

Maastricht-Belvédère fauna 5 postdates the Eemian Rocourt palaeosol and is correlated with an earlier part of the Weichselian on the basis of for instance the "primitive" evolutionary stage of *Dicrostonyx torquatus* (Van Kolfschoten, 1985). Agadjanian and Von Koenigswald (1977) have indicated that more "advanced" molars occur during the middle and late Weichselian.

IV.5. CORRELATION BETWEEN THE BIOZONATION AND THE CHRONOSTRATIGRAPHICAL SUBDIVISION

The correlation between the biozones and the Dutch standard division of the Pleistocene as presented in Fig. 26 is based on the correlation between some of the discussed faunas and the chronostratigraphical subdivision.

The Noordbergum locality yielded *Arvicola* molars from deposits which have been dated, palynologically, to Interglacial IV of the "Cromerian complex". Therefore, we can say that at least part of the *A. terrestris cantiana* Range-zone correlates with Interglacial IV of the "Cromerian complex" and that a number of faunas assigned to the first subzone, the *A. terrestris cantiana - Sorex (Drepanosorex)* sp. Concurrent-range-zone should be correlated with this interglacial.

The second zone, the *A. terrestris cantiana* Partial-range-subzone, comprises the fauna from Neede which is palynologicaly dated to the Holsteinian. The macrofloral data from the Bilzingsleben locality also indicate a Holsteinian Age for that fauna.

One of the oldest associations of the *Arvicola terrestris* Partial-range-zone is the fauna Ariendorf 1. The fauna indicates glacial conditions and is correlated with the Saalian. Therefore, the transition from the *A. terrestris cantiana* Range-zone to the *A. terrestris* Partial-range-zone should be more or less contemporaneous with the Holsteinian-Saalian transition.

Because of the occurrence in M-B 2 of *Coelodonta antiquitatis*, which migrated from Asia to Europe during the early Saalian, it is obvious that the fauna and the superimposed ones have a post-Holsteinian Age. This is confirmed by the evolutionary stages of the *Arvicola* populations. The *Arvicola* molars from M-B 3-4 and Wageningen-Fransche Kamp II have lower SDQ values than those from Neede but higher SDQ values than the *Arvicola* molars from Rhenen which also date to the Saalian. This implies that the fauna from Wageningen-Fransche Kamp II should be correlated with the Early Saalian and because we are dealing with an interglacial fauna we correlate this fauna with the Hoogeveen Interstadial, the first temperate/warm phase of the Saalian period.

The chronostratigraphical correlation of the smaller mammal fauna from Rhenen is based on the evolutionary stage of the *Arvicola* molars (they are more evolved than those from Wageningen - Fransche Kamp II and Maastricht - Belvédère 3 - 4) and on the knowledge that the sediments were pushed by the Saalian inland ice.

The third group of *Arvicola terrestris* ssp. faunas of the *A. terrestris* Partial-range-zone, characterized by *Arvicola* with SDQ values which are higher than those from Rhenen, should be correlated with the Eemian. This correlation is based on a large number of faunas from England and some from The Netherlands with a post-Saalian Age, with amongst others *Hippopotamus*.

The last group of faunas date to the Weichselian and the Holocene. The fauna M-B 5 dates to the Weichselian. It is obtained from a unit above a paleosol which is correlated with the Eemian "Sol de Rocourt".

IV.6. CORRELATION BETWEEN THE LOCAL STRATIGRAPHY OF THE MIDDLE RHINE AREA AND THE GENERAL SUBDIVISION OF THE PLEISTOCENE

The correlation between the deposits located in the Middle Rhine Area and the Standard Division of the Pleistocene is problematical. Ideas about the correlations, put forward by authors of various disciplines, are controversial.

The faunas Miesenheim I and Kärlich Gb are placed in the *Arvicola terrestris cantiana - Sorex (Drepanosorex)* sp. Concurrent-range-subzone. This subzone is correlated with Interglacial IV of the "Cromerian complex" and at least part of the Elsterian. This indicates a correlation between the Ariendorf Interglacial (to which the Miesenheim I fauna is correlated (Brunnacker, in: Boscheinen *et al.*, 1984)), with an absolute age of about 420 ± 30 ka, and Interglacial IV of the "Cromerian complex".

The Ariendorf 1 fauna is correlated to the lower part of the *A. terrestris* Partial range zone, which postdates the Holsteinian. The fauna is correlated with the Early Saalian. This correlation implies that in the section in the Ariendorf pit, there is a stratigraphical hiatus between the Ariendorf-Interglacial deposits and the layer yielding the oldest mammal fossils.

Whether the same hiatus is also present in the Kärlich section is nor clear. The fauna from Kärlich Unit Gb is correlated to Interglacial IV of the "Cromerian complex", and with the Ariendorf Interglacial. The Kärlich Interglacial postdates the Ariendorf Interglacial. On the basis of pollen analyses correlation between the Kärlich Interglacial and the Holsteinian can be excluded (Urban, 1983, Bittman, 1988).

Therefore, there are at least two possibilities to correlate the Kärlich Interglacial to the standard subdivision of the Pleistocene. The first possibility is that the Kärlich Interglacial should be correlated to the Early Saalian Hoogeveen Interstadial. This implies that there is a hiatus in the part of the Kärlich section between Unit Gb and the top of Unit H, from where the palynological data were obtained.

However, the pollendiagram obtained from the type section of the Kärlich Interglacial and the diagram from the clay layer in Wageningen-Fransche Kamp which is, on the basis of the mammal fauna, correlated to the Hoogeveen Interstadial, show a number of differences which make correlation problematical (de Jong, pers. comm., 1988). Whether the differences are due to the differences in geographical position is not clear at the moment.

The second possibility is that the Kärlich Interglacial should be correlated to a warm phase of the Elsterian or to an interglacial postdating Interglacial IV of the "Cromerian complex" and predating the Holsteinian, an interglacial which is not represented in the standard division so far. This implies that the Kärlich section above the top of Unit H is incomplete.

Mammal paleontological data may solve this problem in the near future.

The lower part of the stratigraphical scheme (Fig. 12) shows the presence of another four paleosols between the Brunhes Matuyama boundary and the paleosol at the top of Unit Gb. These paleosols cannot simply be correlated with the remaining Cromerian interglacials because as far as we know at the moment there are only two interglacial phases between the Brunhes-Matuyama boundary and Interglacial IV of the "Cromerian complex".

In summary it can be said that the Ariendorf Interglacial can be correlated to Interglacial IV of the "Cromerian complex" and that the correlation between the local stratigraphy of the Middle Rhine area and the standard subdivision of the Pleistocene is still problematical. But the Kärlich section provides us with good opportunities to obtain more information about the faunal history in N.W. Europe, which will be useful for solving part of the correlation problems.

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APPENDIX

LARGER MAMMAL FOSSILS FROM RHENEN (KWINTELOOIJEN AND LECCIUS DE RIDDER PITS)

Introduction

The pits near Rhenen (Kwintelooijen, Vogelenzang and Leccius de Ridder) yielded a large number of larger mammal remains, mainly found by amateur collectors.

The exact stratigraphical provenance of the larger mammal remains is unknown, therefore, the stratigraphic value of these fossils is restricted. Most of these fossils have already been described (Van Kolfschoten, 1981). In the period after 1981 more material has been collected from sediments which were obtained from the Kwintelooijen and Leccius de Ridder pits, which are still being worked. All the fossils, except for a mandibula of *Trogontherium cuvieri*, belong to species which were already known from these pits. The most interesting of these recently collected finds are described here.

SYSTEMATIC DESCRIPTIONS

RODENTIA

Castoridae
***Trogontherium cuvieri* Fischer, 1809**
(Fig. 27.1)

Material (Kwintelooijen): mandibula dext. with i, p4 and m1 (Coll. D. Mol, 's-Heerenberg)

Measurements:
p4: length 14.5 mm., width 11.2 mm.
m1: length 8.1 mm., width ±11.0 mm.

Description and remarks
The incisor is compressed and broken off at both ends. Therefore, no measurements can be taken. The

anterior side of the incisor is round; its enamel is rough. The p4 is in an intermediate state of wear. The tooth shows 4 enamel islands representing the four main folds. The accessory, antero-internal fold extends downward from the occlusal surface to a depth of about 5 mm. There is no trace of cement in the islands on the crown surface or in the folds on the sides. The m1 is damaged at the inner side. It has two folds, one is isolated from the margin, the other fold was probably isolated too, but this cannot be ascertained because of the damage.

Based on the measurements of the teeth it can be concluded that the specimen from Kwintelooijen is larger than the ones from Tegelen, Neede and Miesenheim I (see Table 5).

PROBOSCIDEA

Elephantidae

***Elephas antiquus* (Falconer and Cautley, 1845)**
(= *E. namadicus*)
(Straight-tusked elephant)
(Fig. 27.2)

Material: (Kwintelooijen): 2 fragments of upper molars, 1 fragment of a lower molar sin. (Coll. Van IJmeren, Opheusden)

(Leccius de Ridder): M3 dext. (incomplete) (Coll. Koolen, Maartensdijk), one fragment of a deformed molar (Coll. R.G.M., Leiden no. 64909)

Description and remarks
All the molar fragments have strongly folded and thick (2.2 to 3.5 mm.) enamel. The enamel patterns are lozenge-shaped rising above the cement. The lamellar frequency of the upper molar fragments is about 6 - 6.5, that of the lower molar fragments 4.5 - 5. The width of the incomplete M3 is 87 mm which is within the range of the M3 of *E. antiquus* (width M3: 62.0 - 93.0 (N = 9, various localities) (Maglio, 1973)).

PERISSODACTYLA

Equidae

In Van Kolfschoten (1981) the horse remains are only briefly described and are assigned to two different species, a larger robust type *Equus* sp. A and a smaller one *Equus* sp. B. The smaller type is represented by a single molar, which is figured in the article mentioned. Later it was realized that the molar is very similar to the molars of *Equus hydruntinus* (Van Kolfschoten, 1985). *Equus* sp. B is, therefore here assigned to *Equus* cf. *hydruntinus* (see below).

The remains of *Equus* sp. A have not been restudied. They are provisionally assigned to *Equus* sp.

***Equus* cf. *hydruntinus*, Stehlin & Graziosi, 1935**

Material: m1/m2 sin. (see Van Kolfschoten, 1981; plate 2, fig. 3)

Measurements: length 24.0 mm., width 12.0 mm.

Description and remarks
The molar has a stenonid type of morphology characterized by the deep penetration of the vestibular groove into the so-called double-knot, such that the groove nearly touches the V-shaped margin of the double-knot. In this character it is very similar to the m2 of *Equus hydruntinus* from Maastricht-Belvédère (van Kolfschoten, 1985) and the m2 of *E. hydruntinus* from its type locality Grotta Romanelli (Italy) and Heiligenstadt (Austria) (Stehlin & Graziosi, 1935). The specimen from Rhenen has about the same dimensions as the m2 (length 25.2 mm., width 12.5 mm.) of *E. hydruntinus* from Felines-Termenes (France) (Eisenmann & Patou, 1980).

Rhinocerotidae

***Coelodonta antiquitatis* (Blumenbach, 1799)**
(Woolly rhinoceros)
(Fig. 27: 3-7)

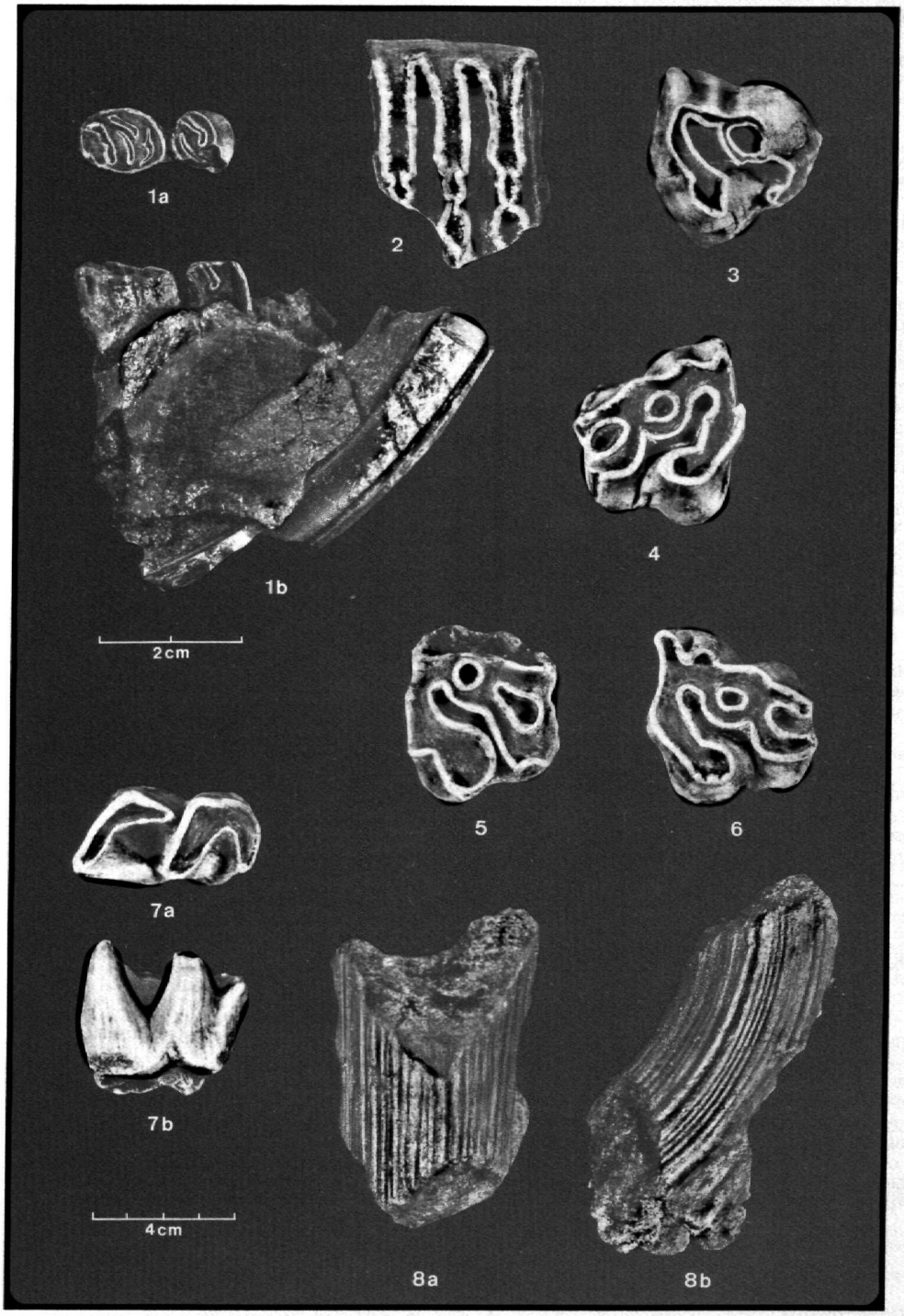
Material: Kwintelooijen; M2 sin., M3 dext., M3 sin., m2 sin., (Coll. Van IJmeren, Opheusden); M3 sin. (Coll. Van de Bovenkamp, Veenendaal).

Measurements:
M2 sin. (Coll. Van IJmeren) length ± 47 mm., width -
M3 dext. (Coll. Van IJmeren) length ± 51 mm., width 56.5 mm.
M3 sin. (Coll. Van IJmeren) length ± 51 mm., width 54 mm.
M3 sin. (Coll. Vd Bovenkamp) length ± 53 mm., width 49.8 mm.
m2 sin. (Coll. Van IJmeren) length 52.3 mm., width 32.8 mm.

Description and remarks
The upper molars have a closed medifossette, undulating ectolophs and "leathery", rather rough enamel. Two M3's in the collection of Van IJmeren have a rectangular outline, the one in the collection of Van de Bovenkamp has a more triangular outline.

The triangular specimen has been recovered from the Saalian deposits of the Units 9 or 10. This implies that the triangular shape of the M3 of *Coelodonta antiquitatis* is not conclusive evidence for a post Saalian age, as suggested by Guérin (1970).

Fig. 27. Rhenen - Kwintelooijen: 1: *Trogontherium cuvieri*: mandibula dext. with i, p4 and m1 (Coll. Mol, 's-Heerenberg): a: occlusal view; b: buccal view: 2: *Elephas antiquus*: fragment of an upper molar (Coll. Van IJmeren, Opheusden): 3 - 7: *Coelodonta antiquitatis*: 3: M3 sin. (Coll. Van de Bovenkamp, Veenendaal); 4: M3 dext.; 5: M2 sin.; 6: M3 sin.; 7: m2 sin.: a: occlusal view; b: lingual view (4 - 7: Coll. Van IJmeren, Opheusden): 8: *Hippopotamus* sp.: pseudo-morphosis of a lower canine fragment (Coll. Franssen, Bennekom).


1a
2
3
1b
4
2cm
5
6
7a
7b
4cm
8a
8b

ARTIODACTYLA

Hippopotamidae
Hippopotamus sp.
(Fig. 27.8)

Material: Kwintelooijen; pseudo-morphosis of a lower canine fragment (Coll. C.J.H. Franssen, Bennekom)

Measurements: length of the fragment ± 115 mm., diameter > 50 mm.

Description and remarks
The pseudo-morphosis consists of cemented sand of the Urk Formation (Zandstra and Ruegg, pers. comm, 1986). It has the same shape and size as a part of a lower canine of a hippo and shows the characteristic fine longitudinal grooves (Fig. 27.8).

A previous find, a canine fragment from the Vogelenzang pit, was assigned to *Hippopotamus* cf. *amphibius* (Van Kolfschoten, 1981). However, the investigations of Faure (1983) indicate that *Hippopotamus amphibius* did not occur in Western Europe during the Pleistocene. She distinguishes two different species amongst the Pleistocene Hippopotamidae of Western Europe: *Hippopotamus major* and *H. incognitus*. The scarce remains from Rhenen do not allow a specific assignment to be made.

Cervidae
Megaloceros giganteus (Blumenbach, 1803)
(Giant deer)

Material: Kwintelooijen; antler fragment, mandible dext. with m3, first phalange (Coll. Van IJmeren, Opheusden)

Measurements: m3: length	46.5 mm.
width (at the base of the crown)	22.0 mm.
phalange: length	87.6 mm.
proximal width	38.5 mm.
prox. antero-post. diam.	37.2 mm.
distal width	33.5 mm.
distal antero-post. diam.	29.2 mm.

Description and remarks
The antler fragment consists of the proximal part of a shed antler. There is a fragment of the brow tine at a small distance above the burr. The diameter of the burr is at least 94 mm. and comparable in size with the largest antler known so far from Rhenen. The m3 is low crowned and has a distinct ectostylid. The first phalange shows the characters which, according to Heintz (1970), are typical for cervids.

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