

M	<i>Equus</i> sp.				<i>Equus steinheimensis</i>		
	Neede	M-B 3	Rhenen RV 107	Heppenl. 7590	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 Kolschoten, 1981). Most of the ectolophs of the M1 of *D.*

*hemitoechus* are also more deeply undulated than those of *D. mercki* (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

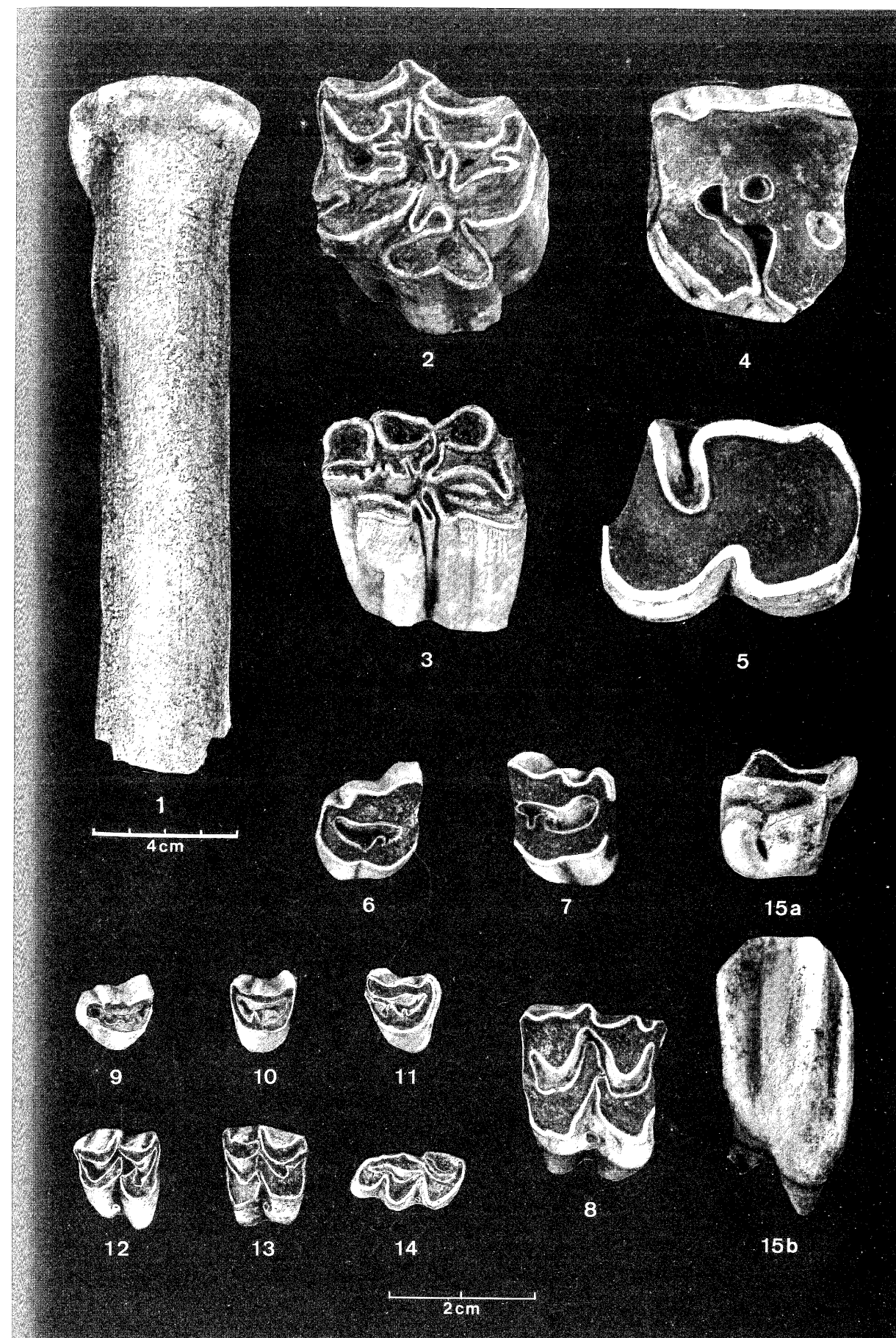


Fig. 18. Maastricht-Belvédère: M-B 3: 1: *Equus* sp.: metatarsus dext.; M-B 2: 2 - 3: *Equus* sp.: upper premolar dext.; 3: lower premolar dext.; M-B 4: 4 - 5: *Dicerorhinus hemitoechus*: 4: DP2 sin.; 5: m1/2 dext.; 6 - 8: *Cervus elaphus*: 6: P3 sin.; 7: P4 dext.; 8: M1 dext.; 9 - 14: *Capreolus capreolus*: 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.

	N	P4 RANGE	MEAN	N	M1 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).

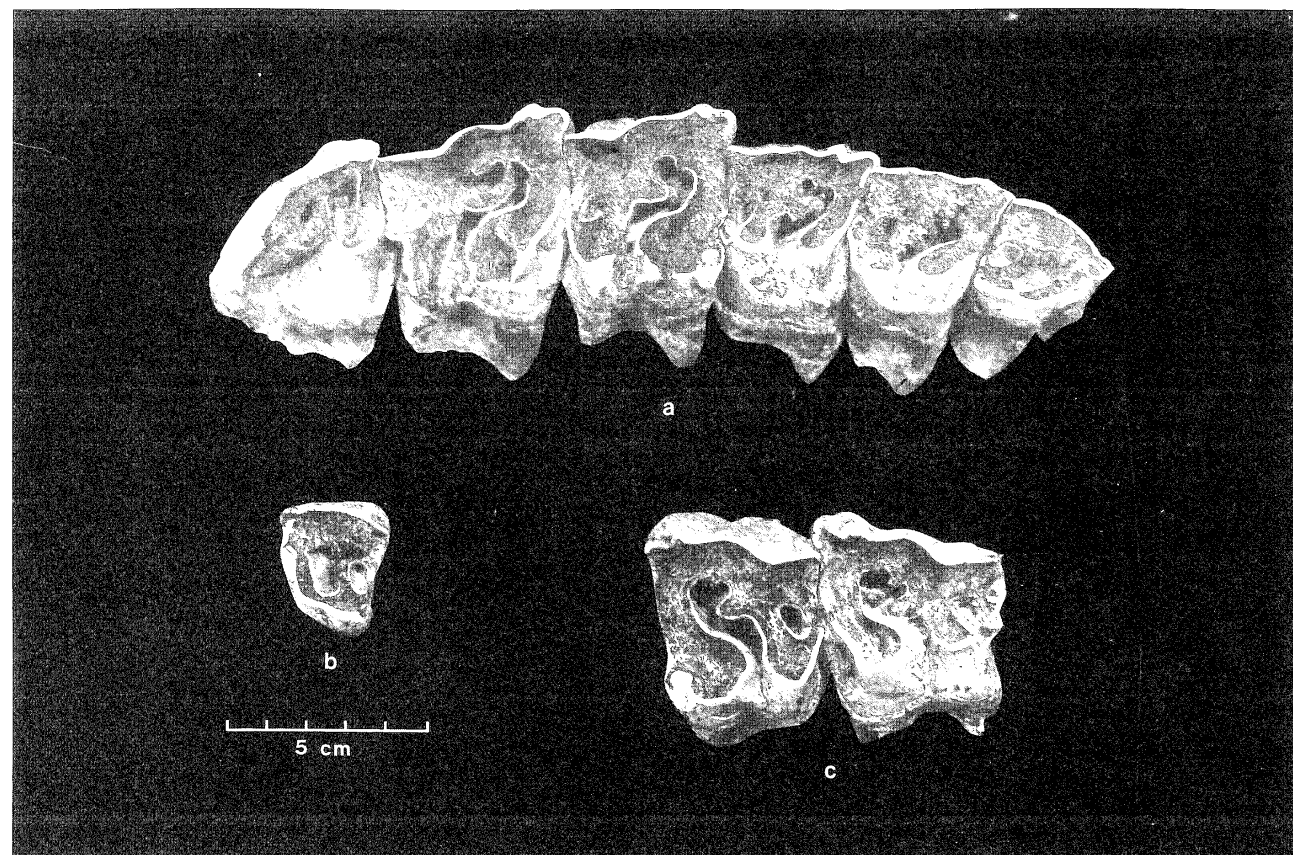


Fig. 19. *Dicerorhinus hemitoechus* (Maastricht-Belvédère fauna 3C): a: P2 - M3 dext.; b: P2 sin.; c: M1 and M2 sin.

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 ectolophes (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 ectolophes 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

	<i>D. mercki</i>	<i>D. hemitoechus</i>		
	Neede P4/M1	Rhenen P4	P4	Maastricht-Belvédère 3C 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., navicuboid 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* LACÉPÈDE, 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 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 salient 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 sedi-

ments, 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		N
	m1	M3	
<i>A. terrestris amphibius</i> (Great Britain: Shropshire)	72.5	70.7	19
<i>A. terrestris terrestris</i> (West Germany: northern part)	74.3	74.6	35
<i>A. terrestris sherman</i> (West Germany: Bonn)	78.1	76.9	54
<i>A. terrestris sherman</i> (West Germany: Trier)	75.7	76.1	11
<i>A. terrestris sherman</i> (France: eastern part)	65.7	71.9	16
<i>A. terrestris exitus</i> (Switzerland: Interlaken)	68.8	69.4	33
<i>A. terrestris exitus</i> (Liechtenstein)	71.6	75.2	8
<i>A. terrestris sherman</i> (Hungary: Fehérvár)	93.8	94.3	4
<i>A. terrestris italicus</i> (Northern Italy: Turin)	94.2	93.0	13
<i>A. terrestris musignani</i> (Southern Italy: Camigliatello)	98.4	106.0	7
<i>A. terrestris persicus</i> (Turkey: Tatvan)	124.6	131.9	5
<i>A. terrestris persicus</i> (Iran)	134.4	148.1	3
<i>A. terrestris monticola</i> (Northern Spain: Reinos)	73.3	68.1	12
<i>A. sapidus sapidus</i> (Western Spain: Salamanca)	119.7	119.0	31
<i>A. sapidus sapidus</i> (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 that the 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 course 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

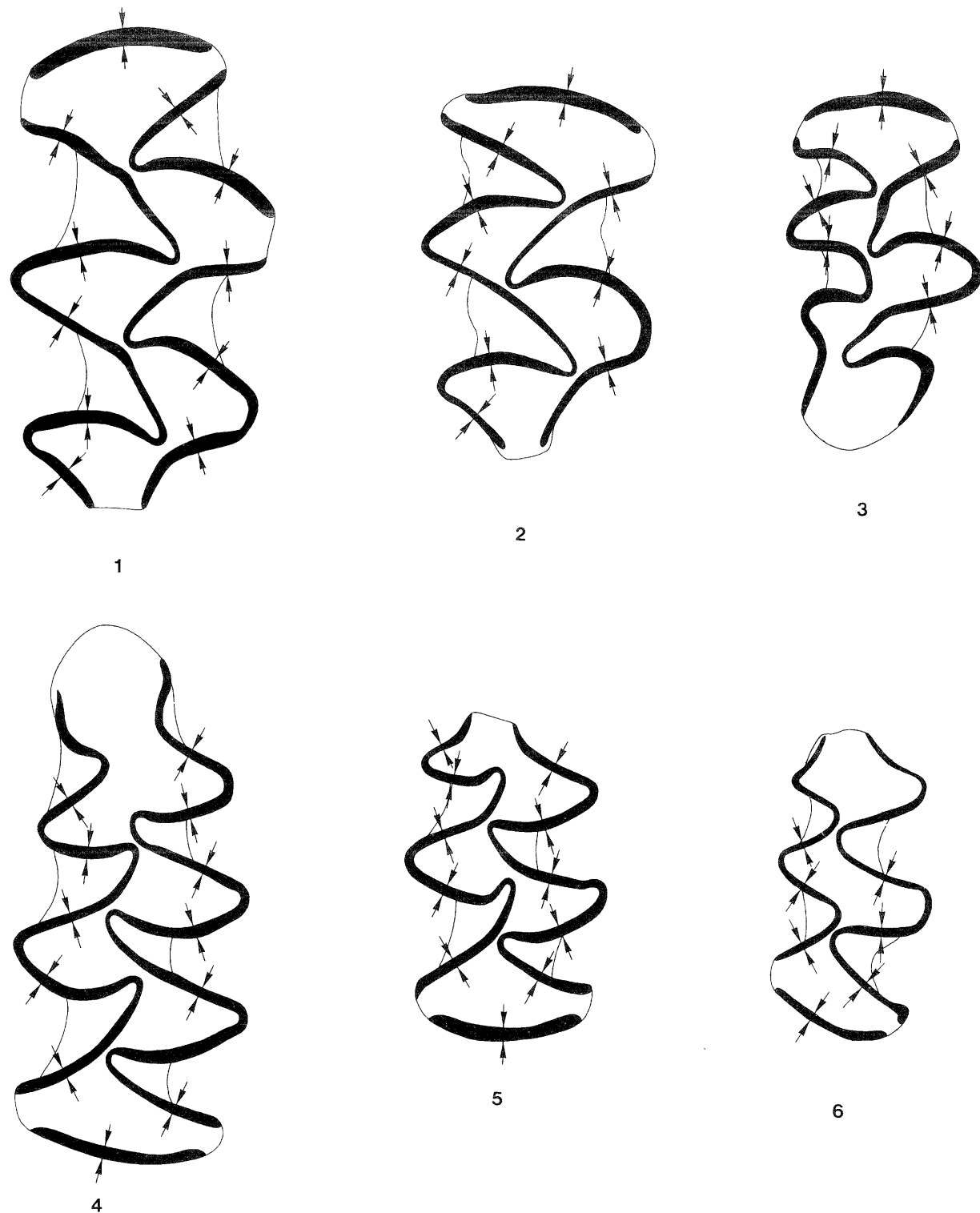


Fig. 20. The places where the thickness of the enamel band of the upper (1 - 3) and lower (4 - 6) *Arvicola* molars are measured in order to calculate the enamel thickness quotient of the molars. 1: M1; 2: M2; 3: M3; 4: m1; 5: m2; 6: m3.

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

#### Miesenheim I

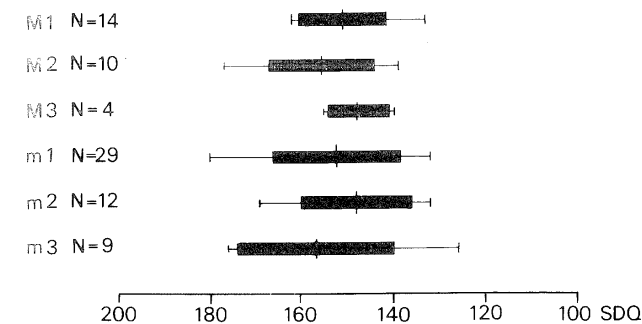


Fig. 21. The range, standard deviation and mean of the enamel thickness quotient (SDQ values) of the molars of *Arvicola terrestris cantiana* from Miesenheim I.

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 "Miomys-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 *Miomys*-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 *Miomys*-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 and 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 *Miomys 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 *Miomys 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*.

HOLOCENE		POPULATIONS FROM CENTRAL EUROPE		POPULATIONS FROM THE NETHERLANDS AND THE MIDDLE RHINE AREA						
PLEISTOCENE	LATE PLEISTOCENE	Weichselian	<i>Arvicola</i>			<i>Arvicola</i>				
			Euerwanger Bühl H	83.03	(74 - 94)		Maastricht-Belvédère 5	88.67 (75 - 99)		
			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)							
	MIDDLE PLEISTOCENE	Eemian				Plaidter-Hummerich I	82.17 (66 - 94)			
			Untertürkheim	100.81	(89 - 133)					
			Adlerberg/Nördlingen	100.83	(91 - 109)					
		Saalian	Taubach	105.15	(97 - 115)			Ariendorf 2	76.50 (74 - 79)	
			Schönfeld	106.02	(96 - 117)					Rhenen
Weimar-Ehringsdorf UT	112.30	(102 - 126)	Wageningen-F. Kamp II	114.38 (111 - 120)						
Holsteinian					Maastricht-Belvédère 4	102.04 ( 86 - 113)				
	Dobrkovice 2	123.21					(113 - 139)	Maastricht-Belvédère 3	102.66 ( 94 - 114)	
Elsterian					Ariendorf 1	118.50 (112 - 128)				
	Bilzingsleben	132.52	(121 - 145)	Neede			146.58 (124 - 169)			
"Cromerian Complex"	Mosbach	133.54			Miesenheim I	152.03 (126 - 180)				
			<i>Mimomys</i>							
			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

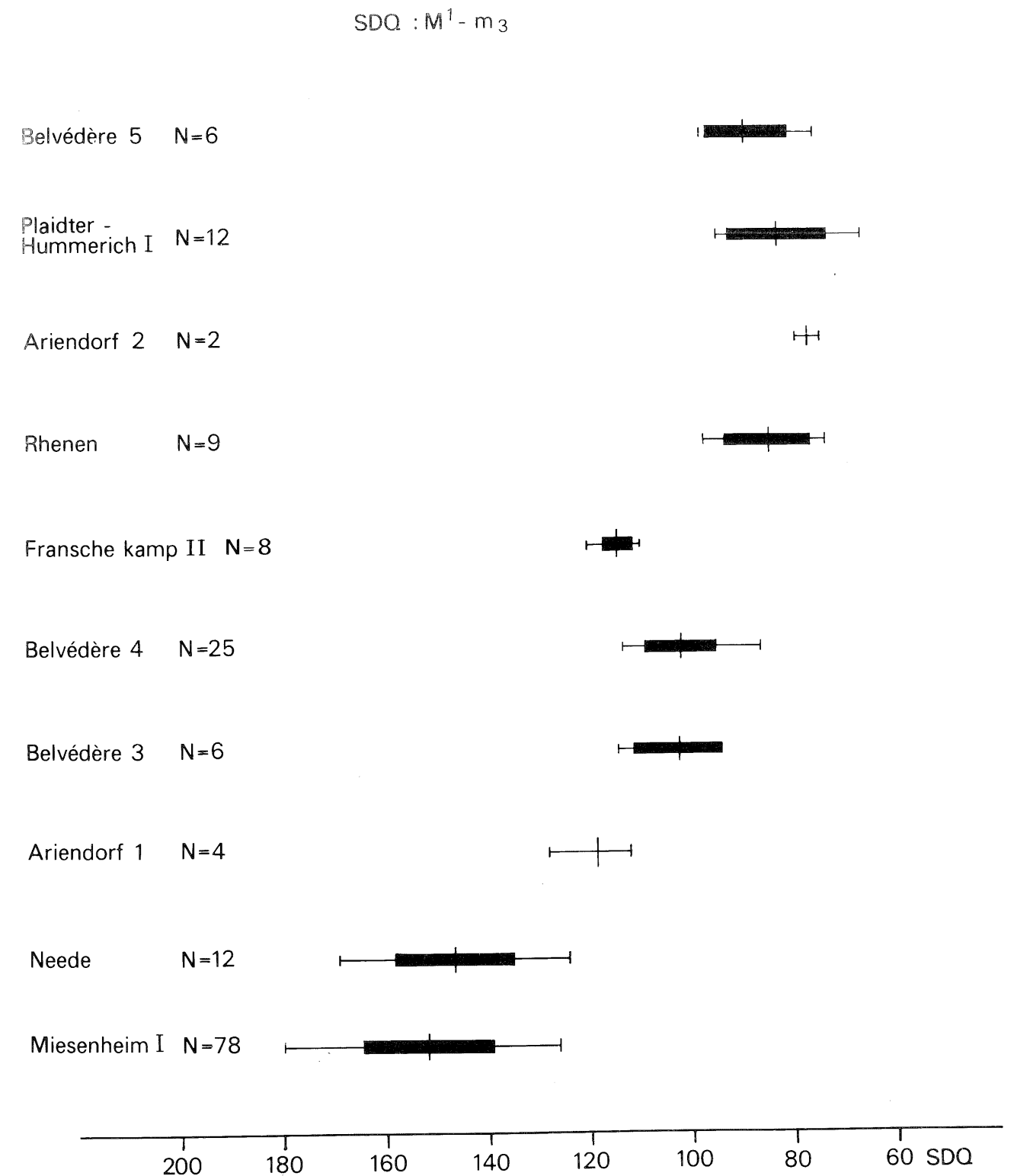


Fig. 22. The range, standard deviation and mean of the enamel thickness quotient (SDQ values) of the *Arvicola* molars from the discussed assemblages.

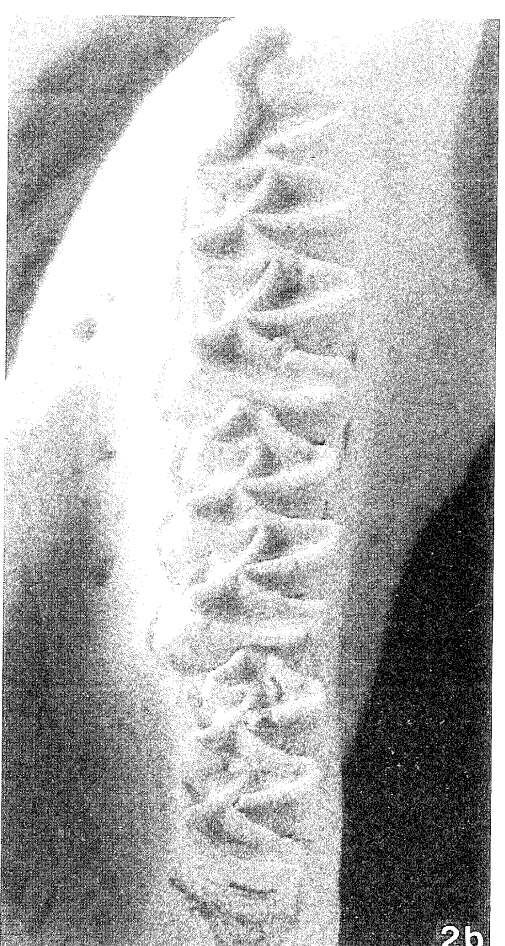
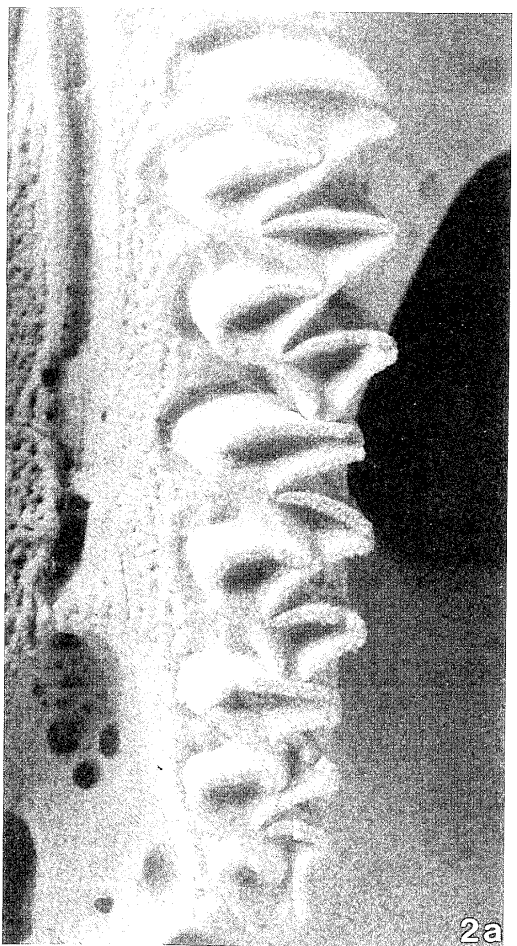
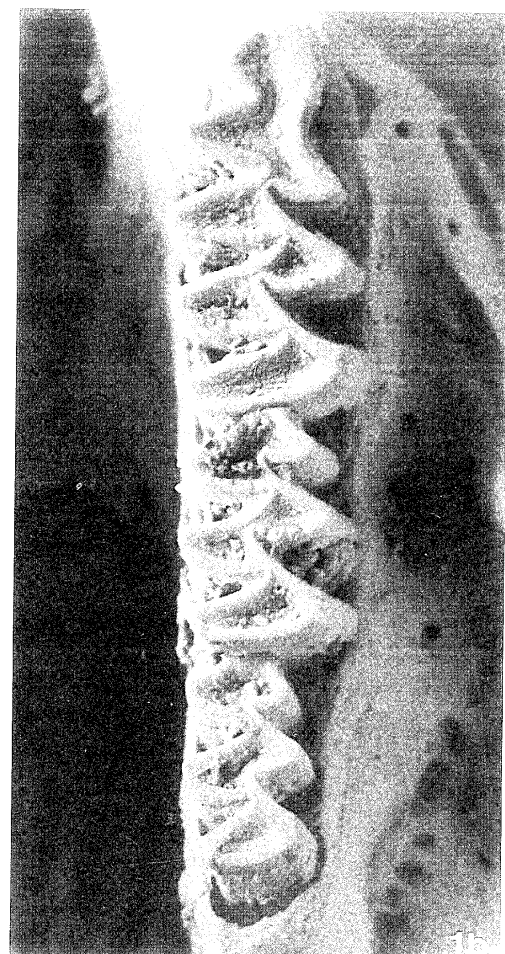
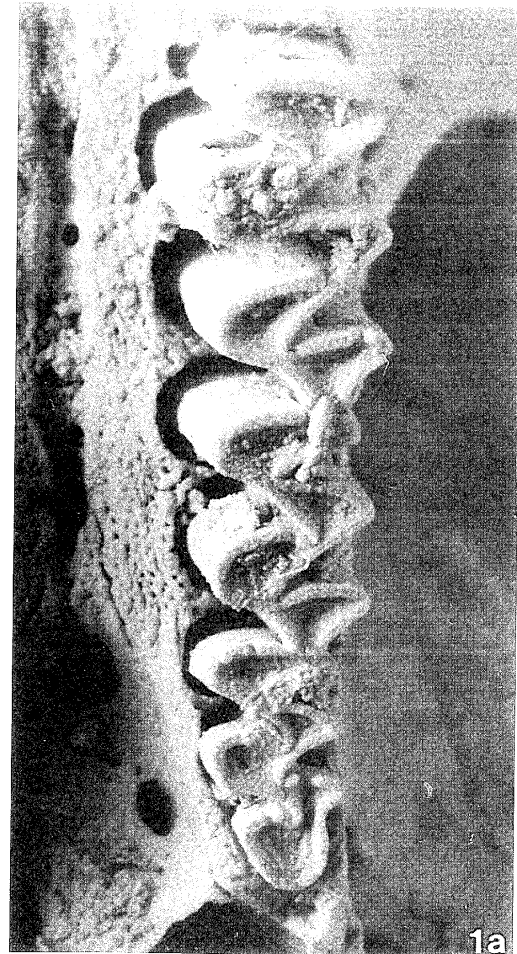


Fig. 23. The upper and lower dentition of *Arvicola terrestris persicus* from Turkey (nr. 1) (Coll. Koenig Museum, Bonn; nr. 68.284) and Iran (nr. 2) (Coll. Senckenberg Museum, Frankfurt; nr. 35407). (Photos made by Mr. G. Oleschinski, Bonn)

	N	Range	Mean	SD
Maastricht-Belvédère 5	1	—	3.80	—
Plaidter Hummerich I	5	3.56 - 3.97	3.796	0.180
Rhemen	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. Length of the m1 of *Arvicola* from the localities discussed in this paper.

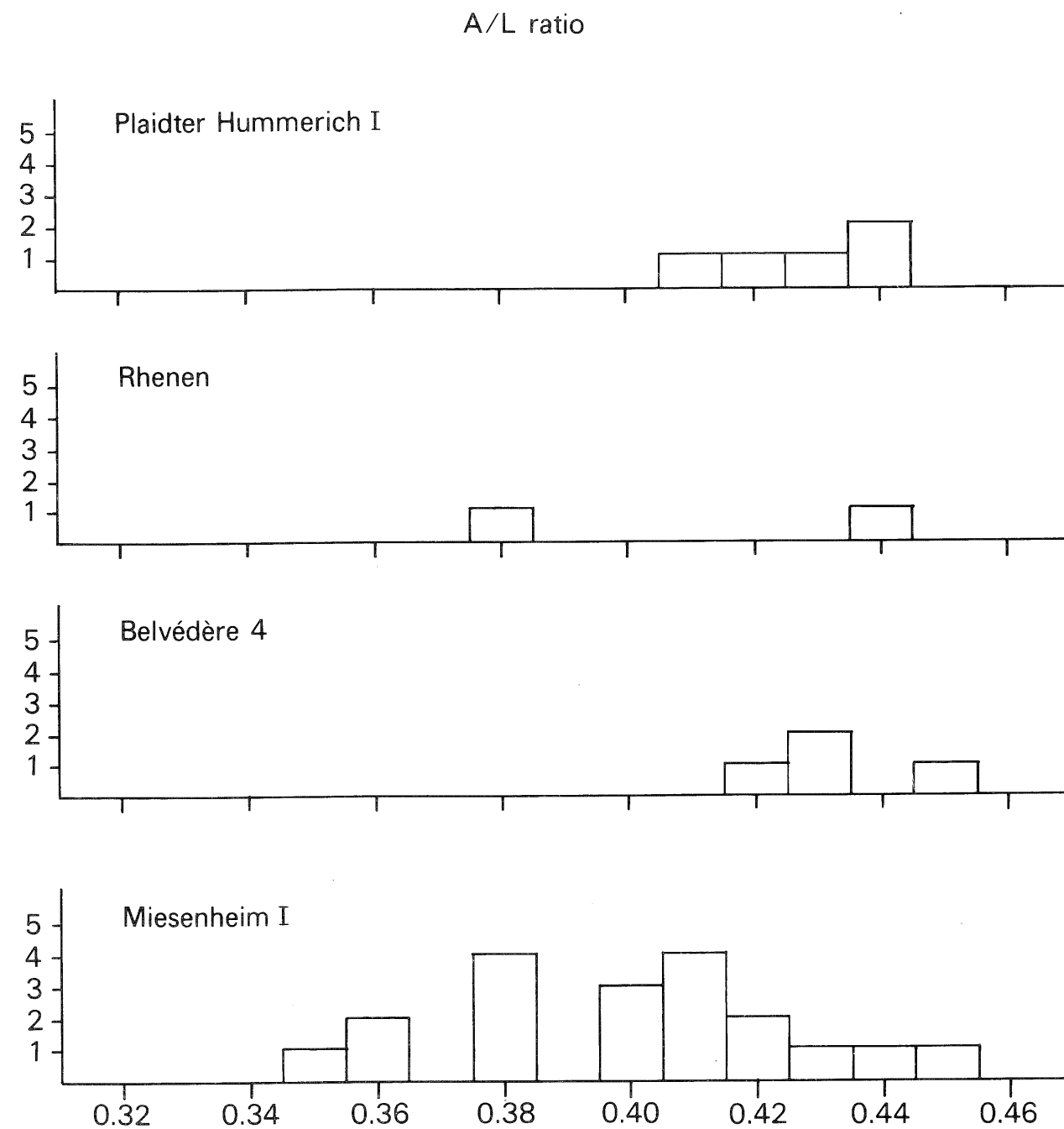


Fig. 24. The A/L ratio of the *Arvicola* m1 from the faunas Miesenheim I, Maastricht-Belvédère 4, Rhemen and Plaidter-Hummerich I.

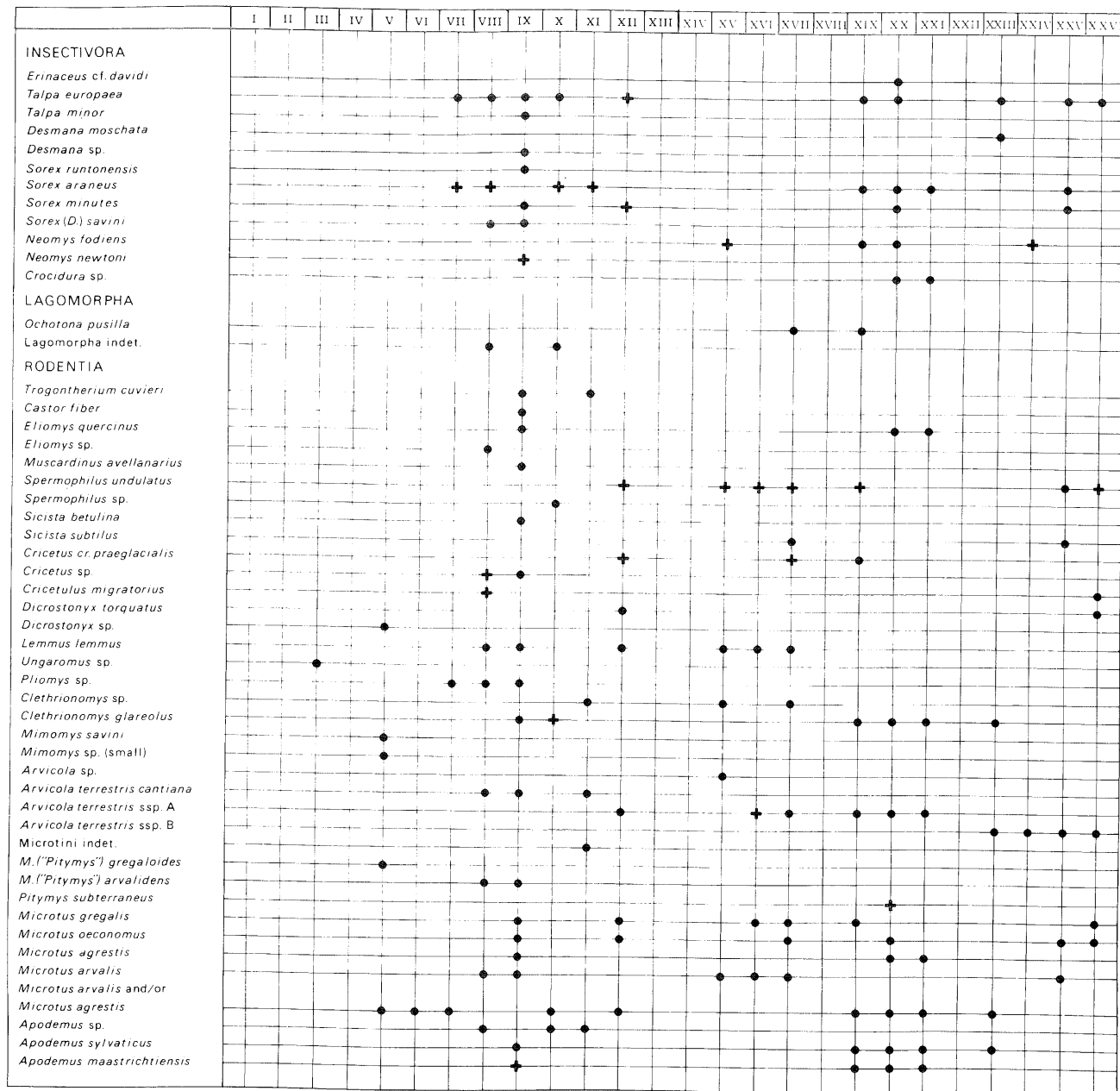


Fig. 25. The distribution of the mammal species in the studied faunas. I = Kärlich A; II = Kärlich Ba; III = Kärlich Bb; IV = Kärlich C; V = Kärlich D-E; VI = Kärlich F; VII = Kärlich Ga; VIII = Kärlich Gb; IX = Miesenheim I; X = Kärlich H; XI = Neede; XII = Ariendorf 1; XIII = Wageningen-Fransche Kamp 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

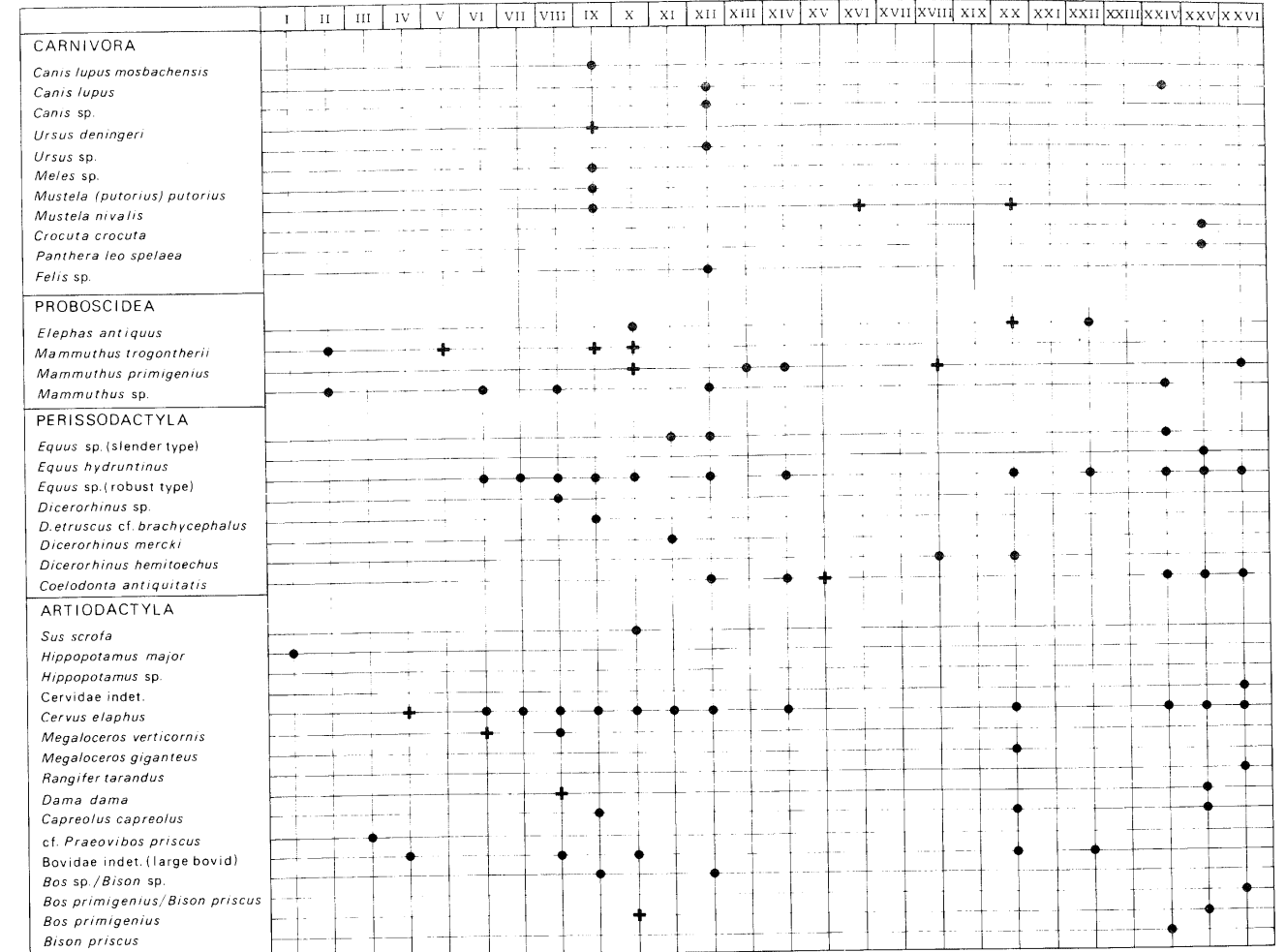


Fig. 25. Continuation.

we have proper data regarding the lithostratigraphical provenance.

##### IV.2. STRATIGRAPHICAL RANGES OF SPECIES WHICH ARE RELEVANT FOR THE BIO-STRATIGRAPHY 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 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 avella-*

*narius*, *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 maastrichtensis*, *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 subtilis*, *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.) praeearaneus*, 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

*Trogotherium 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. can-*

*tiana*. 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 arvicolid molars 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 Kolschoten, 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 ± 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 Kolschoten 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 "acornate" 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 *Miomys* 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 "*Miomys 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 *Miomys*, the Biharian faunas by a *Microtus* dominance. In the Biharian "Stage" one has distinguished two substages: Lower and Upper Biharian. The disappearance of *Miomys* 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 "Istállóskő/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 *Miomys*. 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 where 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 successive 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-occurrence 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.

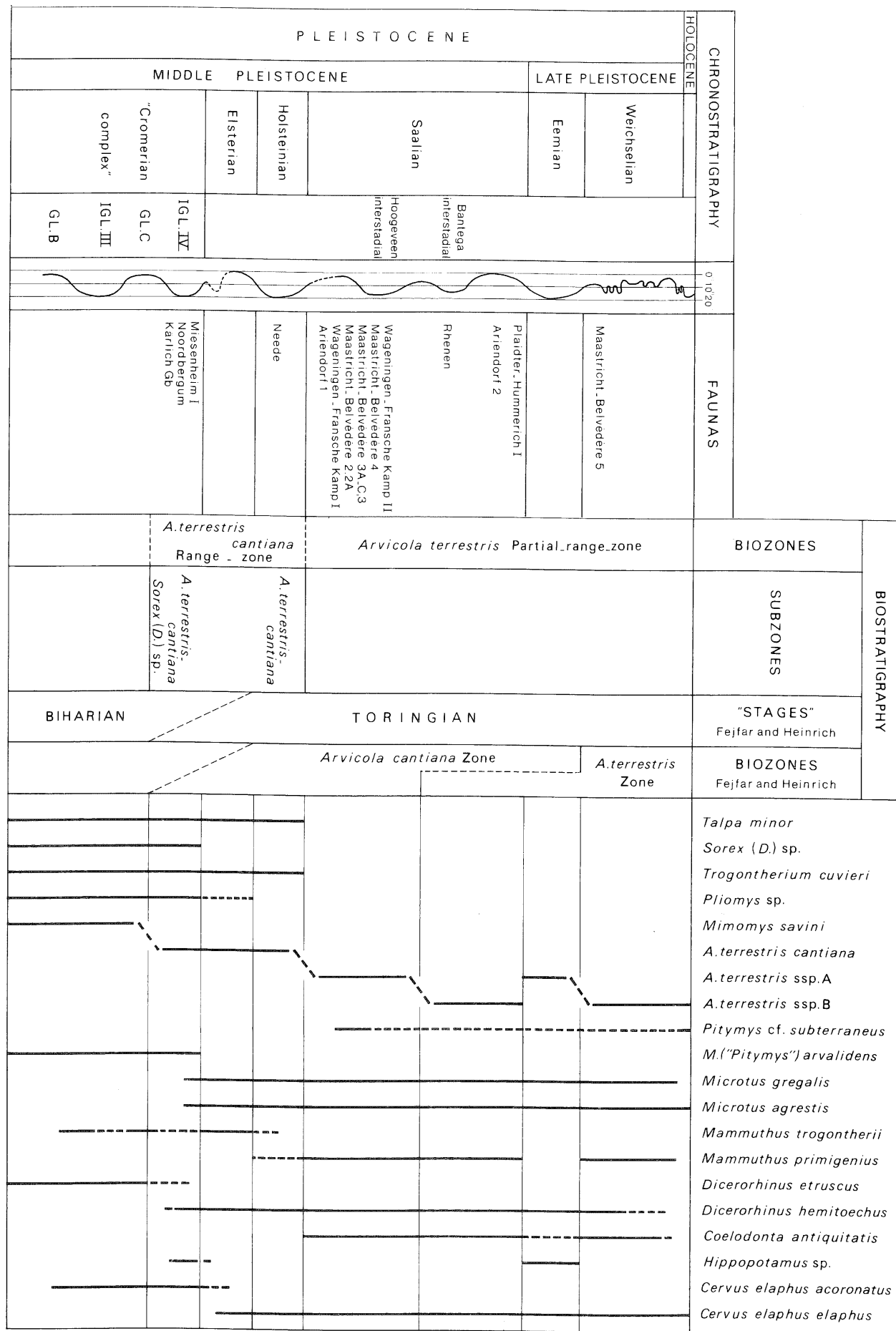
##### Remarks

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* (Jánosy, 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 contemporaneous. 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 (Jánosy, 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* (Jánosy, 1976). Heinrich (1982) rejects Jánosy'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, Weinberghöhle 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 palynologically 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  $420 \pm 30$  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 not 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.

#### ACKNOWLEDGEMENTS

The author would like to express his sincere thanks to many persons for their help and advice and for the stimulating discussions. In particular I want to thank Prof. Dr. P. Marks, Dr. A.J. van der Meulen, Dr. P.Y. Sondaar and Dr. W.H. Zagwijn for their continued support and interest, and for the close reading of the manuscript and their constructive criticism.

I have benefited from the contributions and discussions with Dr. H. de Bruijn, Dr. C.J. Rümke, Mr. A.J. Burger, Mr. J. de Jong, Mr. T. Meijer, Mr. G.H.J. Rugg, Mr. J. Zandstra, Mr. E.A. van de Meene and Dr. J. Vandenberghe for which I am grateful. The author expresses his sincere gratitude to Mr. W. Roebroeks for his interest, the stimulating discussions and his permission to study the material from Maastricht-Belvédère. I am also indebted to Mr. K. Groenendijk and Mr. J.P. de Warrimont who recovered and sampled a number of faunas in the pit Maastricht-Belvédère. I also should like to express my gratitude to the members of the N.I.V.O.N. association, department Neede, for their assistance and their cooperation.

Prof. Dr. G. Bosinski gave me permission to study the collections from the localities in the Middle Rhine area for which I am grateful. I have appreciated the discussions with Prof. Dr. G. Bosinski, Prof. Dr. W. von Koenigswald and Prof. Dr. W. Boenigk. The author also wants to thank Mrs. E. Turner, Mr. M. Street, Mr. K. Kröger and Mr. J. Schäfer for their cooperation and the stimulating discussions.

The author grateful acknowledges the curators Dr. G. Storch (Senckenberg Museum, Frankfurt (B.R.D.)), Prof. Dr. J. Niethammer (Museum Alexander Koenig, Bonn (B.R.D.)), Dr. J. de Vos (R.G.M. Leiden), Mr. P. Venema (N.H.M. Enschede), Mr. J. Veenvliet (N.D. Denekamp), Mr. L.W.A. Meijer (N.H.M. Maastricht) for the opportunity to study the collections. I also

wish to express my gratitude to Mr. A. Buter (Borne), Dr. C.J.H. Franssen (Bennekom), Mr. D. Mol ('s Heerenberg) and Mr. B. van IJmeren (Opheusden) for their permission to study their collections.

I should like to thank Mr. H.P. Brinkerink, Dr. K.J. Steensma and Mr. L. van de Hoek Ostende for their assistance in the field; the former also for the preparation of part of the fossils the latter two for their help to finish the manuscript. Mr. J. Luteijn made the drawings and Mr. W.A. den Hartog the pictures, for which I am grateful. Sincere thanks are due to Mrs. S. McNab who corrected the English text. Finally I gratefully acknowledge the Dutch Organization for the Advancement of Pure Research (Z.W.O.) for its financial support.

#### APPENDIX

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

##### Introduction

The pits near Rhenen (Kwinteloijen, 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 Kolf-schoten, 1981). In the period after 1981 more material has been collected from sediments which were obtained from the Kwinteloijen and Leccius de Ridder pits, which are still being worked. All the fossils, except for a mandibula of *Trogotherium 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

##### *Trogotherium cuvieri* Fischer, 1809 (Fig. 27.1)

Material (Kwinteloijen): 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  $\pm 11.0$  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 Kwinteloijen 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: (Kwinteloijen): 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 re-studied. 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: Kwinteloijen; 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  $\pm$  47 mm., width - M3 dext. (Coll. Van IJmeren) length  $\pm$  51 mm., width 56.5 mm.

M3 sin. (Coll. Van IJmeren) length  $\pm$  51 mm., width 54 mm.

M3 sin. (Coll. Vd Bovenkamp) length  $\pm$  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).

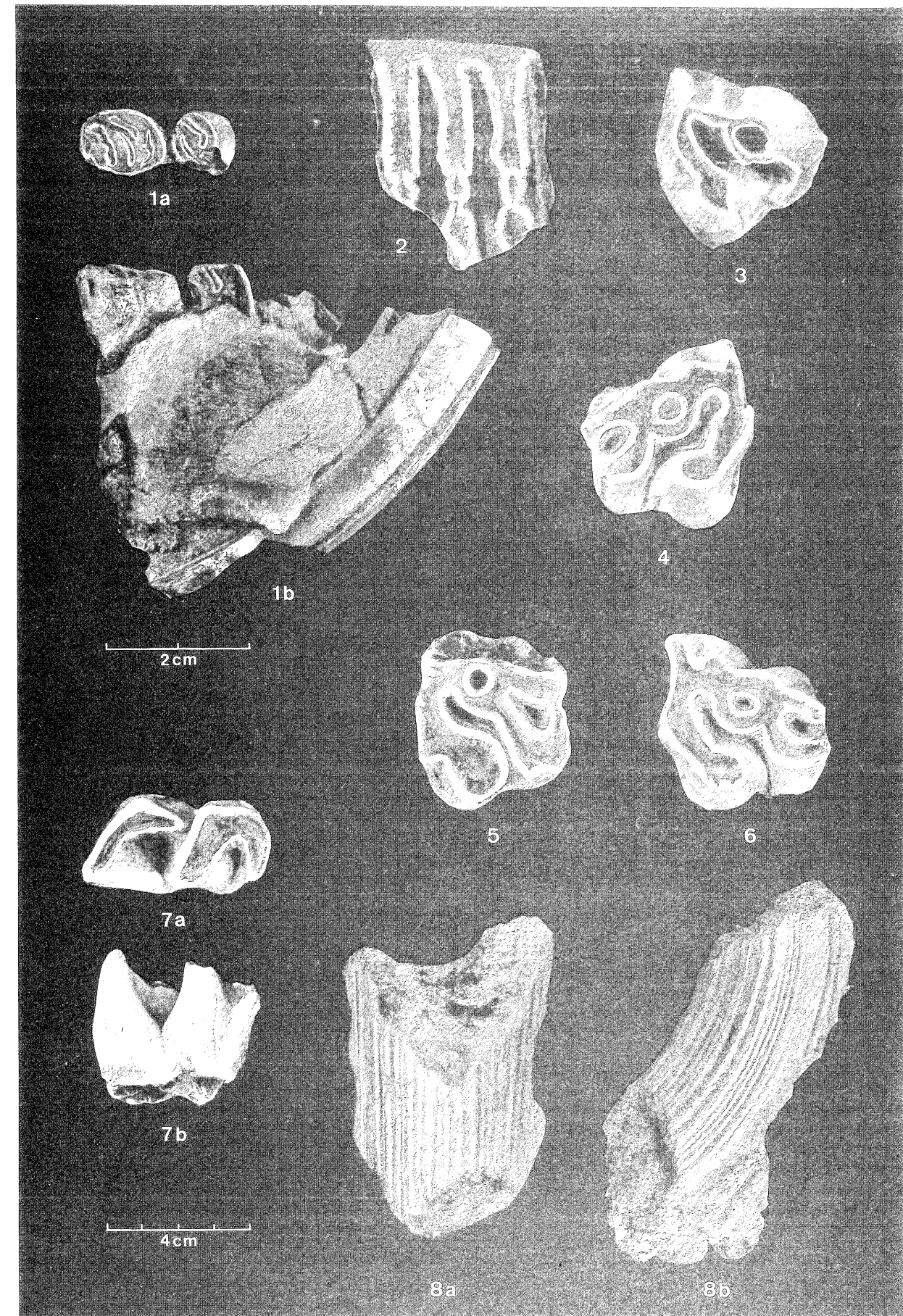


Fig. 27. Rhenen - Kwinteloijen: 1: *Trogontherium cuvieri*: mandibula dext. with i, p4 and m1 (Coll. Mol, 's-Heerenberg): a: occlusal view; b: buccal view; 2: *Elephas antiquus*: fragment of an upper molar (Coll. Van IJmeren, Opheusden); 3 - 7: *Coelodonta antiquitatis*: 3: M3 sin. (Coll. Van de Bovenkamp, 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).

## ARTIODACTYLA

### Hippopotamidae

#### *Hippopotamus* sp. (Fig. 27.8)

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

Measurements: length of the fragment  $\pm$  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 Vogelzang 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: Kwinteloijen; 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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