THE SAALIAN MAMMAL FOSSILS FROM WAGENINGEN-FRANSCHE KAMP

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SAMENVATTING

In de groeve Wageningen-Fransche Kamp is een aantal schubben met vroeg- en midden-pleistocene sedimenten ontsloten. In twee nivo's van de lithostratigrafische eenheid 3 zijn zoogdierresten aangetroffen. Een kiesfragment van de mammoet *Mammuthus primigenius* is opgenomen in het onderste deel van eenheid 3. De tamelijk primitieve kenmerken van de mammoet kies wijzen op een Vroeg-Saalien ouderdom.

Het bovenste nivo leverde een rijke kleine zoogdierfauna op. De fauna met Sorex araneus, Crocidura sp., Eliomys quercinus, Clethrionomys glareolus, Arvicola terrestris ssp. A. Microtus agrestis, Microtus arvalis en/of Microtus agrestis, Apodemus sylvaticus en Apodemus maastrichtiensis is tamelijk modern. Al de soorten, met uitzondering van Arvicola terrestris ssp. A en Apodemus maastrichtiensis komen ook tegenwoordig in Nederland voor. De fauna indiceert interglaciale klimaatsomstandigheden en een bosrijke omgeving en wordt op grond van het evolutionaire ontwikkelingsstadium van de Arvicola terrestris kiezen met het Vroeg-Saalien gecorreleerd.

SUMMARY

In the pit Wageningen-Fransche Kamp a number of thrust sheets with Early and Middle Pleistocene sediments is exposed. Mammal fossils have been collected from two levels of the lithostratigraphical unit 3. A molar fragment of Mammuthus primigenius has been incorporated in the lowermost level of unit 3. The rather primitive characters of the Mammuthus primigenius molar point to an Early Saalian age.

The upper level yielded a rich smaller mammal fauna. The fauna with Sorex araneus, Crocidura sp., Eliomys quercinus, Clethrionomys glareolus, Arvicola terrestris ssp. A, Microtus agrestis, Microtus arvalis and/or Microtus agrestis, Apodemus sylvaticus and Apodemus maastrichtiensis is rather modern. All the species, except for Arvicola terrestris ssp. A and Apodemus maastrichtiensis also inhabit The Netherlands nowadays. The fauna indicates interglacial conditions and a mainly wooded environment and is correlated with the Early Saalian on the basis of the evolutionary stage of the Arvicola terrestris molars.

1. INTRODUCTION

The sandpit "Fransche Kamp" at Wageningen is located in the highest part of the ice-pushed ridge, which is formed during the Saalian and is situated to the east of Lunteren-Ede-Wageningen and the Gelderse Vallei (see fig. 1). The discovery of a number of molluscs in the sandpit by Dr. C.J.H. Franssen (Bennekom) in 1981 led to the palaeontological investigations of the sediments exposed in this pit.

The loam and clay layer, containing the molluscs, at the top of unit 3 (see Ruegg, this volume), is exposed in the pit in several places. A sample of about 3 tons of clay was taken at the most westerly outcrop (see fig. 2) from a layer which is part of thrust sheet D (see Ruegg, this volume). This sample yielded about 650 identifiable vertebrate fossils (mainly mammals) and a large molluscan fauna. The mammals are described in this paper, together with an incomplete molar of an elephant, found by Mr. G.H.J. Ruegg (Geological Survey, Haarlem) at the base of unit 3 in a layer of stones and coarse gravel.

The vertebrate fossils are stored in the Institute of Earth Sciences, Utrecht University.

2. TERMINOLOGY AND MEASUREMENTS

The elements of the upper jaw are indicated by an upper case character, the elements of the lower jaw by a lower case character.

The dental elements and lower jaw of the Soricidae are measured and described after Reumer (1984). The terminology and measurements of the dental elements of the Gliridae are after Daams (1981), those of the Arvicolidae (fig. 3) after Van der Meulen (1973) and those of the Muridae after Van der Weerd (1976). The remains of the Elephantidae are described and measured after Maglio (1973).

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

ABBREVIATIONS

There are a number of standard abbreviations such as: N = number of observations; min. = minimum, smallest measurement; max. = maximum, largest measurement; dext. = dextral; sin. = sinistral; SE = standard error; SD = standard deviation.

3. SYSTEMATIC DESCRIPTIONS

3.1. INSECTIVORA SORICIDAE Gray, 1821

Sorex araneus Linnaeus, 1758 (Common shrew)

Material: 10 I dext., 9 I sin., maxillary fragment with P4 and M1 sin., 9 P4 sin., 8 M1 dext., 10 M1 sin., 11 M2 dext., 12 M2 sin., M3 dext., 3 M3 sin., 12 i dext., 12 i sin., mandibular fragment with m1-m3 dext., mandibular fragment with m1-m2 dext., 3 mandibular fragments with m2 dext., 8 mandibular fragments dext., 2 mandibular fragments with m1-m3 sin., 2 mandibular fragments with m1-m2 sin., mandibular fragment with m1 sin., 3 mandibular fragments with m2 sin., 10 mandibular fragments sin., 4 m1 dext., 10 m1 sin., 5 m2 dext., 4 m2 sin., m3 dext., m3 sin.

Measurements: see table 1

Description and remarks

The presence or absence of pigmentation of the teeth is an important diagnostic character for the genera of the family of the Soricidae. Unfortunately the soricid material from Wageningen-Fransche Kamp does not show any trace of the pigmentation. Therefore, the determination is based purely on morphological characters and on size.

The upper incisors are not fissident, the lower

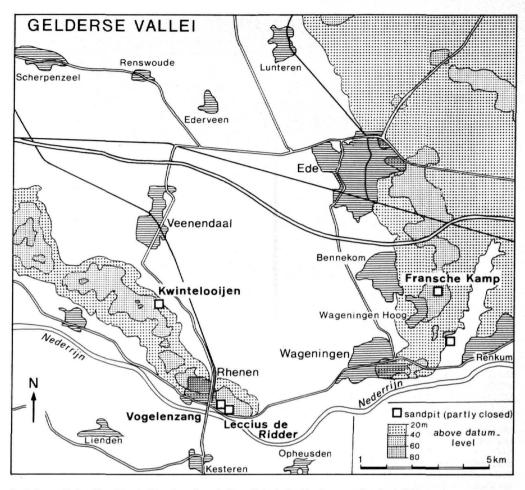


Fig. 1. Geographical position of the pits Wageningen-Fransche Kamp, Kwintelooijen, Vogelenzang and Leccius de Ridder.

incisors are tricuspulate, the foramen mentale is located below the trigonid of the m1. The size and the morphology of the dental material and the condyle of the mandibular fragments are very similar to recent material of *S. araneus* with which the fossils have been compared. The dimensions of the mandibulae and the lower dentition correspond to those of *Sorex araneus* from recent Central European populations as presented by Heinrich (1983) Jánossy (1969) and Von Koenigswald (1970).

On the basis of the ramus height (table 2) it can be stated that the material from Wageningen-Fransche Kamp is larger than that of *Sorex runtonensis* from the Upper Freshwater Beds of West Runton, the specimen of *Sorex runtonensis* from Miesenheim I and *Sorex* sp. A from Petersbuch. The material cannot be referred to *Sorex kennardi*, which occurs,

for instance, in La Fage, because this species is about the same size as *S. runtonensis* (Jammot, 1974a; Von Koenigswald, 1970). The living *Sorex articus*, which nowadays occurs nearly all over the U.S.S.R. and which has been described from the Middle Pleistocene fauna from Cagny (France), is likewise somewhat smaller than *Sorex araneus* (Jammot, 1974b).

The rami of Sorex (Drepanosorex) savini from the Upper Freshwater Beds of West Runton and from Miesenheim I are much higher than those from Wageningen-Fransche Kamp indicating that the former belong to a larger species (table 2).

Crocidura sp. (figs. 4.1 and 4.2)

Material: M1 dext, M1 sin, M2 sin, i dext.

Measurements:

	PE	LL	BL	AW	PW
M1 dext	1.20	_	1.62	1.77	
M1 sin	1.28	1.60	1.55	1.72	1.91
M2 sin	1.25		1.36	1.72	-
i length	= 3.82	mm			

	N	RANGE	MEAN	SE	SD
I1 LT	13	0.95 - 1.18	1.061	0.016	
11 length	9	1.71 - 2.03	1.862	0.030	
I1 height	13	0.94 - 1.34	1.113	0.029	0.104
P4 PE	6	0.96 - 1.18	1.030	0.030	
P4 LL	6	1.09 - 1.36	1.177	0.036	0.087
P4 BL	10	1.41 - 1.64	1.558	0.023	0.074
P4 width	6	1.38 - 1.67	1.542	0.039	0.095
M1 PE	15	0.99 - 1.30	1.101	0.018	0.070
M1 LL	15	1.26 - 1.49	1.377	0.017	0.064
M1 BL	17	1.22 - 1.45	1.387	0.014	0.058
M1 AW	18	1.37 - 1.58	1.478	0.013	0.055
M1 PW	14	1.50 - 1.72	1.613	0.018	0.067
M2 PE	15	0.97 - 1.18	1.033	0.015	0.057
M2 LL	14	1.20 - 1.45	1.281	0.018	0.069
M2 BL	13	1.19 - 1.38	1.272	0.013	0.046
M2 AW	15	1.42 - 1.62	1.519	0.017	0.066
M2 PW	11	1.37 - 1.56	1.461	0.019	0.062
M3 length	3	0.70 - 0.75	0.720	0.012	0.022
M3 width	4	1.10 - 1.29	1.177	0.035	0.071
i1 length	5	3.66 - 4.04	3.780	0.060	0.134
m1 TRW	19	0.66 - 0.89	0.809	0.013	0.056
m1 TAW	20	0.82 - 0.97	0.898	0.009	0.040
m1 length	17	1.50 - 1.68	1.574	0.011	0.047
m2 TRW	19	0.73 - 0.88	0.803	0.010	0.045
m2 TAW	19	0.76 - 0.91	0.837	0.011	0.047
m2 length	19	1.25 - 1.46	1.377	0.013	0.055
m3 length	6	1.06 - 1.22	1.112	0.021	0.052
m3 width	6	0.60 - 0.71	0.635	0.017	0.042
m1-m3 length	1 2	3.82 - 3.83	3.825	0.004	0.005
ramus length	4	4.96 - 5.75	5.370	0.172	0.345
ramus height	4	4.51 - 4.67	4.600	0.029	0.058
ramus LUF	6	0.70 - 0.97	0.843	0.023	0.107
ramus LLF	7	1.05 - 1.27	1.161	0.030	0.080
Julius LLI		1.00-1.27	1.101	0.000	0.000

Table 1: Measurements of Sorex araneus from Wageningen-Fransche Kamp Fauna II.

ramus HC 7 1.33 - 1.92 1.653 0.075 0.199

Description and remarks

The upper molars are relatively wider than those of Sorex araneus from the same locality. The lower incisor is acuspulate. In these characters the fossils from Fransche Kamp correspond to recent material of Crocidura russula with which the fossils have been compared. However, the upper molars are larger than those of C. russula. They are also larger than those of C. kornfeldi known from the Early Biharian faunas Villány 3 and Osztramos 3/2 (Hungary) (Reumer, 1986). Our material has about the same dimensions as the upper molars of C. leucodon from the Late Pleistocene and Holocene fauna from Pisede (Germany) (Heinrich, 1983). However, the posterior width (PW) of the M1 and the anterior width (AW) of the M2 from our locality are much smaller than, and fall outside the range of variation observed at a large number of specimens from Pisede (Heinrich, 1983).

The material cannot be referred to the Middle Pleistocene C. zorzii, C.obtusa or C. robusta because they have larger dimensions than C. leucodon (Jammot, 1974a). According to Jánossy (1969) C. zorzii and C. robusta must be regarded as synonym of C. obtusa.

Jammot (1974a, 1975) described from the locality La Fage (France) the occurrence of C. zorzii and Crocidura sp., the latter species being smaller than the former one. The length of m1-m3 of Crocidura sp. from La Fage corresponds well with that of material of C. leucodon populations living in Central Europe (Heinrich, 1983). The dimensions of our material also resemble those of the same C. leucodon populations. This correspondence suggests a relation between the fossils from la Fage, assigned to Crocidura sp. and our material

The remains from Wageningen-Fransche Kamp are referred to Crocidura sp. and not to the living C. leucodon on the basis of the differences in the measurements found for M1 and M2. Furthermore, it is generally accepted that C. leucodon invaded Europe from the Near East for the first time after the Weichselian (Heinrich (1983), Catzeflis (1984) in Reumer (1986).

3.2. RODENTIA

GLIRIDAE Thomas, 1897

Eliomys quercinus Linnaeus, 1776 (Garden dormouse)

Material: P4 sin, 2 M2 sin, M3 sin, p4 dext, m1 sin, m2 dext, m2 sin, 2 m3 dext, m3 sin. (fig. 4.3)

Measurements:

	N	RANGE	MEAN	SE	SD
P4 length	1	¥ .	0.990	-	-
P4 width	1	-	1.440		
M2 length	2	1.32-1.33	1.325	0.004	0.005
M2 width	2	1.67-1.70	1.685	0.011	0.015
M3 length	1		1.260	1 1 11-61	- 13
M3 width	1		1 470		

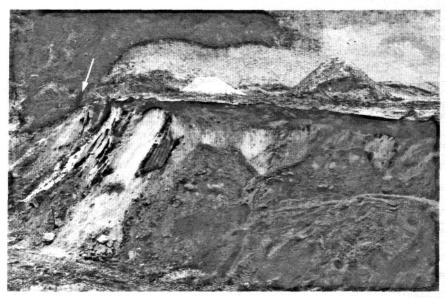


Fig. 2. Wageningen-Fransche Kamp: View of the northwestern section of the pit. The arrow indicates the location where the samples were taken.

p4 length	1	-	1.190	-	-
p4 width	1	-	1.240	-	-
m1 length	1	-	1.380		-
m1 width	1	*	1.660	-	-
m2 length	2	1.35 - 1.38	1.365	0.011	0.015
m2 width	2	1.59 - 1.64	1.615	0.018	0.025
m3 length	3	1.23 - 1.32	1.283	0.022	0.039
m3 width	3	1.34 - 1.39	1.363	0.012	0.021

Description and remarks

The size of the elements and the morphology of the few little worn (pre)molars correspond well to the living *E. quercinus*. The dimensions also resemble those of the fossils from Sudmer-Berg-2 and Hohensülzen (Germany) referred to *Eliomys quercinus* and *Eliomys* cf. *quercinus* respectively (Von Koenigswald, 1972; Storch *et al.*, 1973). The material has smaller dimensions than the late Middle Pleistocene fossils from Balaruc VII (France) which are assigned to the subspecies *Eliomys quercinus helleri* (Brugal, 1981).

ARVICOLIDAE Gray, 1821

Clethrionomys glareolus (Schreber, 1780) (Bank vole)

Material:14 M1 dext, 8 M1 sin, 12 M2 dext, 17 M2 sin, 9 M3 dext, 14 M3 sin, 12 m1 dext, 16 m1 sin, 16 m2 dext, 17 m2 sin, 13 m3 dext, 16 m3 sin. (fig. 4.4)

M	ea	SU	ren	ner	its

	Ν	RANGE	MEAN	SE	SD
M1 length	18	1.72 - 2.22	1.919	0.026	0.110
M1 width	19	0.84 - 1.11	0.998	0.017	0.073
M2 length	25	1.24 - 1.42	1.332	0.009	0.045
M2 width	24	0.70 - 0.95	0.860	0.012	0.061
M3 length	20	1.38 - 1.68	1.538	0.014	0.062
M3 width	21	0.69 - 0.80	0.746	0.006	0.027
m1 length	20	1.85 - 2.37	2.097	0.028	0.127
m1 width	13	0.68 - 0.80	0.743	0.012	0.045
m1 ACC	20	0.67 - 1.00	0.841	0.018	0.081
m1 B	13	0.12 - 0.24	0.167	0.011	0.039
m1 C	13	0.02 - 0.19	0.082	0.012	0.042
m2 length	24	1.24 - 1.49	1.360	0.011	0.056
m2 width	26	0.70 - 0.93	0.846	0.010	0.049
m3 length	25	1.08 - 1.44	1.257	0.018	0.092
m3 width	28	0.51 - 0.78	0.688	0.011	0.060

Description and remarks

The little worn specimens are rootless and have thin enamel, the worn ones have thicker enamel and two roots each. One very worn M1 has three roots, which is diagnostic for the subspecies *Cl. glareolus combieri* found in Orgnac-3 and described by Jeannet, 1981. The salient angles of the molars are rounded at their tips; the re-entrant folds of the molars are partly filled with crown-cementum.

The morphology of the M3 is variable. Most of them have two deep buccal re-entrant angles. The third one is shallow or absent. There are at least two rather deep lingual re-entrant angles. About half of the M3 have three such angles. The morphology of the M3 corresponds very well with that of CI. glareolus and is

	N	RANGE	MEAN
Sorex araneus			
Wageningen-Fransche Kamp	4	4.51 - 4.67	4.600
Sorex araneus			
Maastricht - Belvédère Fauna 4	4	4.67 - 4.80	4.755
Sorex runtonensis			
Miesenheim I	3	4.01 - 4.25	4.110
Sorex (D.) savini			
Miesenheim I	3	5.67 - 5.80	5.723
Sorex runtonensis			
England - Cromer Forest Bed	21	3.7 - 4.3	4.004
Sorex (D.) savini			
England - Cromer Forest Bed	24	5.3 - 5.9	
Sorex sp. A			
Petersbuch	72	3.7 - 4.4	3.958
Sorex araneus			
The Netherlands - recent	7	4.32 - 4.78	4.476
Sorex araneus			
G.D.R rec. (Heinrich, 1983a)	87	4 20 - 4 90	4 532

Table 2: Height of the coronoid process of mandibulas from different localities, assigned to various species of the genus *Sorex*. The information about the fossils from the English localities is adopted from Jánossy, 1969; the measurements of the material from Petersbuch from Von Koenigswald, 1970.

more simple than the morphology of the M3 of *Cl. rutilus* presented by Ognev (1950).

The m1 have four triangles which in most cases are narrowly confluent. In the older specimens T1 and T2, as well as T3 and T4, are more confluent. The morphology of the anteroconid complex shows some variation. All specimens have a rather shallow to deep fourth lingual re-entrant angle. Some have a deep third buccal re-entrant angle and a short anterior cap, whereas others have a shallow third buccal re-entrant angle and a relatively long anterior cap.

In size and morphology our material (notably M3) agrees well with the fossil material from Maastricht-Belvédère 3 and 4 (Van Kolfschoten, 1985).

The length of the m1 from Wageningen-Fransche Kamp resembles that of the m1 of Cl. glareolus from Petersbuch which varies between 1.8 and 2.3 mm. (N= 1442; mean 2.0 mm.)(Von Koenigswald, 1970). These dimensions are distinctly smaller than those of fossil (Holocene and Late Pleistocene) and recent molars of Cl. glareolus from Poland: the mean lengths of the m1 varie between 2.29 and 2.52 mm. (Nadachowski, 1982). The Holocene material from Pisede and the molars from a recent population living in the area of Mecklenburg also have larger dimensions than our material (m1: mean length 2.35 and 2.38 mm. respectively) (Heinrich and Maul, 1983).

In summary it can be said that the Middle Pleistocene *Clethrionomys glareolus* is smaller than those of Late Pleistocene or Holocene age.

Arvicola Lacépéde, 1799

The genus Arvicola is represented in the extant European fauna by two species, A. terrestris and A. sapidus. A. sapidus ranges from Portugal through Spain and southern France eastwards to the Italian border. Arvicola terrestris has an extremely wide, Palaearctic, distribution. The species is present over 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; Röttger, 1986).

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 differences in the occlusal patterns of the m1 of the oldest representatives of Arvicola led Hinton (1926) to distinguish a number of morphotypes upon which he based a number of species. However, the different morphotypes occur together in assemblages from localities such as Petersbuch (Von Koenigswald, 1970) and Miesenheim I (Van Kolfschoten, Therefore, all primitive representatives of Arvicola such as A. bactonensis, A. greenii, A. praeceptor and A. mosbachensis were included in A. cantiana, because the name Arvicola cantiana (Hinton, 1926) has priority (Sutcliffe and Kowalski, 1976).

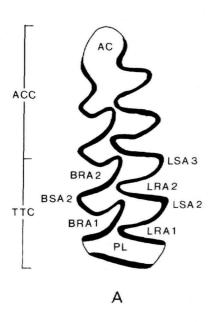
A. cantiana is characterized mainly by its so-called Mimomys enamel differentiation (the enamel of the trailing edges is markedly thicker than that of the leading edges) and by its relative small size.

Carls (1986) defined a new species, Arvicola hunasensis from late Middle Pleistocene deposits at Hunas (Southern Germany). The molars of this species are characterized by equally thick enamel on both sides of the dentine fields, a morphology intermediate between the fossil A. cantiana and the living N.W. European A. terrestris. 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).

Almost all the fossil species have been defined on dental characteristics, such as: thickness of the enamel of one or more molars, morphology of m1 and M3, and size of the molars (m1 in particular).

To quantify the differences in the thickness of the enamel Heinrich (1978; 1982) proposed to measure the thickness at both sides of the salient angles of the m1 and to divide the value of the trailing edge (the posterior edge at the lower molars) by the one of the leading edge and multiply the quotient by 100. The result is the socalled SDQ value.

Röttger (1986, 1987) studied extant Arvicola popu-



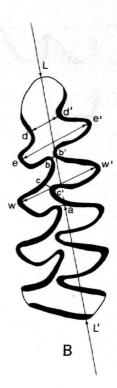


Fig. 3. Occlusal surface of *Microtus* m1 sin. illustrating the terminology (A) used in this paper (AC=anterior cap; ACC=anteroconid complex; BRA=buccal re-entrant angle; LRA=lingual re-entrant angle; LSA=lingual salient angle; PL=posterior lobe; TTC=trigonid - talonid complex) and the measured parameters (B) (L-L'=L; W-W'=W; a-L=a; b-b'=b; c-c'=c; d-d'=d; e-e'=e).

lations from Europe, Turkey and Iran to investigate the interspecific variation in the molars. Her results show that there is a large variation in the differentiation of the enamel thickness in the extant Arvicola subspecies. The Western European populations of A. terrestris sherman show the so-called Microtus enamel differentiation (mean SDQ values of the m1 ranges between 65.7 and 78.1) whereas the populations from Iran (A. terrestris persicus) show the Mimomys enamel differentiation (mean SDQ m1: 134.4). The values for Hungary and Italy are intermediate.

Röttger's results indicate 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 characteristics too, such as the variation in the frequency of morphotypes. However, it appears that the differences in the frequency of the morphotypes present in Middle and Late Pleistocene populations are only minor.

Therefore, the large variation in the SDQ values of the modern *Arvicola* populations and the minor differences in other dental characteristics (morphology of m1 and M3, dimensions) lead to the conclusion

that all the fossil N.W. and Central European assemblages of the genus *Arvicola*, should be considered as belonging to a subspecies of *A. terrestris* (Van Kolfschoten, 1990a).

The Middle Pleistocene representatives of the genus Arvicola are therefore assigned to Arvicola terrestris cantiana. This subspecies is mainly characterized by a Mimomys enamel differentiation of the molars, by the occurrence of a relatively high percentage of "primitive" m1 morphotypes, and by a relatively small size.

This 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) 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* as defined by Carls (1986) in her unpublished thesis). The fossil assemblages showing a *Microtus* enamel differentiation (SDQ < 95) are assigned to *Arvicola terrestris* ssp. B.

The nature of the relationship of the fossil

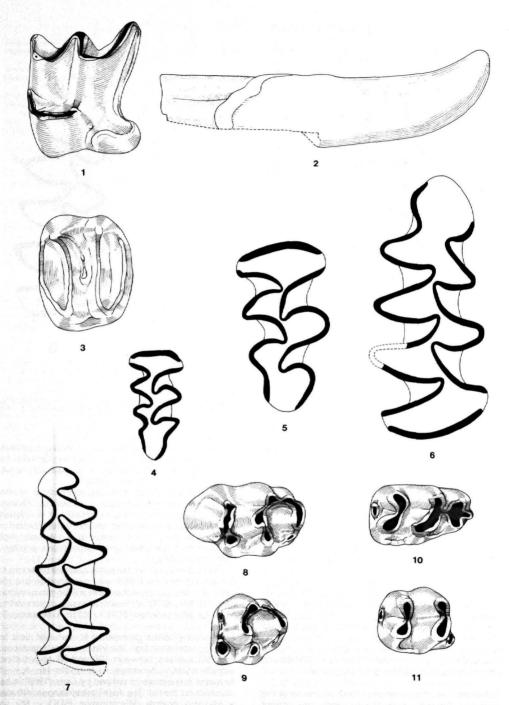


Fig. 4. Wageningen-Fransche Kamp: 1 and 2: Crocidura sp.: 1: M1 sin. (Fk 341); 2: i dext. (Fk 331); 3: Eliomys quercinus: M2 sin. (Fk 361); 4: Clethrionomys glareolus: M3 dext. (Fk 491); 5 and 6: Arvicola terrestris ssp. A; 5: M3 dext. (Fk 731); 6: m1 dext. (Fk 741); 7: Microtus arvalis or M. agrestis: m1 sin. (Fk 681); 8 - 11: Apodemus maastrichtiensis: 8: M1 sin. (Fk 811); 9: M2 sin. (Fk 874); 10: m1 dext. (Fk 918); 11: m2 dext. (Fk 978).

assemblages to 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 on molars with values close to 95, it can be seen that we are dealing with a Microtus differentiation as the trailing edges lack the strengthening elements in the third dimension (Von Koenigswald, 1980) and therefore wear much more than the leading edges, even when the trailing edge is only a little thinner than the leading edges.

Arvicola terrestris ssp. A

Material: M1 dext, M2 sin, M3 dext, M3 sin, 2 m1 dext, 2 m1 sin, m2 dext, m3 dext.

Measureme	nts: N	RANGE	MEAN	SE	SD
M1 length	1	HANGE	3.04	SE	30
M1 width	1	-	1.79	-	-
WIT WIGHT	36	-	1.75	-	-
M2 width	1		1.51		
IVIZ WIUTI		-	1.51	-	
M3 length	1	_	2.42	-	_
M3 width	1		1.29		
IVIS WIGHT	1	-	1.29	-	-
m1 length	1	-	3.68	-	_
m1 width	1	-	1.53	-	-
m1 ACC	1	_	1.30	_	_
m1 B	1	_	0.39	_	-
m1 C	1	_	0.28	-	-
1111 0			0.20		
m2 length	1	_	2.32	~	-
m2 width	1	_	1.38	_	_
IIIZ WIGHT			1.50		
m3 length	1		2.05		_
ino longin			2.00		

1.15

Description and remarks

m3 width

All the molars are rootless, their re-entrant folds are partly filled with crown-cementum. Both M3 have two lingual re-entrant angles, one molar has three buccal re-entrant angles (the third one is very shallow), the other molar has only two. The m1 (fig. 4.6) has a posterior loop, three well closed triangles and an anteroconid complex with a lingual re-entrant angle which is a little shallower than the buccal one. The length of the m1 falls within the ranges of the Arvicola m1 from Miesenheim I (the molar is markedly larger than the mean length of the molars from Miesenheim I), Maastricht-Belvédère 4 and Plaidter Hummerich I (table 3). The anteroconid complex is relative short. The A/L ratio of 0.35 is lower than the values of the molars from Maastricht-Belvédère 4 (0.42 - 0.45) and those of the molars from Plaidter Hummerich I (0.41 -0.44) and fall within the range of the molars from Miesenheim I (0.35 - 0.45). (Van Kolfschoten, in press).

The molars show a slight difference in the thickness of the enamel at both sides of the dentine fields. The enamel of the so-called trailing edges (in the lower molars the posterior, concave edges) is slightly thicker than that of the so-called leading edges.

	N	Range	Mean	SD
Maastricht-				
Belvédère 5	1		3.80	200
Plaidter Hummerich I	5	3.56 - 3.97	3.796	0.180
Rhenen	2	3.45 - 3.65	3.550	0.141
W Fransche Kamp II	1		3.68	
Maastricht-				
Belvédère 4	5	3.60 - 3.90	3.738	0.116
Miesenheim I	18	3.21 - 3.71	3.495	0.143

Table 3: Lenght of the m of *Arvicola* from the localities discussed in this paper.

All the elements from Wageningen-Fransche Kamp have been measured and not only the m1 as some authors such as Heinrich (1982) and Röttger (1986) do, because after calculating the SDQ values of all elements of *Arvicola* of a large sample from Miesenheim I it appeared that there are no significant differences between the obtained ratios and that measuring all elements is useful to increase the statistical sample (Van Kolfschoten, 1990a). The molars from Wageningen-Fransche Kamp have a mean SDQ-value of 114.38 (range: 111 - 120; N=8) and are therefore referred to the subspecies *A. terrestris* ssp. A.

The SDQ-value is lower than that of the molars from Neede, assigned to *Arvicola terrestris cantiana* and higher than the value of the molars from Rhenen, assigned to *Arvicola terrestris* ssp. B (fig. 5):(van Kolfschoten, 1990a).

Microtus Schrank, 1798

The living *M. arvalis* and *M. agrestis* can be distinguished on the basis of the morphology of the M2: the latter species has an extra postero-lingual salient angle in the M2. This extra part may also be present in the M1 of *M. agrestis*. The m1 of *M. arvalis* is generally more symmetrical and has a somewhat simpler anterior loop than the m1 of *M. agrestis*. However, there is a considerable overlap in the range of morphological variation. The other elements are indistinguishable. Therefore in this paper the M2 and the M1, having the proper diagnostic features of *M. agrestis*, will be determined as such, but the other elements will be described as *M. arvalis* and/or *M. agrestis*.

Microtus agrestis Linnaeus, 1791 (Short-tailed vole)

Material: M2 dext.

Measurements: length: 1.76 mm, width: 1.05 mm.

Description and remarks

The M2 has three salient angles lingually. The posterior one is small and is diagnostic for *M. agrestis*, which is the only *Microtus* species with an extra postero-lingual salient angle.

The specimen from Wageningen-Fransche Kamp is a little longer than the specimens from Maastricht-Belvédère 4 (Van Kolfschoten, 1985); the dimensions

of the latter are: length: 1.20 - 1.74 mm (mean: 1.55 mm; N=11); width: 0.71 - 1.09 mm (mean: 0.96 mm; N=14)

Microtus arvalis and/or M. agrestis (Short-tailed vole and/or common vole)

Material: M1/M2 sin, 3 M3 sin, 4 m1 dext, m1 sin, 5 m2 sin, 4 m3 dext, m3 sin. (fig. 4.7)

Measurements:

	N	RANGE	MEAN	SE	SD
m1 length	1	-	3.03	-	~
m1 width	3	0.93 - 1.04	0.983	0.026	0.045
m1 ACC	2	1.45 - 1.66	1.555	0.074	0.105
m1 B	3	0.01 - 0.03	0.020	0.005	0.008
m1 C	2	0.02 - 0.03	0.025	0.004	0.005
m1 D	4	0.11 - 0.32	0.240	0.041	0.082
m1 E	4	0.75 - 0.79	0.770	0.008	0.016
m2 length	3	1.26 - 1.54	1.443	0.075	0.130
m2 width	3	0.77 - 0.99	0.900	0.054	0.094
m3 length	2	1.57 - 1.74	1.655	0.060	0.085
m3 width	2	0.84 - 0.90	0.870	0.021	0.030

Description and remarks

The two almost complete m1 have five closed triangles and a well developed T6 and T7. This type of morphology is characteristic for the living species *M. agrestis* and *M. arvalis*. Two out of the five anterior loops of m1 have deep fourth buccal and fifth lingual re-entrant angles, in the others these angles are very shallow.

The fossils are rather large in comparison to the material from Maastricht-Belvédère 3 and 4 (Van Kolfschoten, 1985) but they fall within the variation of the Maastricht-Belvédère collection.

MURIDAE

On the basis of size and morphology the murid material can be divided into two different groups both belonging to the genus *Apodemus*. The larger specimens have been assigned to *A. sylvaticus*, the smaller to *A. maastrichtiensis*. The M3 and m3 of *Apodemus* show some variation in size (see fig. 6) but there are no diagnostic characters to classify these elements.

Apodemus sylvaticus Linnaeus, 1758 (Wood mouse)

Material: 28 M1 dext, 29 M1 sin, 22 M2 dext, 13 M2 sin, 8 M3 dext*, 6 M3 sin*, 25 m1 dext, 28 m1 sin, 23 m2 dext, 28 m2 sin, 10 m3 dext*, 13 m3 sin*.

Measurements:

100 050 000	N	RANGE	MEAN	SE	SD
M1 length	54	1.81 - 2.30	1.945	0.012	0.085
M1 width	53	1.10 - 1.40	1.203	0.007	0.053
M2 length	34	1.12 - 1.33	1.207	0.010	0.060
M2 width	34	1.05 - 1.27	1.128	0.008	0.049

M3* length	12	0.71 - 0.90	0.780	0.016	0.056
M3* width	12	0.70 - 0.93	0.829	0.016	0.057
m1 length	50	1.63 - 2.02	1.776	0.011	0.078
m1 width	50	0.88 - 1.30	1.063	0.008	0.060
m2 length	46	1.10 - 1.31	1.216	0.006	0.043
m2 width	48	0.96 - 1.16	1.046	0.007	0.047
m3* length	23	0.84 - 1.05	0.953	0.010	0.050
m3* width		0.74 - 0.97	0.865	0.009	0.042

*These molars belong either to A. sylvaticus or to A. maastrichtiensis.

Description and remarks

The size and the morphology of the material correspond to those of the living *A. sylvaticus*; the material is very similar to material from Maastricht-Belvédère fauna 3 and 4 which is also assigned to *A. sylvaticus* (Van Kolfschoten, 1985).

Apodemus maastrichtiensis Van Kolfschoten, 1985 (figs. 4.8 - 4.11 and fig. 6)

Material: 2 M1 dext, 3 M1 dext, 2 M2 sin, m1 dext, 4 m2 dext.

Measurements:

TVIOUDUI OITIC					
M1 length M1 width	N 5 5	RANGE 1.63 - 1.74 1.03 - 1.11	MEAN 1.698 1.078	SE 0.017 0.013	SD 0.039 0.030
M2 length M2 width	2	1.08 - 1.10 1.00 - 1.09	1.090 1.045	0.007 0.032	0.010 0.045
m1 length m1 width	1	1.42 - 1.42 0.85 - 0.85	1.420 0.850	0.000 0.000	0.000
m2 length m2 width	4	0.94 - 1.02 0.85 - 0.96	0.973 0.918	0.015 0.021	0.029 0.041

Description and remarks

The tubercles t7 and especially t9 of M1 and M2 and t3 of M2 are small. The m1 and m2 are characterized by the steepness of the cusps. The angle formed by the posterior sides of the parts of the chevrons is large. The anterior cusps of the m1 have only a low connection with the posteriorly located cusps. The m2 has a small antero-labial cusp and a small terminal heel

In all morphological characters the material described here is similar to *A. maastrichtiensis* from Maastricht-Belvédère 3 and 4.

A. maastrichtiensis seems to be related to "Parapodemus" coronensis, a species described by Schaub (1938) on the basis of a maxillary fragment with M1 and M2 from the late Early Biharian locality of Brassó (Rumania). The lengths of the molars of the type- (and only) specimen of "P." coronensis (M1=1.6, M2=1.0) fall within the range of variation found at the type locality of A. maastrichtiensis (Maastricht-Belvédère 4). As in the latter, t7 is reduced in "P." coronensis.

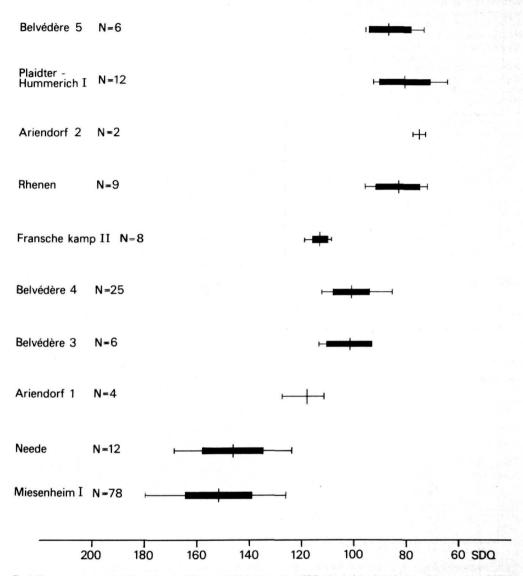


Fig. 5. The range, standard deviation and mean of the enamel thickness quotient (SDQ values) of the Arvicola molars from a number of Middle and Late Pleistocene assemblages.

On the other hand there are features of "P." coronensis which are not present in A. maastrichtiensis: 19 is developed well enough so as to produce a bulge in the outline of M1; 13 of M2 of "P" coronensis is present as a distinct and rounded tubercle. On the basis of these differences A.

maastrichtiensis is maintained as a separate species.

In the single find of "P." coronensis (a M1) from the late Early Biharian locality Sudmer-Berg-2, the t9 seems to be more reduced than in the holotype of the species (Von Koenigswald, 1972, fig. 11). The molar from Sudmer - Berg-2 resembles A. maastrichtiensis.

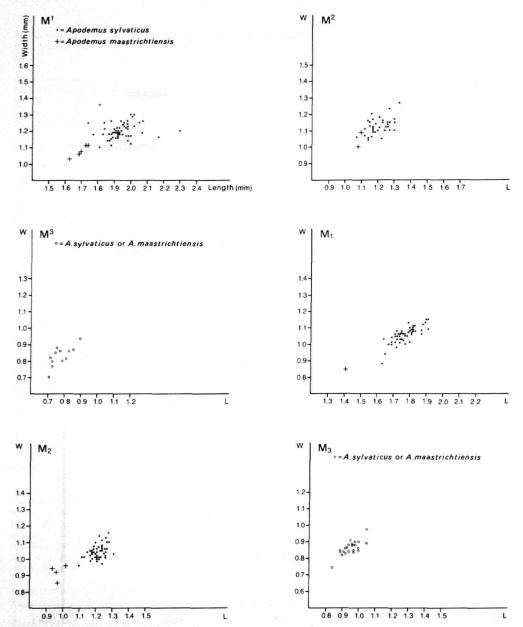


Fig. 6. Wageningen-Fransche Kamp: Length-width scatter diagrams of molars of Apodemus sylvaticus and Apodemus maastrichtiensis.

Judging from the description and figure of the m1 of Apodemus sp. from Sudmer - Berg-2, this molar should be associated with the above-mentioned upper molar. The m1 is small (1.50 mm), has reduced accessory tubercles and a wide angle between the posterior parts of the chevrons, as in A. maastrichtiensis. Several remains of "P." coronensis have been reported (by Heller, 1983) from Hunas

(Germany), a fauna which seems to be approximately contemporaneous with Wageningen-Fransche Kamp II and Maastricht - Belvédère 3 and 4. Investigation of part of the murid remains, collected during the more recent excavations, showed that at least the studied material should be assigned to Apodemus maastrichtiensis.

3.3. PROBOSCIDEA ELEPHANTIDAE

Mammuthus primigenius (Blumenbach, 1799) (Woolly mammoth)

Material: fragment of an upper M2 or M3 dext. (fig. 7)

Measurements: number of plates 6.5; length 93 mm; width ca.75 mm; height 145 mm; lamellar frequency 7.5; enamel thickness 1.8 mm.

Description and remarks

The incomplete molar, found among the gravels at the base of unit 3 (see above), is rather well preserved. It is eroded mainly on the lingual and buccal sides. The enamel is not strongly folded, as it is in the molars of *Elephas (Palaeoloxodon) antiquus*,

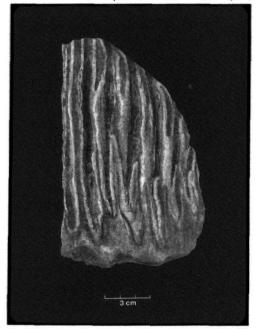


Fig. 7. Wageningen-Fransche Kamp: Mammuthus primigenius: M2 or M3: buccal view.

and the enamel pattern corresponds to that of *Mammuthus primigenius*. The lamellar frequency of the specimen from Fransche Kamp is low, even a little lower than the lamellar frequencies of the upper molars from Rhenen which have values ranging from 8.0 to 9.0 (Van Kolfschoten, 1981). The lamellar frequency and the enamel thickness correspond fairly well with those of an m2 from Maastricht-Belvédère fauna 2 with a lamellar frequency of 7.5 and and enamel thickness of 2.0 mm. (Van Kolfschoten, 1985). Generally there is an increase in the lamellar frequency and a decrease of the enamel thickness during the evolution of *Mammuthus trogontherii* (=*M. armeniacus*) to *Mammuthus primigenius* (Maglio,

1973). The M3 of *Mammuthus primigenius* have a lamellar frequency which varies from 6.5 - 11.1 (mean: 9.0) and an enamel thickness of 1.3 - 2.0 (mean: 1.6) (N=17, from several localities with late Middle Pleistocene and Late Pleistocene faunas); the lamellar frequency and enamel thickness of the M3 of *M. trogontherii* from various Cromerian to Saalian faunas are 5.0 - 8.2 (N= 26; mean 6.5) and 1.5 - 3.0 (N= 36; mean 2.2) respectively (Maglio, 1973).

The molars of *M. trogontherii* from Mosbach, most probably of Elsterian age, have a lamellar frequency of 5.0 - 8.3 and an enamel thickness between 2.3 and 2.8 (Guenther, 1968). Especially the enamel of the Fransche Kamp specimen is thinner than that of the molars from Mosbach. In this character the mammuth from Fransche Kamp can be regarded as more advanced than *M. trogontherii* from Mosbach. Because of this, the author prefers to refer the molar to *M. primigenius*.

The low lamellar frequency of the specimen from Fransche Kamp suggests that we are dealing with a rather primitive representative of *M. primigenius*. However, we must realise that there is a very large variation in the molars of *Mammuthus*.

4. COMPOSITION OF THE FAUNAS

WAGENINGEN-FRANSCHE KAMP I

A single fossil molarfragment has been collected from the base of unit 3.

Mammalia

Proboscidea Mammuthus primigenius

WAGENINGEN-FRANSCHE KAMP II

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

Number of

Pisces	Cyprinidae			
Esocidae	Esox lucius			

Aves Passeriformes indet.

Mammalia

	specimens		individuals	
Insectivora				
Sorex araneus	154	25.75%	15	19.74%
Crocidura sp.	4	0.67%	1	1.32%
Rodentia				
Eliomys quercinus	11	1.84%	2	2.63%
Clethrionomys glareolus	164	27.42%	17	22.37%
Arvicola terrestris ssp. A	10	1.67%	2	2.63%
Microtus agrestis	1	0.17%	1	1.32%
Microtus arvalis and/or				
Microtus agrestis	19	3.18%	5	6.58%
Apodemus sylvaticus	223	37.29%	29	38.16%
Apodemus				
maastrichtiensis	12	2.01%	4	5.26%
	598	100.00%	76	100.01%

min. no. of

REMARKS

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

5. PALAEO-ENVIRONMENTAL AND PALAEO-CLIMATOLOGICAL INTERPRETATIONS OF THE FAUNA-ASSOCIATIONS

WAGENINGEN-FRANSCHE KAMP I

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

The presence of *Mammuthus primigenius* in the gravels might suggest that the climate was relative cold during the deposition of the gravels at the base of unit 3. However, unit 3 has an interglacial origin (Ruegg, this volume) which implies that the molar probably has been incorporated in the gravels; a hypothesis which is supported by the eroded surface of the molar fragment.

WAGENINGEN-FRANSCHE KAMP II

Clethrionomys glareolus and Apodemus sylvaticus which are very common in the small mammalian fauna from Fransche Kamp unit 3 point to the presence of woods. The other abundant species Sorex araneus has a wide range of habitats. Eliomys quercinus prefers to live in deciduous and mixed forests. The living water voles in Western Europe, Arvicola terrestris terrestris and A. t. sherman, are more or less aquatic.

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

The composition of the fauna, notably the relative frequency of Cletrionomys glareolus and Apodemus sylvaticus as compared to Microtus, indicates a predominance of woods alternating with some open areas. In The Netherlands the garden dormouse (Eliomys quercinus) only occurs in the extreme southwestern part of the province of Limburg, about 100 kilometres south of Wageningen (Foppen, et al., 1989). The presence of the garden dormouse Eliomys quercinus and Crocidura sp. in the fauna Wageningen-Fransche Kamp II leads us to the conclusion that the climatic conditions during the deposition of the clay were like those of today, probably even a little warmer.

The pollen and the molluscan fauna from the same clay layer support this interpretation. The pollen association points to interglacial conditions and a wooded environment and, because of the low

percentage of *Alnus*, to rather a dry environment (De Jong, this volume).

The mollusc assemblage from the clay layer is characterized by the dominant occurrence of woodland species. Fresh-water species are represented too. The association of molluscs is characteristic for a mainly forested environment and interglacial conditions (Meijer, this volume).

6. THE STRATIGRAPHICAL POSITION OF THE FAUNAS

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

WAGENINGEN-FRANSCHE KAMP I

The single specimen which represents Fauna I is referred to the woolly mammoth *Mammuthus primigenius*. This species occurred in N.W. Europe from the Early Saalian and became extinct at the very end of the Weichselian. The specimen shows characters (see description) which suggest that we are dealing with a rather primitive representative of *M. primigenius*. These characters are comparable with those of a molar from Maastricht-Belvédère fauna 2, assigned to *M. primigenius*, with a Early Saalian age (van Kolfschoten, 1985). The molar from Wageningen-Fransche Kamp seems to be more advanced than molars of *M. trogontherii* from Mosbach which have, most probably, a Elsterian age.

WAGENINGEN-FRANSCHE KAMP II

The smaller mammal fauna is a modern fauna composed of species which, except for Apodemus maastrichtiensis also inhabit The Netherlands at the present day. Some species (Crocidura sp., Eliomys quercinus, Clethrionomys glareolus, Microtus arvalis and Apodemus sylvaticus) have a rather long stratigraphical range and occurred in N.W. Europe in the Early Pleistocene. Arvicola terrestris appears during the Upper part of the Cromerian. The boreholes Noordbergum 13 and 14 yielded from Cromerian Interglacial IV deposits molars of A. terrestris cantiana (Van Kolfschoten, 1990b). Microtus agrestis also appears during the Cromerian. Its presence has been observed in the fauna Miesenheim I with a Cromerian Interglacial IV age (fig. Sorex araneus probably occurs since the Holsteinian, It has been recorded from the faunas Neede (Van Kolfschoten, 1990a) Bilzingsleben (Heinrich, 1989) both correlated with the Holsteinian. Older faunas, for instance the one from Miesenheim I, yielded the smaller Sorex runtonensis and the larger Sorex (Drepanosorex) savini. The stratigraphical range of A. maastrichtiensis is not well known at the moment. The species has been

recorded from the Early Saalian faunas Maastricht-Belvédère 3 and 4 (Van Kolfschoten, 1985) and Hunas (Germany). Related forms occur in the fauna of Miesenheim I and Grabschütz (Benecke *et al*, 1990).

Arvicola terrestris is the only species which shows an evolution which can be used biostratigraphically. There appears to be an increase in the length of the m1 of A. terrestris after its appearance. One of the earliest populations (the one from Miesenheim I) contains m1 with a length of 3.21 - 3.71 mm which corresponds with the dimensions of the latest Mimomys savini populations (Heinrich, 1987). The m1 of younger Central and N. W. European A. terrestris populations show temporally fluctuating lengths between 3.45 and 4.4 mm. (Stuart, 1982; Carls, 1986; Heinrich, 1987; Van Kolfschoten, 1990a).

More obvious is the evolution in the degree of enamel differentiation in the N.W. and Central European Arvicola populations. There is a change in the enamel differentiation which in general, results in a decrease in SDQ values. However, based on the combination of the data presented by Heinrich (1982, 1987) and the data obtained from localities in The Netherlands and the Neuwied Basin (Germany) it appears that the trend in enamel differentiation is not a simple progressive one, of decreasing SDQ values, but one with an important fluctuation (Kolfschoten, 1990a). This fluctuation might be the result of an invasion of less derived Arvicola populations from southern Europe during the Eemian after the withdrawal of the inland ice-sheet which covered northern Europe during the Saalian.

This trend forms the base for a biozonation of the late Middle and Late Pleistocene deposits of N.W. Europe (Kolfschoten, 1990a). Two biozones have

been defined:

- the Arvicola terrestris cantiana Range-zone (total-range-zone characterized by the occurrence of Arvicola terrestris cantiana)

- the *Arvicola terrestris* Partial-range-zone (partial-range-zone characterized by the occurrence of *Arvicola terrestris* ssp. A and B)

Because of the presence of Arvicola terrestris ssp. A the smaller mammal fauna from Wageningen-Fransche Kamp is correlated with the Arvicola terrestris Partial-range-zone. The Arvicola terrestris Partial-range-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 (see fig. 8). 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*. 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.

The smaller mammal fauna from Wageningen-Fransche Kamp has been collected from sediments ice-pushed during the Saalian. Therefore, it belongs to the group of pre-Eemian faunas with for instance Ariëndorf I, Weimar-Ehringsdorf, Hunas, La Fage, Lazaret, the fauna from the lower loess deposits of Achenheim, Mesvin IV and Maastricht-Belvédère 2-4 (Van Kolfschoten, 1990a).

The Holsteinian faunas from Neede and Bilzingsleben with Arvicola terrestris cantiana are older than the fauna Wageningen-Fransche Kamp II. The pre-Eemian smaller mammal faunas from Rhenen, Ariendorf 2, Plaidter-Hummerich I and and Uppony 1/1-2, containing Arvicola terrestris ssp. B, date from a younger period. These stratigraphical data force the conclusion that the smaller mammal fauna dates from an Early Saalian warm phase. A warm phase which may be the equivalent of the Hoogeveen Interstadial. However, although palynological data do not exclude a Hoogeveen Interstadial Age, the data at least suggest an earlier warm phase: Cromerian IV or possibly Holsteinian (De Jong, this volume). A Cromerian IV age is, on the basis of the smaller mammal fauna, very unlikely. The Arvicola terrestris is far too advanced and the presence of Sorex araneus instead of Sorex runtonensis or Sorex (Drepanosorex) savini exclude a Cromerian IV age.

Holsteinian faunas are unfortunately only poorly known. However, a correlation with the Holsteinian seems to be unlikely because of the occurrence of the more primitive *Arvicola terrestris cantiana* in the faunas from Neede and Bilzingsleben, both correlated with the Holsteinian.

The fauna Wageningen-Fransche Kamp II is very similar to the fauna Maastricht-Belvédère 4. The latter one is correlated to the Early Saalian also because of the occurrence of *Coelodonta antiquitatis* in deposits below the sediments which yielded the fauna Maastricht-Belvédère 4. *Coelodonta antiquitatis* migrated from Asia to Europe during the Early Saalian (Kolfschoten 1985, 1990a).

Both faunas Wageningen-Fransche Kamp II and Maastricht-Belvédère 4, indicate full interglacial conditions. They probably represent the same warm phase; the one which might be correlatable with isotopic Stage 7.

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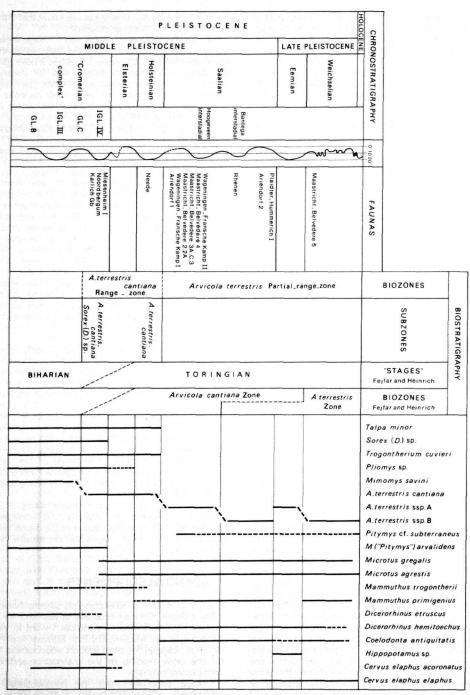


Fig. 8. Range-chart of a number of Middle and Late Pleistocene mammal species, a tentative biozonation of the late Middle and Late Pleistocene deposits of N.W. Europe and the correlation between the zonation and a number of mammal faunas and the chronostratigraphic subdivision of the Pleistocene.

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8. REFERENCES

BENECKE, N., BÖHME, G. & HEINRICH, W.-D., 1990: Wirbeltierreste aus interglazialen Beckensedimenten von Gröbern (Kr. Gräfenhainichen) und Grabschütz (Kr. Delitzsch) - Altenbg. nat. wiss. Forsch., 5, 231-281.

BURGER, A.W., 1991: Sedimentary petrology and lithostratigraphy of ice-pushed Pleistocene deposits in the Fransche Kamp sandpit near Wageningen - Meded. Rijks Geol. Dienst, 46, 27-35 (this volume).

BRUGAL, J.P., 1981: Balaruc Vii (Séte, Hérault). Un nouveau remplissage de fissure de la fin du Pleistocène moyen -Quartemaria 23, 99-141.

CARLS, N., 1986: Arvicoliden (Rodentia, Mammalia) aus dem Mittelund Jungpleistoz\u00e4n S\u00fcdeutschlands - Diss. Univ. Erlangen, 103 pp, 59 Pl.

DAAMS, R., 1981: The dental pattern of the dormice Dryomys, Myomimus, Microdyromys and Peridyromys - Utrecht Micropal. Bull. Spec. Publ. 3, 1-115.

FOPPEN, R.P.B., BERGERS, P.J.M. & van GELDER, J.J., 1989: Het voorkomen van de eikelmuis *Eliomys quercinus* in Nederland -Lutra, vol. 32, p. 42 - 53, 3 figs., 2 tbl.; Leiden.

GUENTHER, E. W., 1968: Elefantenbackenzähne aus den Mosbacher Sanden - Mz. Naturw. Arch. 7, 55-73.

HEINRICH, W.-D., 1982: Zur Evolution und Biostratigraphie von Arvicola (Rodentia, Mammalia) im Pleistozan Europas. Z. geol. Wiss. Berlin, 10, 6, 683-735.

HEINRICH, W.-D., 1983: Untersuchungen an Skelettresten von Insectivoren (Insectivora, Mammalia) aus dem fossilen Tierbautensystem von Pisede bei Malchin. Teil 1: Taxonomische und biometrische Kennzeichnung des Fundgutes - Wiss. Z. Humboldt-Univ. Berlin Math.-naturwiss. R., 32, 6, 681-698.

HEINRICH, W.-D., 1987: Neue Ergebnisse zur Evolution und Biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Quartăr Europas - Z. geol. Wiss. 15, 3, 389-406. HEINRICH, W.-D., 1989: Biostratigraphische Untersuchungen an

HEINRICH, W.-D., 1989: Biostratigraphische Untersuchungen an fossilen Kleinsäugerresten aus dem Travertin von Bilzingsleben. -EAZ Ethnogr. - Archäol. Z. 30, 379-393.

HEINRICH, W.-D., und L. Maul, 1983: Skelletreste von Nagetieren (Rodentia, Mammalia) aus dem fossilen Tierbautensystem von Pisede bei Malchin. Teil 1. Taxonomische und biometrische Kennzeichnung des Fundgutes. - Wiss. Z. Humboldt-Univ. Berlin Math.-naturwiss. R., 32, 6, 729-745.

HELLER, F. 1983: Die H\u00f6lenruine Hunas bei Hartmannshof (Landkreis N\u00fcrnberger Land) - Quart\u00e4r-Bibliothek, 4, 1-407.

HINTON, M.A.C., 1926: Monograph of the voles and lemmings (Microtinae) living and extinct - Vol. 1, British Museum (Natural History), London, 488 pp.

JAMMOT, D., 1974a: Les Insectivores (Mammalia) du gisement Pleistocène moyen des abîmes de la Fage à Noailles (Corrèze) -Nouv. Arch. Mus. Hist. nat. Lyon., 11, 41-51.

JAMMOT, D., 1974b: Les Insectivores de Cagny (Somme) Soricidae (Insectivora, Mammalia) - Bull. l'Ass. f. l'et. Quat. 40-41, 187-190.

JAMMOT, D., 1975: Les Insectivores (Mammalia) du gisement Pleistocène moyen des abîmes de la Fage à Noailles (Corrèze); complément - Nouv. Arch. Mus. Hist. nat. Lyon., 13, 5-11.

JÁNOSSY, D., 1969: Stratigraphische Auswertung der europäischen mittelpleistozänen Wirbeltierfauna II - Ber. deutsch. Ges. geol. Wiss., A, Geol. Paläont., 14, 5, 573-643. JEANNET, M., 1981: Les Rongeurs du Gisement Acheuléen D'Orgnac 3 (Ardeche). Essai de Paléoécologie et de Chronostratigraphie. -Bull. de la Coc. Linnéenne de Lyon, 50e année, 2, 49-71.

Jong, J. de, 1991: Pollen-analytical investigation on sediments of Pleistocene age at Wageningen (The Netherlands) - Meded. Rijks Geol. Dienst, 46, 65-70 (this volume).

KOENIGSWALD, W. von (1970): Mittelpleistozäne kleinsäuger aus der Spaltenfüllung Petersbuch bei Eichstätt - Mitt. Bayer. Staatssamml. Paläont. hist. Geol., 10 407 - 432, 40 Abb., München.

KOENIGSWALD, W. von, 1972: Sudmer-Berg-2, eine Fauna des frühen Mittelpleistozäns aus dem Harz - N. Jb. Geol. Paläont. Abh., 141, 194-221.

KOENIGSWALD, W. von, 1973: Veränderungen in der Kleinsäugerfauna von Mitteleuropa zwischen Cromer und Eem (Pleistozän) -Eiszeitalter u. Gegenw., 23/24; 159-167, 2 Abb., Öhringen.

KOENIGSWALD, W. von, 1980: Schmelzstruktur und Morphologie in den Molaren der Arvicoliden (Rodentia) - Abh. Senckenberg. Naturforsch. Ges., 539, 1-94.

KOLFSCHOTEN, T. van, 1981: On the Holsteinian? and Saalian mammal fauna from the ice-pushed ridge near Rhenen (The Netherlands) -Meded. Rijks Geol. Dienst N.S. 35, 223-251.

KOLFSCHOTEN, T. van, 1985: The Middle Pleistocene (Saalian) and Late Pleistocene (Weichselian) mammal faunas from Maastricht-Belvédère, Southern Limburg, the Netherlands) - Meded. Rijks Geol. Dienst, 39-1, 45-74.

KOLFSCHOTEN, T. van, 1986: Zoogdierpaleontologisch onderzoek in groeve "De Fransche Kamp" (Wageningen), - Cranium 3 (1), 30-34.

KOLFSCHOTEN, T. van 1990a: The evolution of the mammal fauna in the Netherlands and the middle Rhine Area (Western Germany) during the late Middle Pleistocene - Med. Rijks Geol. Dienst, 43-3, 1-69.

KOLFSCHOTEN, T. van, 1990b: Review of the Pleistocene Arvicolid Faunas from The Netherlands - Institute of Earth Sciences, Int. Symp. Evol. Phyl. Biostr. Arvicolids, 255-274, 10 Figs, 1 pl.; Praha.

MAGLIO, V.J., 1973: Origin and evolution of the Elephantidae -Transaction of the American Philosophical Society, N.S., 63 (3), 1-149.

MEULEN, A.J. van der, 1973: Middle Pleistocene Smaller Mammals from the Monte Peglia (Orvieto, Italy) with Special Reference to the Phylogeny of Microtus (Arvicolidae, Rodentia) - Quaternaria, XVII, Roma, 1-144.

MEUER, T., 1991: Molluscan investigation of ice-pushed Pleistocene deposits near Wageningen, The Netherlands - Meded. Rijks Geol. Dienst, 46, 55-64 (this volume).

NADACHOWSKI, A., 1982: Late Quaternary Rodents of Poland with special references to morphotype dentition analysis of voles -PWN, Warszawa-Krako'w, 108 pp.

OGNEV, S.I., 1950: Mammals of the U.S.S.R. and adjacent countries.
Vol. V. Rodents, 626 pp. Israel program for Scientific Transl.,
Jerusalem, 1964.

REICHSTEIN, H., 1982: Gattung Arvicola Lacépède 1799 - Schermäuse in: Niethammer, J. & F. Krapp (Hrsg.): Handbuch der Säugetiere Europas. Bd. 2/I, Nagetiere II - Akademische Verlagsgesellschaft, Wiesbaden, 209-252.

REUMER, J.W.F. 1984: Ruscinian and Early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary - Scripta Geolica, 73, 1-173.

REUMER, J.W.F., 1986: Notes on the Soricidae (Insectivora, Mammalia) from Crete. I. The Pleistocene species Crocidura zimmermanni - Bonn. zool. Beitr., 37 (3), 161-171.

RÖTTGER, U., 1986: Schmelzbandbreiten an Molaren der Gattung Arvicola Lacépède 1799 - Med. Dissertation, Bonn, pp. 12.

RÖTTGER, U., 1987: Schmelzbandbreiten an Molaren von Schermäusen (Arvicola Lacépède, 1799) - Bonn. zool. Beitr., 38, 2, 95-105.

RUEGG, G.H.J., 1991: Pleistocene fluviatile deposits in ice-pushed position, Wageningen, The Netherlands - Meded. Rijks Geol. Dienst, 46, 3-25 (this volume).

SCHAUB, S., 1938: Terti\u00e4re und quart\u00e4re Murinae - Abh. Schweiz. Pal. Ges., 61, 1-38.

STORCH, G., J.L. FRANZEN, J.L. & MALEC, F., 1973: Die altpleistozene Säugerfauna (Mammalia) von Hohensülzen bei Worms -Senckenbergiana lethaea, 54 (2/4), 311-343.

STUART, A.J., 1982: Pleistocene Vertebrates in the British Isles -Longman, London/New York, pp. 221.

SUTCLIFFE, A.J. & KOWALSKI, K., 1976: Pleistocene Rodents of the British Isles - Bull. Br. Mus. Nat. Hist. (Geol), 27, 2, 31-147.