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Small mammals from the Late Pliocene Oosterschelde dredgings

Reumer, J.W.F., Mayhew, D.F. & Van Veen, J.C., 2005 - Small mammals from the Late Pliocene Oosterschelde dredgings - DEINSEA 11: 103-118 [ISSN 0923-9308]. Published 29 December 2005

A description is given of the fossil small mammal remains that were found during dredging activities in the Oosterschelde estuary, the Netherlands. The following taxa are encountered in the samples: Mimomys pliocaenicus, Mimomys reidi, Mimomys tigliensis, Mimomys newtoni, Trogontherium sp., Beremendia fissidens, Sorex (Drepanosorex) praearaneaus, and Galemys kormosi. The find of one m1 of Microtus oeconomus is considered to be a contamination. The fauna is of Late Pliocene age, and may appear slightly older than the classic Tegelen fauna. In terms of mammal zonation, we consider the age to be MN17.

Keywords: Late Pliocene, Early Pleistocene, Arvicolidae, Soricidae, Desmaninae, MN16-17, the Netherlands.

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INTRODUCTION

From 1951 onwards, once every year a fishing vessel ventures out on the Oosterschelde estuary in order to dredge for fossil mammals. Strata containing such fossils of supposedly Tiglian age crop out below the water level in trenches at a depth of some 35-40 m below the water level. The fishing vessel, a mussel cutter with the registration number ZZ8 or (lately) ZZ10 - where ZZ stands for its port, the town of Zierikzee, province of Zeeland - pulls two dredge-nets behind the ship over the bottom of the Oosterschelde. A horizontal iron bar in front of the net acts as a knife and penetrates a few centimetres into the sediment. Subsequently, the net becomes filled with mussels, oysters, starfish, fish, stones, and, occasionally, mammalian fossils. Up until 1997 only larger mammals had been recorded belonging to a fauna of Tiglian age, correlated to the TC3 pollen zone according to De Vos et al. (1998): Mammuthus meridionalis, Anancus arvernensis, Equus sp., Stephanorhinus cf. etruscus, Cervus rhenanus, Eucladoceros ctenoides, Leptobos sp., Homotherium sp., cf. Hyaena perrieri, and Sus strozzii.

Since 1997 this procedure has been extended by attaching iron pipes to the dredge-net (Reumer *et al.* 1998), named 'Van Veen tubes' after their inventor, mr Joop van Veen of Teylers Museum, the third author of this paper. A 'Van Veen tube' typically consists of a c. 75 cm long pipe of 7.8 cm bore, which is attached to a grip on the metal bar in front of the dredge-net. The pipe scrapes through the sediment and collects some of it, which can

subsequently be washed, sieved, and picked for fossils. By this method we were able to collect a first series of small mammal fossils that were published a year after their discovery (Reumer et al. 1998): Galemys kormosi, Mimomys cf. pliocaenicus and M. cf. tigliensis. Since, we have collected considerable quantities of sediment, whereas the number of Van Veen tubes used for dredging increased from only one (per pull of two nets) to four tubes per pull in 2001 and 2002. Here we report on the mammalian fossils thus far collected.

MATERIAL AND METHODS

The sediment we obtained from the Van Veen tubes was washed and sieved on board the ship, later to be dried, treated with acetic acid, rewashed, and picked in the laboratory. The amount of (wet) sediment thus processed is estimated between 600 - 800 kg in total. Nomenclature of teeth and dental details are after Van der Meulen (1973) for the arvicolid occlusal surface and after Rabeder (1981) for the arvicolid linea sinuosa, and after Reumer (1984) for dental details in the Soricidae. Measurements were made on a Leitz Ortholux binocular microscope fitted with a movable stage and measuring clocks at the Department of Earth Sciences of Utrecht University; drawings (by the first author) were made on a Wild M5 binocular microscope fitted with a drawing prism.

TAXONOMY

order Rodentia family Arvicolidae Gray, 1821 genus *Mimomys* Forsyth Major, 1902

Mimomys pliocaenicus Forsyth Major, 1902

(Figures 1, 2 and 3)

Available material 2 m1 (plus one detached anteroconid complex), 1 m2, 3 M1, 3 M2 (one of which only fragmentary), 2 M3.

Measurements See Table 1.

Description

m1 The first lower molar consists of the anteroconid complex, three triangles and the posterior loop. An enamel islet is present in two of the three available anteroconid complexes, it is absent in the third. The Mimomys-ridge is well developed in one specimen but only weakly so in the other two. The triangles and the posterior loop are well separated and not confluent in both complete specimens. The linea sinuosa shows high anterosinuids, hyposinuids and a somewhat lower hyposinulid. In one specimen the hyposinulid is not yet reached by the abrading occlusal surface (Fig. 1-2c), resulting in a posterior loop with only one enamel-free zone at the buccal side. M. pliocaenicus from Tegelen (Tesakov 1998: fig. 6-1, 6-2, 6-3) also have a hyposinulid that is lower than the hyposinuid. There are small but distinct

Table I Sizes (in mm) of the Oosterschelde Arvicolidae teeth (arranged by element).

element	species	length	width
m l	M. pliocaenicus	3.49	1.67
ml	M. pliocaenicus	3.20	1.40
ml	M. reidi	2.92	1.27
ml	M. tigliensis	2.69	1.18
ml	Microtus oeconomus	3.00	1.14
m2	M. pliocaenicus	1.92	1.15
m2	M. reidi	1.54	0.93
m3	M. reidi	1.38	0.65
m3	M. reidi	1.43	-
MI	M. pliocaenicus	2.80	1.61
MI	M. pliocaenicus	2.82	1.53
MI	M. pliocaenicus	2.99	1.78
MI	M. tigliensis	2.37	c. 1.37
M2	M. pliocaenicus	2.39	1.56
M2	M. pliocaenicus	2.35	1.42
M2	M. tigliensis	>1.53	0.90
M2	M. newtoni	1.88	1.15
M3	М. pliocaenicus	2.16	1.11
M3	M. pliocaenicus	2.04	1.14
M3	M. reidi	1.81	0.99
M3	M. reidi	1.80	0.88
M3	M. reidi	1.88	1.00

mimosinuids. Cementum is well developed in all re-entrants. Size of our m1's agrees well with those from Tegelen (Table 1; Tesakov 1998).

m2 The only available m2 (Fig. 3-1) is slightly smaller than the m2's from Tegelen (Table 1), but morphologically identical. The posterior

loop has two enamel-free zones, at its buccal and lingual side, and one at the anterior tip where it touches m1. The t1-t2 and t2-t3 are completely separated, while t3-t4 are confluent; cementum is present.

M1 Three upper first molars are preserved, in size they are slightly smaller than the

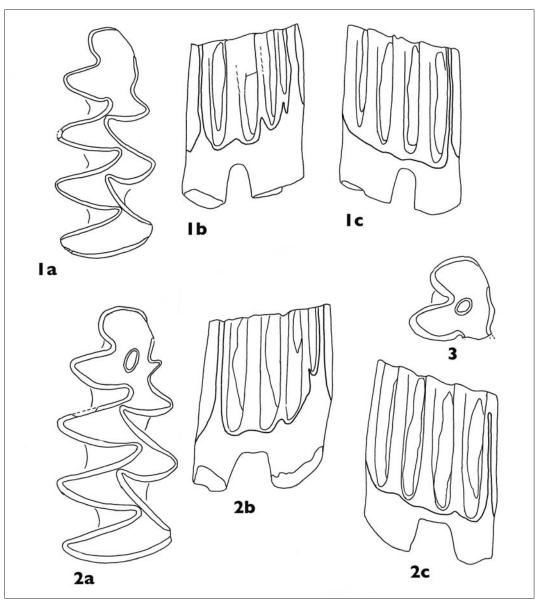


Figure 1 Mimomys pliocaenicus I m1 dex., found 2001, a occlusal, b buccal, c lingual views; 2 m1 dex., found 2002, same views as 1; 3 m1 dex., found 1998, anteroconid complex in occlusal view.

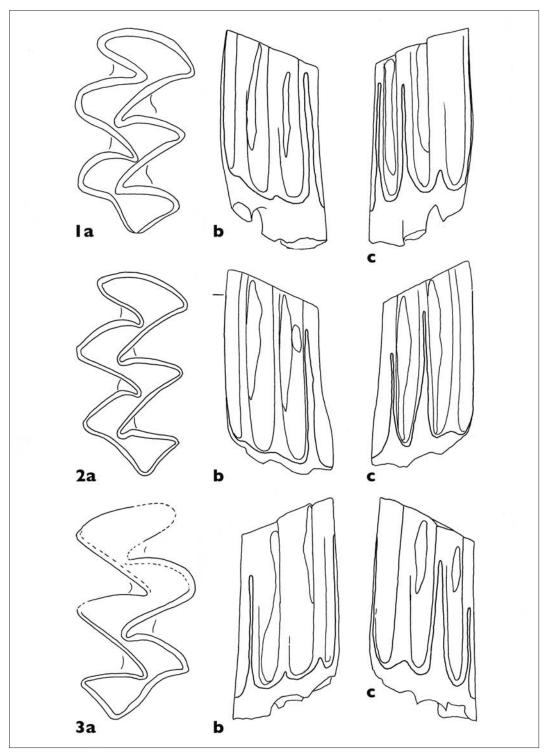


Figure 2 Mimomys pliocaenicus I M1 sin., found 1998, **a** occlusal, **b** buccal, **c** lingual views; **2** M1 sin., found 2001, same views as 1; **3** M1 dex., found 2000, same views as 1.

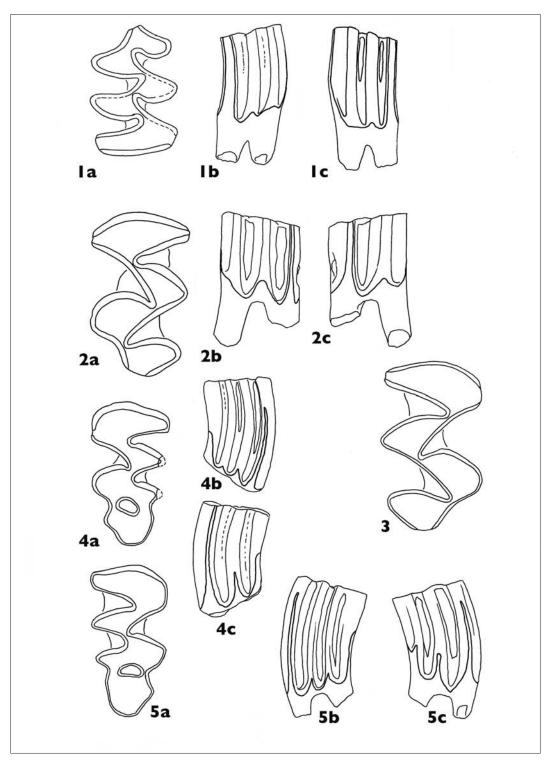


Figure 3 Mimomys pliocaenicus I m2 dex., found 1998, a occlusal, b buccal, c lingual views; 2 M2 sin., found 1997, same views as 1; 3 M2 dex., found 2001, in occlusal view; 4 M3 sin., found 2000, same views as 1; 5 M3 dex., found 2001, same views as 1.

Tegelen specimens (Table 1; Tesakov 1998) again, although some overlap in size-ranges occurs. Especially the length is smaller. Root formation is as described from Tegelen: either three separate roots, or the anterior root and the smaller centrally located protocone root are connected. All our three specimens are slightly worn young teeth; the anterosinus and anterosinulus are still untouched by wear. Protosinus is high, higher than the anterosinus in two of the three specimens, but slightly lower in the third.

M2 We also have three upper second molars, two of which are measurable. Their lengths fall within the range of the Tegelen M2's (Table 1; Tesakov 1998). The only specimen with developed roots shows a two-rooted situation. The linea sinuosa shows a moderately well developed parasinus and hyposinus.

M3 There are two upper third molars which, again, fall within the size-range for Tegelen. The tooth consists of the anterior loop, one separate triangle (T1) and the posterior complex. This seems to contradict Tesakov's (1998) description, who stated that the M3 consists of the anterior loop, followed by two triangles (T1 and T2) and the posterior complex. This description is, however, in contradiction with Tesakov's (1998) figures 11-1 and 11-2. It appears that T2 becomes separate as an individualised triangle only in older specimens (his figure 11-5 and 11-6 in particular). In our two teeth too, T2 is not yet individualised and is broadly integrated into the posterior complex. Both teeth have an enamel islet, that is ovoid to kidney-shaped (reniform) and not connected to the re-entrant (LRA2). In one specimen there are two roots (the other tooth is still rootless). Linea sinuosa as in Tegelen, with a rather high hyposinus.

Remarks Morphologically, our specimens and the material from Tegelen are extremely similar. Most of our specimens agree in size with the Tegelen material, but sometimes our specimens are in the lower reaches of, or below,

the Tegelen size-range. This could imply a taxonomic difference, but there are slight morphological features hindering attribution to another, related, taxon such as M. praepliocaenicus Rabeder, 1981 (e.g. the non-confluent t1-t2 in m2 of our sample) or M. polonicus (the linea sinuosa which is more advanced in our sample). On the other hand, M. praepliocaenicus is a species that is -apart from the triangle confluences- hardly distinguishable from M. pliocaenicus. The only character to be found in the diagnosis (Rabeder 1981) is the linea sinuosa and the related HH-index, an index that can be measured with certainty in unworn specimens only, and that is therefore less useful. Both taxa are morphologically identical and have similar sizes. Comparison of our material, its morphology, its linea sinuosa and its sizes with the material of Rabeder's (1981) type series reveals the confluence of the triangles in the lower molars as the only distinguishing feature. The development of the linea sinuosa in our material is rather similar to Rabeder's material, especially the size and shape of the mimosinuid in m1 shows more resemblance to Rabeder's material than to Tesakov's (1998) Tegelen material. Another possible reason to explain the sometimes smaller sizes of our samples in comparison with the Tegelen material is a geological age difference (i.e., an older sample) due to the general trend of size increase in these arvicolids. Our decision to identify our sample as M. pliocaenicus is thus entirely based on the lack of triangle confluences in the lower molars, otherwise M. praepliocaenicus would have been quite as possible.

M. pliocaenicus is present in Late Villanyian localities of the MN17 zone (Fejfar 2001); the Late Villanyian Mimomys (Mimomys) pliocaenicus zone sensu Fejfar & Heinrich 1990; Tesakov restricts the species to the MN17b subzone (Tesakov 1998: p.84) or the MN17-2 subzone (ibid.: figure 54); he also notes that the entire MN17 is the biozone of M. pliocaenicus sensu lato (which includes M. praepliocaenicus, M. pliocaenicus and the larger M. ostramosensis). Rabeder (1981) on

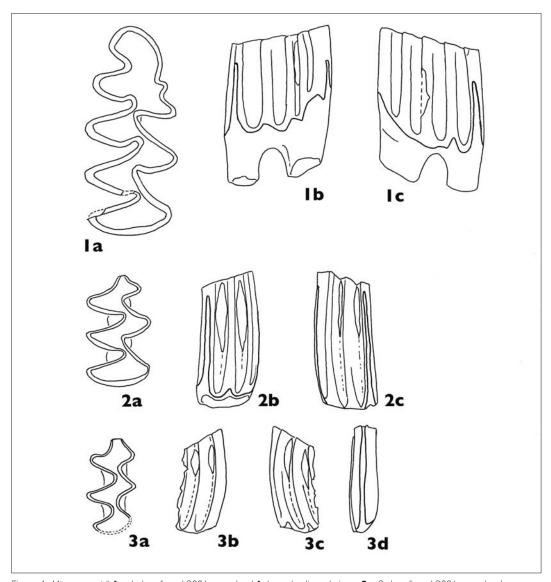


Figure 4 $Mimomys\ reidi\ I\ m1\ dex.$, found 2001, **a** occlusal, **b** buccal, **c** lingual views; **2** m2 dex., found 2001, **a** occlusal, **b** buccal, **c** lingual views; **3** m3 dex., found 2001, **a**, **b**, **c** same views as 1, **d** anterior view

the other hand places *M. praepliocaenicus* in the Early Villanyian, i.e. MN16B in MN terms. Repenning *et al.* (1990) indicate an MN16B ("Early Odessan") age for both *M. pliocaenicus* and *M. reidi* in Russia.

Mimomys reidi HINTON, 1910 (Figures 4 and 5)

Available material 1 m1, 1 m2, 2 m3, 3 M3.

Measurements See Table 1.

Description

m1 A medium-sized m1, without enamel islet and possessing a *Mimomys*-ridge (Fig. 4-1). The molar is composed of the posterior loop,

of three dentine triangles of which the first and second (t1 and t2) are confluent, and an anteroconid complex. The re-entrants, especially BRA1 and LRA1-3, are bent towards the anterior, which is an advanced character state. There is hardly any crown cementum, only in the buccal re-entrant angle between the second triangle and the anteroconid complex (BRA2) a little cementum is to be found. The linea sinuosa shows a rather primitive state. On the buccal side, the anterosinuid is relatively low and narrow, the hyposinuid is unconspicuous and hence rather undetectable; it may reach up till two thirds of the preserved tooth and does not seem to reach the wear surface; on the lingual side the hyposinulid mirrors the hyposinuid. it is better visible and reaches till two thirds of the crown: in front of it is a low entosinuid. Neither of the sinu(l)ids reaches the occlusal surface in the preserved tooth; as a result, the enamel runs uninterrupted around the occlusal surface of the entire tooth. This is unique in the Oosterschelde arvicolids and appears to be a rather primitive state for *M. reidi*. There are two roots, the posterior one is a little shorter in comparison to the anterior one.

m2 Considerably smaller than the corresponding tooth of *M. pliocaenicus*; the tooth (Fig. 4-2) consists of the posterior loop, a broadly confluent t1-t2 complex, and a broadly confluent t3-t4 complex. Cement is present in all re-entrants. The tooth is of a young individual and apart from anterosinuid none of the other sinu(l)ids have been touched by abrasion.

m3 Both available specimens are somewhat damaged. The tooth, like m2, consists of a posterior loop and two confluent triangle complexes (t1-t2 and t3-t4). Sizes as in the Tegelen sample (Table 1; and Tesakov 1998).

M3 The slightly undulate anterior margin of the anterior loop is also to be seen in the three upper third molars. The three teeth (Fig. 5), of remarkably similar size, all possess two roots. Two have an enamel islet between BRA3 and LRA2, while the other tooth lacks the islet.

Crown cementum is present in most re-entrants. The anterior loop and T1 are strongly confluent; between T1 and T2 (the posterior complex) there is no connection in two specimens, and a very narrow connection in the third one. Sizes are in the upper reach of the Tegelen size-range (Table 1; Tesakov 1998).

Remarks *Mimomys reidi* is a known companion of *M. pliocaenicus*; according to Fejfar & Heinrich (1990) their total ranges parallel eachother. This implies an MN17 age. In a later paper however, Fejfar (2001: tables 1 and 2) also includes *M. reidi* in MN16B. Also, Repenning *et al.* (1990) give an MN16B age for *M. reidi* in both Russia and Western/Central Europe. Our m1 is rather primitive in the configuration of its linea sinuosa, which could mean that it concerns a relatively older sample.

Mimomys tigliensis Tesakov, 1998 (Figure 6)

Available material 1 m1, 1 M1, 1 M2.

Measurements See Table 1.

Description

m1 There is one lower first molar, of a size (L = 2.69, W = 1.18) that closely resembles the mean sizes of the type sample from Tegelen (mean L = 2.59, mean W = 1.10). There is abundant cementum in the re-entrants of this moderately worn tooth. It consists of the posterior loop, three distinct triangles not being confluent, and a separate anteroconid complex lacking the Mimomys-ridge. This latter situation was also described for the type sample (Tesakov 1998). The broad anterosinuid, and the hyposinuid and hyposinulid are all touched by abrasion, hence the enamel rim shows three interruptions of which the anterior one reaches to the anterior tip towards the lingual side. The tooth is in a rhizodont stage, the anterior root is the slightly more robust one.

M1 The upper first molar we have available

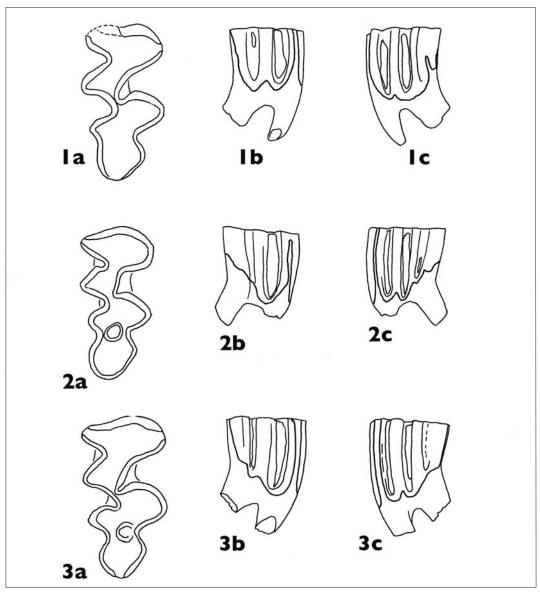


Figure 5 Mimomys reidi 1 M3 dex, found 2001, **a** occlusal, **b** buccal, **c** lingual views; **2** M3 dex., found 2001, same views as 1; **3** M3 dex., found 2002, same views as 1.

is preserved within its alveolus, with part of the palatal region and side of the maxilla (the zygomatic plate showing a small foramen). The lingual side of the tooth is somewhat damaged. The anterior loop and the four alternating triangles ar all closed off. The enamel rim shows three enamel-free areas: at the sides of the anterior loop (anterosinus and anterosinulus) and at the posterior end (distosinus). We have not observed the root situation. Cementum is abundant. Size (L = 2.37, W = c. 1.37) agrees well with the means of the Tegelen sample (mean L = 2.37, mean W = 1.28).

M2 The upper second molar was already mentioned in our earlier paper (Reumer *et al.* 1998) to which description we here refer. The occlu-

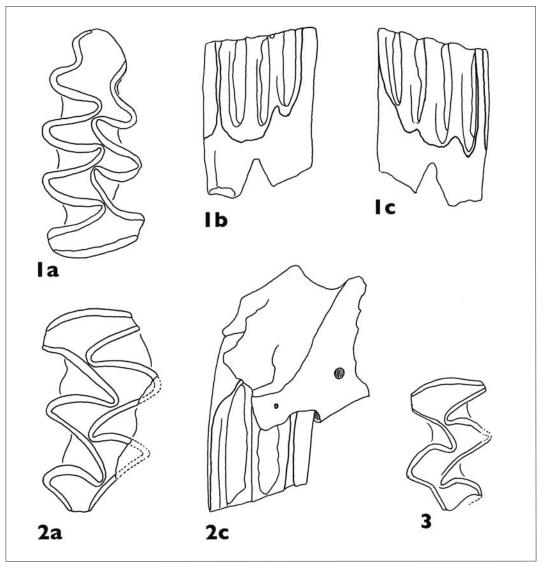


Figure 6 Mimomys tigliensis I m1 dex., found 2001, a occlusal, b buccal, c lingual views; 2 M1 dex., found 2001, a occlusal, b buccal view of the tooth embedded in part of the right maxilla; 3 M2 dex., found 1997, in occlusal view.

sal surface is depicted here (Fig. 6-3); it shows better than the earlier illustration (Reumer *et al.* 1998: fig. 4) the slight damage to the tooth. Length and width agree with the values of the type series (Tesakov 1998) even though the length (here given as >1.53; as >1.57 in Reumer *et al.* 1998 indicating it would not be exceeding that value by more than 0.1 mm; length is thus safely given as between 1.53 and 1.67 mm) is at its lower eaches. The cementum

is abundant.

Remarks In 1998 we mentioned the presence of *M. tigliensis* as a *confer* identification only, based on the M2. We now have more material of the taxon, allowing us to remove the uncertainty about its presence in the Oosterschelde sample. The size of the teeth, the presence of abundant crown cementum, absence of an enamel islet in m1, and the shape of the ante-

rior complex in m1 all indicate *M. tigliensis*. *M. tigliensis* is a new name given to a taxon previously known in the literature up to 1985 under the name of *M. newtoni* (see Mayhew & Stuart 1985 for discussion).

Mimomys newtoni Major, 1902 (Figure 7-1)

Available material 1 M2.

Measurements See Table 1.

Description

M2 The only available upper second molar is entirely without crown cementum. It has an undulated anterior border of the anterior loop. In addition to the loop, there are three separate triangles. The tooth has a low but distinct parasinus and hyposinus.

Remarks The tooth has no crown cementum. In this regard, it resembles the British type material of *M. newtoni*, but differs from some other material attributed to this species in the literature (see Mayhew & Stuart 1985 for discussion). For example, Freudenthal *et al.* (1976) described this taxon from Tegelen, but this same material was later transferred to the new name *M. tigliensis* by Tesakov (1998). As far as we can see, this is the first time that true *M. newtoni* (i.e., small and without cement) is been described from the Netherlands, although earlier publications may contain the species under other denominations.

genus Microtus SCHRANK, 1798

Microtus oeconomus (PALLAS, 1776) (Figure 7-2)

Available material 1 m1.

Measurements See Table 1.

Description One lower first molar is indisputably that of a *Microtus oeconomus*: the (recent)

root vole. The species is known from Recent (Van Apeldoorn 1999) as well as Holocene and Late Pleistocene deposits in the Netherlands (e.g., Van Kolfschoten 1985) and still exists in the very region where the Oosterschelde is located. We cannot but consider the presence of one molar in our sample to be due to contamination, either of a tooth from Late Pleistocene or Holocene levels that slid down the slope of the trench, or of a Recent specimen that was drowned or became washed offshore.

family Castoridae Hemprich, 1820 genus *Trogontherium* FISCHER VON WALDHEIM, 1809

Trogontherium sp.

Remark Two remains are found that belong to the extinct beaver *Trogontherium*, part of a tibia and a fragment of the lower incisor. These remains will be described and depicted in a forthcoming paper on fossil Castoridae, but are here mentioned for the sake of completeness, as they form part of the rodent hypodigm of the Oosterschelde dredgings. The Oosterschelde beaver will be subject of a forthcoming paper.

order Insectivora family Talpidae FISCHER VON WALDHEIM, 1817 subfamily Desmaninae THOMAS, 1912 genus *Galemys* KAUP, 1829

Galemys kormosi (Schreuder, 1940) (Figure 8-1)

Available material 1 i inf.

Description This lower incisor of a water mole was already described and illustrated by Reumer *et al.* (1998), to which we here refer. It is here depicted for the sake of completeness only.

family Soricidae FISCHER VON WALDHEIM, 1817 genus *Beremendia* KORMOS, 1934

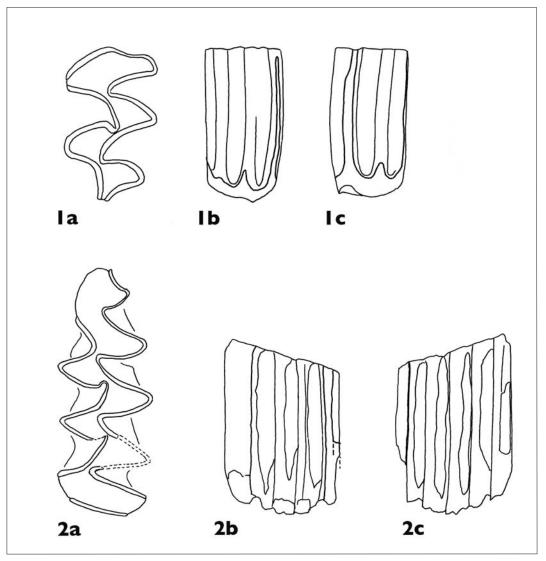


Figure 7 Mimomys newtoni I M2 sin, found 2001, **a** occlusal, **b** buccal, **c** lingual views; Microtus oeconomus **2** m1 sin, found 2001, same views as 1.

Beremendia fissidens Petényi, 1864 (Figure 8-2)

Available material 1 upper antemolar

Measurements L = 1.74, W = 1.01

Description We have a right upper antemolar, A1 or A2, showing one central cusp (paracone) surrounded by a cingulum. At the lingual side

this cingulum widens and becomes separated from the paracone by a valley, but it does not develop a (secondary) cuspule.

genus *Sorex* Linnaeus, 1758 subgenus *Drepanosorex* Kretzoi, 1941

Sorex (Drepanosorex) praearaneaus Kormos, 1934

(Figures 8-3 and 8-4)

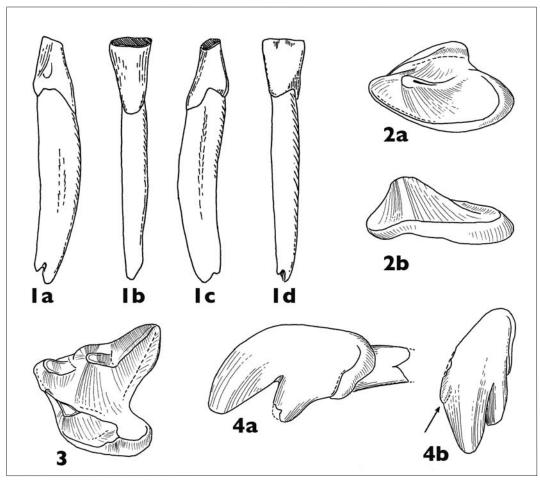


Figure 8 Galernys kormosi I i inf. dex., found 1997, a lateral, b anterior, c medial, d posterior views; Beremendia fissidens 2 A sup. dex., found 2000, a occlusal, b buccal views; Sorex (Drepanosorex) praearaneus 3 P4 sin., found 2001, in occlusal view; 4 I sup. sin., found 2001, a lateral (buccal) view, b frontal view with secondary median tine indicated by arrow.

Available material 1 I sup., 1 P4.

Measurements I sup: L = 1091, LT = 1.15, H = 1.16

P4: PE = 0.94, LL = 1.08, BL = 1.56, W = 1.42

Note Unfortunately, the P4 became lost during the study after it was drawn at a x25 magnification. The measurements of P4 are taken from the drawing and divided by 25. The reliability of this method was checked using the illustrations of the *Mimomys* molars, and was tested positively (average deviation 0.46 %). The measurements of our P4 are therefore reliable

within a 99.54 - 100.46 % range compared to the other measurements in this publication, and can be taken at face value.

Description

I sup. The apex is lightly but clearly fissident (see arrow in figure 8-4b); the upper margin is convex but straightens in its posterior part. The posterior margin is undulate and leans considerably towards the back, is possesses a wide cingulum.

P4 The worn protocone has a triangular shape.

Two low but distinct ridges connect it to the low hypocone; a little depression is enclosed by these ridges. Another low ridge runs from the protocone in antero-buccal direction to the inconspicuous cingulum surrounding the parastyle. A little cuspule is to be seen on this ridge. The hypoconal flange is short, the metaloph is bordered by a distinct and well individualised posteror cingulum. The morphology of this tooth strongly resembles that of a P4 from Tegelen, depicted by Reumer (1984: Plate 9, fig. 5). Also the sizes are very close to the Tegelen means (these mean values are: PE = 0.98, LL = 1.10, BL = 1.52, W = 1.42).

GENERAL DISCUSSION

Discussions about the stratigraphical age of the Oosterschelde mammal assemblage can only be made with the consideration in mind that the faunule is not found *in situ*, that is, it is being assembled by means of nets and Van Veen tubes, and we can only assume that the fossils originate from a single layer of sediment. It is thus what American scholars use to call a 'local fauna', i.e. a fauna that was collected within a certain area and of which we assume a single stratigraphic origin.

The faunal list of the Oosterschelde mammal assemblage can now be composed as follows (leaving out the single tooth of *Microtus oeconomus* considered a contamination):

Rodentia

Mimomys pliocaenicus

M. tigliensis

M. reidi

M. newtoni

Trogontherium sp.

Insectivora

Beremendia fissidens

Sorex (Drepanosorex) praearaneus

Galemys kormosi

Proboscidea

Mammuthus meridionalis

Anancus arvernensis

Perissodactyla

Stephanorhinus etruscus

Equus sp.

Artiodactyla

Cervus rhenanus

Eucladoceros ctenoides

Leptobos cf. L. elatus

Sus strozzii

Carnivora

Homotherium sp.

Hyaena (or Pachycrocuta) perrieri

Figure 9 shows a chart with the known stratigraphical ranges of the mentioned taxa within the MN16/MN17 zones, based on literature sources. Most ranges concentrate in MN17, but in fact the faunal contents of MN16 and MN17 are virtually identical. *M. tigliensis* is lacking

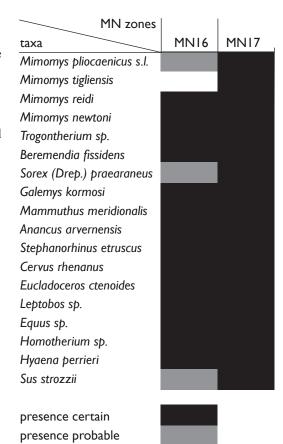


Figure 9 Chart of the known stratigraphical ranges of the 18 mammal taxa encountered in the Oosterschelde. Compiled after Fejfar 2001, Lister 1996, De Vos et al. 1995, Jánossy 1986, Rümke 1985, Reumer 1984, and the NOW database.

in MN16. This appears to be a real difference. This was noted by Mayhew & Stuart (1985) who found the taxon (previously called *M. newtoni*, subsequently *M. blanci*) to be lacking in earlier faunas from the British Crag material ("faunal group 2").

The last result is due to the restricted distribution of the taxon, which is so far known from the type locality only. *M. tigliensis* can of course not be very helpful in resolving stratigraphical matters as it is only known so far from its type locality (Tegelen). The *M. reidi* m1 appears rather primitive with regard to the configuration of the linea sinuosa. Perhaps it is best to correlate our material to a time somewhat earlier than Tegelen itself, but still within MN17.

Earlier correlation with the TC3 pollen zone of the Tiglian (De Vos *et al.* 1998) is here and now considered less appropriate, mainly because the Tiglian pollen zonation used extensively in the Netherlands is presently under detailed study that could reveal its severe limitations (Drees, personal communication).

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ACKNOWLEDGEMENTS

The mayor of the municipality of Schouwen-Duiveland, mr. Jack Asselbergs, invites scientists, among whom the present authors, on a yearly boat-trip to dredge for fossils; the fishing vessel ZZ10 is wholeheartedly provided for this purpose by the Schot family and is skillfully sailed above the fossiliferous sediments by its skipper, mr. Jaap Schot. Without their contribution these expeditions would be impossible. We thank Dirk Slagter, Riet van Veen, Francien Braber, Arthur Oosterbaan and the ZZ10 crew for help with sampling of the sediment during the fishing expeditions. Barbara Reumer helped picking the sediment. Dr. Lars W. van den Hoek Ostende, dr. Albert J. van der Meulen, prof. Oldrich Fejfar, and mr. Andrzej Slupik are to be thanked for giving helpful advice, for reading, and for discussions about the material and its context.

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received 25 March 2004 accepted 15 June 2004

DEINSEA - ANNUAL OF THE NATURAL HISTORY MUSEUM ROTTERDAM P.O.Box 23452, NL-3001 KL Rotterdam The Netherlands