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Mimomys hajnackensis from the Pliocene of the Netherlands

D.F. Mayhew[1,2,*], F.E. Dieleman[2], J. Boele[3], L. Verhaard[4] & L.W. van den Hoek Ostende[2]

1 Natuurhistorisch Museum Rotterdam, Westzeedijk 345, 3015 AA Rotterdam, the Netherlands.
2 Nationaal Natuurhistorisch Museum Naturalis, Darwinweg 2, 2333 CR Leiden, the Netherlands.
3 Joh. Poststraat, 141, 3333 BJ Zwijndrecht, the Netherlands.
4 Geologisch Museum De IJsselvallei, Eikelhofweg 12, 8121 RC Olst, the Netherlands.
* Corresponding author. Email: dfm1@stcatharinescollege.org

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Abstract

We describe the occurrence in the Netherlands of three teeth of *Mimomys hajnackensis* (Arvicolidae, Rodentia) from three separate boreholes extending into marine deposits of the Maassluis Formation. These marine Pliocene/Early Pleistocene deposits at depth are overlain by, and interdigitate eastwards with, the freshwater deposits of the Waalre and Peize Formations (formerly known in part as the Tegelen Formation). Teeth identified as *M. hajnackensis* have not previously been described from the Netherlands although similar material has been reported from Pliocene deposits in Germany at Frechen and Hambach close to the Dutch border. The material described here comes from boreholes at the Polder de Biesbosch near Dordrecht, Diepenveen and Deventer. To our knowledge, these finds represent the oldest described rodent fossils from the Netherlands, corresponding to an absolute age of 2.9 to 3.3 Ma on the basis of comparison with other European localities, implying that the remains are reworked from older deposits.

Keywords: Arvicolidae, *Mimomys hajnackensis*, Netherlands, Pliocene, Maassluis Formation

Introduction

The fossil record for micromammals in the Netherlands is rather patchy. Several assemblages have been gathered from the Middle and Upper Pleistocene of the Belvédère quarry near Maastricht (Van Kolfschoten, 1985). Middle Pleistocene rodents are also known from Franse Kamp near Wageningen, and a faunule, also of Middle Pleistocene age, was collected from the Needse Berg (Van Kolfschoten, 1990). A large Late Pliocene fauna was collected in 1970s at Tegelen (Freudenthal et al., 1976; Tesakov, 1998). A somewhat older fauna was collected from the Maalbeek pit, just south of Tegelen (Westerhoff et al., 1998). These are the only faunas excavated by conventional digging and sieving of exposed stratified layers.

Other, less conventional ways of collecting, can be used to somewhat fill in the gaps. Gathering sediment samples from the base of the channel of the Eastern Scheldt resulted in a faunule, which is considered even somewhat older than Tegelen (Reumer et al., 1998, Reumer et al., 2005). However, the most important sources for micromammal molars, at least in number of locations, are the boreholes. Ever since the days of the Dutch micromammal pioneer Antje Schreuder, micromammal molars were recorded from the cores of the boreholes made by the Dutch geological survey and others (e.g. Schreuder, 1933, 1941, 1943; Van der Meulen & Zagwijn, 1974). Boreholes can even be used to actively collect micromammals, as was proven by amateur geologist Leen Hordijk in his series of boreholes at Zuurland. His collection surpasses even the Tegelen collection in number of specimens, and contains superimposed assemblages from the Tiglian, and several succeeding stages (Reumer & Hordijk, 1999; van Kolfschoten, 1988, 1998; van Kolfschoten & Tesakov, 1998).

The regular finding of micromammal molars in boreholes suggests that these fossils are rather ubiquitous in continental

sediments, and may well represent a continuous, though extremely patchy, record. The absence of such fossils that can be confidently correlated to units such as the Menapian, Eburonian or Waalian seems to have a more fundamental cause (Drees, 2005). Rodents were certainly present throughout the Late Pliocene and Pleistocene, and their remains can be found in the continental deposits of that period. But not only there, for the Pliocene to Early Pleistocene near-shore and marine deposits of the Maassluis Formation have also yielded fossil rodents.

At first sight, one would not expect rodents to be found in marine deposits. The sea, after all, is not part of their natural habitat. Still, micromammal molars are sturdy fossils, and have also been found e.g. in marine deposits in the Middle Miocene locality of Mühlbach (Austria) (Harzhauser et al., 2003). Closer to home, and more relevant to our research, are the marine deposits of the Crags in East Anglia that also consistently yield small mammal remains (Hinton, 1926; Mayhew & Stuart, 1986; Mayhew, 1990; Mayhew & Gibbard, 1998). The correlation of the mammal assemblages from the Crags to those of continental Europe has been notably difficult. Taking the sparse finds from the Maassluis Formation into account, and thus expanding the Dutch record downward, may facilitate the correlation of Late Pliocene mammals across the North Sea.

In this paper we focus on one species only, *Mimomys hajnackensis*. Specimens are described from boreholes at the following localities: Polder de Biesbosch (Dordrecht), Deventer (borehole # 394/9), and Diepenveen.

Taxonomy of the larger *Mimomys* species

Before going into detail concerning the Dutch material, we will briefly discuss the taxonomy of the large *Mimomys* species from the Pliocene presumed to belong to the lineage leading to *M. pliocaenicus*. Although part of an evolutionary lineage which is widely accepted as a useful stratigraphic tool, there still is a lot of confusion about the synonymy, the boundaries between species in this lineage, and some species are in fact by modern standards quite poorly defined.

The species *M. hajnackensis* Fejfar was created in 1961 (Fejfar, 1961; 1964) for material (three teeth) of a large *Mimomys* species from Hajnáčka, Slovakia, which was clearly more primitive than *M. polonicus* Kowalski, 1960. This species in turn had been created for teeth from the Polish locality Rębielice Krolewskie considered to be lower crowned than *M. pliocaenicus* Major, 1902. These species are considered to have an ancestor-descendant relationship.

According to modern standards, the species *Mimomys polonicus* is actually not at all well defined, drawings in the original paper being insufficiently accurate, subsequent descriptions being insufficient or even conflicting in such matters as the amount of crown cement, confluency of the triangles and height of lingual and labial enamel free areas.

The species *M. hassiacus* was described from fissure filling material from Gundersheim, Germany by Heller (1936) who identified two large *Mimomys* species in his assemblage: *M. pliocaenicus* and *M. hassiacus*. The latter species was originally described as lacking crown cement. However, re-examination of the material (Fejfar and Storch, 1990) indicated that crown cement was present in all specimens of larger *Mimomys* in the Heller collection, including the type of *M. hassiacus*. Apparently, Fejfar and Storch have included the specimens originally described by Heller as *M. pliocaenicus* in *M. hassiacus*. According to their description, *M. hassiacus* Heller and *M. hajnackensis* Fejfar would be extremely similar. In their article, Fejfar and Storch (1990) indicated that re-evaluation of the material previously described as *M. hajnackensis* was necessary. Indeed, *M. hajnackensis* is often considered a junior synonym of *M. hassiacus* in the literature (e.g. Mörs et al., 1998; Sabol et al., 2006; Fejfar et al., 1998; but not in Tesakov, 2004).

Tesakov (2004) expressed doubt about the homogeneity of the sample which Storch and Fejfar (1990) assigned to *Mimomys hassiacus*, and warned that the name *hassiacus* should not be used at face value for primitive *polonicus* type assemblages. On the basis of the illustrations in Fejfar and Storch (1990) we concur with Tesakov. This, of course, raises the question whether *M. hajnackensis* is a true synonym of *M. hassiacus*, or whether it is a valid name of its own. We follow Tesakov (2004) in considering *M. hajnackensis* a primitive member of the *M. polonicus - M. pliocaenicus* lineage and use this name until the nature of *M. hassiacus* is clarified.

Mimomys hassiacus is notably absent in published descriptions of French and Spanish Pliocene faunas. It is not clear whether this represents information about the range or whether it is an artefact of nomenclature. In older literature the species *Mimomys occitanus* was considered to be part of the large-sized *Mimomys* lineage, being considered ancestral to *M. polonicus*. Maul (1996) demonstrated that the species *occitanus* is in fact referable to *Dolomys*. Nevertheless, the name *M. occitanus* is still used by some authors, sometimes even including *hajnackensis* as a subspecies (e.g. Chaline et al., 1999; Hurth et al., 2003). It is quite possible that part of the material identified in the literature as *M. occitanus* is in fact referable to *Mimomys* s. str. However, this matter can only be resolved by a complete revision of that material, which is outside the scope of the present article.

The essential difference between the species *M. hajnackensis*, *M. polonicus*, *M. praepliocaenicus* (Rabeder, 1981) and *M. pliocaenicus* is the increase in crown height and overall size, and in the degree of crown cement. This can be expressed by measurement of the basic crown height, by measuring the heights of the enamel free areas and by looking at the timing of disappearance of the enamel islet of the lower first molar/upper third molar.

The best current reference point in the literature is the work of Tesakov (2004) who describes a series of samples from

several localities in Eastern Europe (in the territory of the former USSR) referred to *M. hajnackensis*, *M. polonicus*, *M. praepliocaenicus* and *M.* cf. *pliocaenicus*, and provides measurements for the enamel free areas of teeth assigned to these species. From these numeric data it is clear that the three teeth described here are referable to the most primitive stage of this series, i.e. *M. hajnackensis*. Morphologically these teeth are also similar to those described from Frechen and Hambach (Van Kolfschoten et al., 1998; Mörs et al., 1998), but unfortunately insufficient original data to allow direct comparison have been published. The information does include the HH index and PA index of Rabeder (1981). We propose that these indexes should never replace original measurements in publications, but only be given as supplement, since comparisons at a more precise level are otherwise rendered impossible.

Methods

Measurements were taken on a Leica measuring microscope with digital clocks. All measurements are in mm. The following measurements were taken (as far as possible): Lower molars: AL: Length of anterior loop measured from anterior of tooth to anterior point of second labial re-entrant angle; L: Length of wear surface; W: Width of wear surface; CH: Crown height from wear surface to base of enamel of the first buccal re-entrant angle; ASD: Height of anterior enamel free area (Anterosinuid); HSD: Height of labial enamel free area (Hyposinuid); HSLD: Height of lingual enamel free area (Hyposinulid). Upper molars: L: Length of wear surface; W: Width of wear surface; CH: Crown height from wear surface to base of enamel; PRS: Height of lingual enamel free area (Protosinus); AS: Height of labial enamel free zone (Anterosinus); DS: Height of posterior enamel free zone (Distosinus); HH: HH-index; PA: PA-Index (Rabeder, 1981). Average values are given in brackets, followed by the number of specimens, also between brackets.

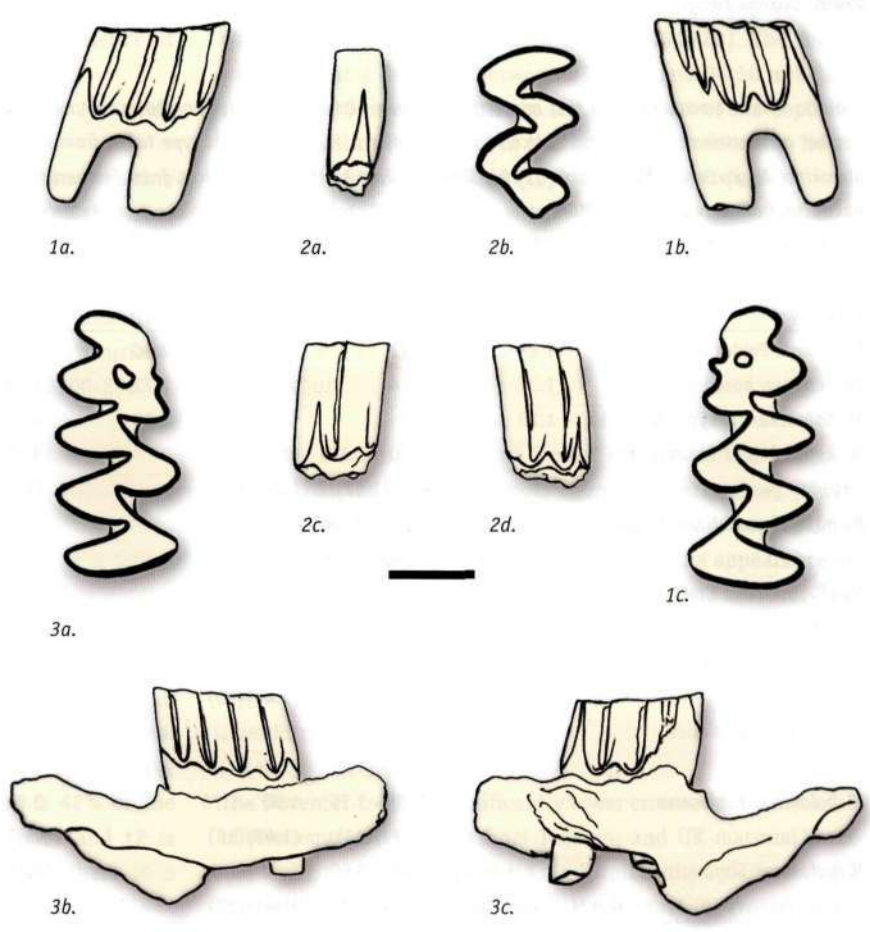
Material attributed to *M. hajnackensis*

1. *Locality: Polder de Biesbosch, Dordrecht*

Screening sediment from a waste dump of a borehole in the Polder de Biesbosch in the vicinity of Dordrecht (province of Zuid-Holland) by one of us (JB) yielded a lower left first molar of *Mimomys hajnackensis* (Collection Naturalis, RGM 195751) (Figs 1a, b, c).

Locality details

Coordinates: (RD2000) ca. 1099 4203. The material was collected in 1992, when the water company Evides set a series of boreholes in the Polder de Biesbosch, about 5 km SE of the city of Dordrecht. The boreholes reached a depth of 145 m. The waste



Figs 1 - 3. Mimomys hajnackensis *from Dordrecht (left m1 Figs 1a, b, c), Deventer (left M2 Figs 2a, b, c, d) and Diepenveen (right m1 and mandible fragment Figs 3a, b, c). Scale line = 1 mm (occlusal views), 2 mm (lateral views).*

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dumps of the drillings were sieved, and proved surprisingly rich in microvertebrates. Unfortunately, the molar was found out of stratigraphical context. In total 26 molars were retrieved, all of them voles. A copy of the borelog was obtained, giving a rough indication of the lithology. It is tantalizing to have such a remarkable find, and not knowing the depth from which it originates. In view of the preservation (slightly rolled and heavily mineralised, compared with undoubtedly geologically younger specimens of other species from the same borehole) it is assumed to come from the Maassluis Formation, the top of which lies in the region at a depth of 80 - 90 metres (NITG-TNO, 2000-2007). The borelog indicates between 80 m and 120 m mainly sands with clayey intercalations, and the regular presence of shells.

Measurements

See Table 1.

Description

m1 – The molar has two plank-shaped roots; the anterior one is stronger developed than the posterior. The crown consists of the posterior loop, three alternating triangles and the anteroconid complex, which makes up 39% of the molar. The *Mimomys*-ridge is well developed. Despite the advanced wear/lower crown height, a small *Mimomys*-island is still present. The enamel differentiation is of a well-developed *Mimomys* type. There is a moderate amount of crown cement. The lingual enamel free zone (hyposinulid) is closed and very low.

Comparison

The anteroconid complex of the Biesbosch m1 is relatively shorter than in *Mimomys pliocaenicus* from Tegelen, similar to *M. polonicus* and *M. hajnackensis* (39% vs. 44 - 49%) .

The hyposinulid is extremely low, falling in the range of *M. hajnackensis* from Nagavskaya and Shirokino, as described by Tesakov (2004). The hyposinuid reaches the wear surface, but its height is also in accordance with identification as *M. hajnackensis*.

2. Locality Diepenveen

The Diepenveen specimen was collected by one of us (LV) in 1969, while sieving material from a borehole that was being made by a water company opposite the house of his parents. For years it was on display in his private museum, the Geologisch Museum de IJsselvallei, where it was noticed in view of its primitive characteristics by FED. The specimen is a right mandible fragment with first molar and associated incisor fragment of *Mimomys*, here attributed to *M. hajnackensis* (Figs 3a, b, c).

Table 1. Measurements of lower first molars from Diepenveen and Biesbosch boreholes compared with material from other localities. Average values and number of specimens in brackets. Source of measurements: M. hajnackensis *type taken from illustration, Fejfar (1964: fig. 21);* M. hajnackensis *from Shirokino, Nagavskaya from Tesakov (2004: Tables 4.2, 4.3);* M. *cf.* polonicus *from Frechen from van Kolfschoten et al. (1998: Fig. 6, Table 2);* M. hassiacus *from Hambach from Mörs et al. (1998: Fig. 7, Table 1);* M. polonicus *from Rębielice, from figures of Chaline (1975); Fejfar and Heinrich (1982);* M. polonicus *Kushkuna and Simbugino from Tesakov, (2004: Tables 4.10, 4.11).*

Locality	AL	L	W	CH	ASD	HSD	HSLD	HH
Biesbosch Polder	1.25	3.23	1.38	2.00	>2.00	>2.00	0.92	
Diepenveen borehole	1.31	3.14	1.42	1.72	>1.72	>1.72	0.57	
M. hajnackensis type Hajnáčka	1.29	3.2	1.48	2.22	>2.22	0.92	0.55	1.1
M. hajnackensis Shirokino		3.00 - 3.50	1.35 - 1.70		3.30 - 3.35	1.55 - 2.35	0.80 - 1.05	1.8 - 2.5
		(3.24)(12)	(1.55)(17)		(3.33)(2)	(2.00)(4)	(0.98)(9)	(4)
M. hajnackensis Nagavskaya		2.80 - 3.35	1.20 - 1.55		2.50 - 3.90	1.60 - 2.20	0.70 - 1.45	1.7 - 2.5
		(3.04)(6)	(1.40)(12)		(3.03)(3)	(1.97)(6)	(0.93)(10)	(6)
M. cf. *polonicus* Frechen		3.31	1.18 - 1.31			1.5 - 3.0		1.5 - 3.4
		(1)	(1.26)(3)			(2)		(2)
M. hassiacus Hambach	1.21 - 1.42	2.93 - 3.57	1.21 - 1.65			0.8 - 1.5	ca. 0.4	1.2 - 2.7
	(1.26)(10)	(3.21)(10)	(1.49)(10)			(2)	(Har5096)	(2)
M. polonicus Rębielice		3.30 - 3.85	1.38 - 1.76		3.00 - 4.10	1.66 - 3.14		
		(3.50)(7)	(1.54)(7)		(3.56)(4)	(2.50)(5)		
M. polonicus Kushkuna		3.00 - 3.75	1.50 - 1.75		3.65 - 3.80	2.30 - 2.90	1.00 - 1.80	2.8 - 3.3
		(3.45)(13)	(1.63)(16)		(3.73)(4)	(2.68)(7)	(1.43)(12)	(3.1)(7)
M. polonicus Simbugino		3.10 - 3.60	1.40 - 1.65		3.60 - 4.20	2.20 - 3.10	1.20 - 2.10	2.7 - 3.7
		(3.33)(23)	(1.53)(23)		(3.97)(9)	(2.82)(21)	(1.50)(23)	(3.2)(21)

Locality details

Coordinates: (RD2000) ca. 2067 4796. Borehole for water by the Water supply Company Overijssel, Olst, October 1969 at Diepenveen, location 80 m south of the Randerstraat and 100 m west of the Molenweg. The borehole was sunk to a depth of ca. 130 m below the surface.

The sequence of deposits measured from the surface recorded at that time was:

0 - 0.5 m:	soil
0.5 - 2.5 m:	fine sands: interpreted as windblown, late Weichselian, Twente Formation
2.5 - 9.5 m:	coarse sands and gravel: interpreted as river deposits, middle Weichselian, Kreftenheye Formation
9.5 - 11.0 m:	clay: interpreted as marine, Eemian
11.0 - 45.0 m:	coarse sands and gravels: interpreted as freshwater, glacial
45.0 - 86.5 m:	laminated clays and silts: interpreted as glacio-lacustrine deposits
86.5 - 86.7 m:	red and brown clays and silts: interpreted as glacio-lacustrine deposits
86.7 - 86.9 m:	dark grey stiff clay: interpreted as glacial deposit
86.9 - 93.0 m:	brown, silty sands: interpreted as freshwater interglacial sediments
93.0 - 117.2 m:	grey sands and silts containing marine shells: interpreted as marine sediments of the Maassluis Formation
117.2 - 117.4 m:	grey clay: interpreted as marine, Maassluis Formation
117.4 - 130 m:	grey sands and silts containing marine shells: interpreted as marine sediments of the Oosterhout Formation.

The tooth assigned here to *Mimomys hajnackensis* came from the part of the section between 93 m and 117 m below surface, i.e. from the Maassluis Formation (cf. NITG-TNO, 2000-2007).

Measurements

See Table 1.

Description

m1 – The tooth is still in the mandible fragment, but the two roots are visible. Despite the low crown height there is an enamel islet, which is long and irregular. The labial enamel free area reaches the wear surface, the lingual enamel free area is closed and very low. The anterior loop is 42% of the wear surface length. The connection between t1 and t2 is open. The enamel is clearly differentiated and there is a moderate amount of crown cement.

Comparison

Compared with material of *M. pliocaenicus* from Tegelen, the m1 from Diepenveen is significantly lower crowned. It still has an enamel islet at a relatively late stage of wear. The height of the lingual enamel free area (hyposinulid) is much lower than in material from the Norwich crag (Bramerton, Bulcamp) referred to *M. pliocaenicus* (Mayhew and Stuart, 1986; Mayhew, 1990) (= *M. praepliocaenicus* in the sense of Rabeder, 1981) and material from Stranzendorf D, Austria, referred to *M. praepliocaenicus* by Rabeder (1981). Comparison with the material described by Tesakov (2004) indicates that the hyposinulid is even lower than in 19 teeth from two localities identified as *M. hajnackensis* (Shirokino: range 0.80 - 1.05 mm, N = 9; Nagavskaya: range 0.70 - 1.45 mm, N = 10).

3. Locality Deventer

A borehole at Deventer in 1927 yielded an upper left second molar of *Mimomys*, originally identified as cf. *Mimomys intermedius* Newton (Collection Naturalis, RGM 87178). The identification can be revised to *M. hajnackensis* (Figs 2a - d).

Locality details

Coordinates (RD2000): 207033 475716. The borehole was made at Deventer, borehole number 3 on the Ceintuurbaan near the Watertower, Number 394/9 (RVD #2401) (27G/29). The tooth was found at a depth of between 85.90 m and 94.50 m below the surface. This corresponds to the upper part of the deposits of the Maassluis Formation, in this borehole considered to lie at a depth of between 85.90 m (top) and 121.50 m (base).

Measurements

See Table 2.

Description

M2 – The tooth has the crown formed, but the roots are broken off, so that the number of roots cannot be determined (there are two alveoli in the dentine). The enamel on the wear surface is thin and not highly differentiated, giving the appearance of a young tooth although the roots had already formed. The lingual, labial and posterior enamel free zones are all closed, and relatively low. There is relatively little crown cementum.

Comparison

The Deventer tooth is significantly lower crowned than material of *Mimomys pliocaenicus* from Tegelen, and UK material from the lower part of the Norwich Crag Formation (e.g. Bramerton, Mayhew & Stuart, 1986; Bulcamp, Mayhew, 1990) (referable to

Table 2. Measurements of upper second molar of Mimomys hassiacus from Deventer borehole 27G/29 compared with material from other localities. Average values and number of specimens in brackets. Source of measurements: Mimomys hajnackensis *from Hajnáčka taken from Sabol et al. (2006: Fig. 9, part 12, figured as* M. hassiacus*);* Mimomys *cf.* polonicus *from Frechen taken from van Kolfschoten et al. (1998);* Mimomys hajnackensis *from Shirokino and* Mimomys polonicus *from Kushkuna taken from Tesakov (2004: Table 4.16).*

Locality	L	W	CH	PRS	AS	DS	PA
Deventer borehole	2.00	1.21	2.99	1.45	1.30	1.90	1.95
***Mimomys hajnackensis* Hajnáčka**	**1.91**	**1.15**	**2.21**	**1.15**	**0.95**	**0.96**	**1.49**
Mimomys cf. *polonicus* Frechen	2.12 - 2.22	1.46 - 1.60					1.56
	(2.18)(4)	(1.55)(4)					(1)
***Mimomys hajnackensis* Shirokino**	**2.06 - 2.25**	**1.35 - 1.55**		**1.35 - 1.70**	**0.85 - 1.10**	**1.30 - 1.50**	**1.72 - 2.02**
	(2.17)(3)	**(1.43)(3)**		**(1.52)(3)**	**(0.98)(2)**	**(1.43)(3)**	**(1.87)(2)**
Mimomys polonicus Kushkuna	2.15 - 2.50	1.45 - 1.75		1.60 - 2.20	1.35 - 1.80	2.20 - 3.00	2.26 - 2.73
	(2.38)(8)	(1.62)(8)		(1.88)(7)	(1.61)(6)	(2.55)(6)	(2.51)(5)

M. praepliocaenicus sensu Rabeder, 1981). According to the detailed measurements Tesakov (2004) provides, we could place this specimen from Deventer between samples assigned by him to *M. hajnackensis* and *M. polonicus*. It is understood from Tesakov (pers. comm.) that the identification of the material described by him as *M. polonicus* was done by reference to a sample in the collections of the Geological Institute Moscow of teeth from the type locality, Rębielice Królewskie in Poland. Unfortunately, the published descriptions of material of this species from the type locality are insufficient for detailed work (Kowalski, 1960). Our molar shows close resemblance to the M2 from Hajnáčka figured by Sabol et al. (2006, fig. 9.12, as *M. hassiacus*).

Discussion

The three teeth here come from different boreholes, and it is not possible to assign them to specific levels. They are all considered to come from the Maassluis Formation. This marine formation occurs at depth through much of the Netherlands and overlies and interdigitates with the Oosterhout Formation (Jansen et al., 2004). The Maassluis Formation is overlain by, and may interdigitate with, deposits of continental / fresh water origin, assigned to the Waalre and Peize Formations (which include those deposits previously known as the Tegelen Formation). The replacement of marine by freshwater sediments was due to a trend for fall in relative sea level, which took place over a considerable period of time during which several transgression/regression cycles have been recognised (see Slupik et al., 2007, for a recent analysis). The above scenario means that the top of the (marine) Maassluis Formation in the eastern Netherlands is of earlier age than the top in the western part of the Netherlands. For example, Jansen et al. (2004) report that in a boring at Apeldoorn, ca. 10 km west of Deventer, the top of the Maassluis Formation may be separated from overlying deposits (Peize Formation) by a hiatus of at least 0.5 my. In the view of Jansen et al. (2004) the base of the Maassluis Formation in the east of the Netherlands may date back as far as 3.4 Ma. However, Wesselingh et al. (2005) consider the base of the Maassluis Formation to be not older than 2.55 Ma.

The deposits of the Maassluis Formation (and the Waalre Formation) are considered to have been laid down in the period Early Gelasian (Late Pliocene) to Early Pleistocene, taking as a definition of the Plio-Pleistocene boundary the International standard at Vrica, Mediterranean area (approx. 1.8 Ma, Gradstein et al., 2004).

The occurrence of fossil vole remains in marine sediments may seem unusual, but finds a parallel in the material from the crags of Eastern England. Undoubtedly there must have been some transport, even reworking. The tooth from the Biesbosch is highly polished, mineralised and the wear surface is slightly rolled. In air it appears shiny black, but viewed under acetone the enamel appears lighter than the more darkly stained dentine. The tooth from Diepenveen (enamel and dentine) and the jaw fragment in which it rests are stained very dark brown/black, but are otherwise not mineralised or rolled. The Deventer M2 has the enamel stained black, and the dentine medium brown. It is not rolled, the wear surface is relatively undamaged, but the roots are broken off. The preservation of the teeth is consistent with some degree of reworking, but not in a high-energy environment.

Two different scenarios can explain the presence of micro-mammal fossils in marine sediments. The remains could have been washed in directly during storms, either through owl pellets or as dead animals. If the large *Mimomys* species had semi-aquatic habits similar to that of present day *Arvicola*, it would in fact have made them more susceptible to drifting into sea through the rivers. Alternatively, the fossil material may have been re-worked, and have been deposited as the original sediment was eroded, for example during a transgression/regression cycle. The extensive reworking at the base of and in the Maassluis Formation is discussed by Slupik et al. (2007).

In the case of the *Mimomys hajnackensis* molars, the second scenario seems to be applicable. The species *M. hajnackensis* is considered to range from ca 2.9 to 3.3 Ma, (roughly equivalent to zone MN 16a: Tesakov, 2004; Sabol et al., 2006). The fossils are therefore substantially older than the accepted dating (Gelasian) for the Maassluis Formation which implies they must have been reworked, which, as we noted, is also apparent from their preservation. They are presumably derived from previously fluvial sediments from the Rhine/Meuse such as found at Frechen and Hambach, just over the Dutch/German border (Van Kolfschoten et al., 1998, Mörs et al., 1998).

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