Gliridae (Rodentia, Mammalia) from the Upper Pliocene of Tegelen (province of Limburg, The Netherlands)

Lars W. van den Hoek Ostende

Hoek Ostende, L.W. van den. Gliridae (Rodentia, Mammalia) from the Upper Pliocene of Tegelen (province of Limburg, The Netherlands). *Scripta Geologica,* **126**: 203-215, 1 pl.; Leiden, November 2003.

L.W. van den Hoek Ostende, Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands (hoek@naturalis.nnm.nl).

Key words — Tegelen, *Muscardinus*, *Glirulus*, Pliocene, The Netherlands.

Two species of dormouse have been found in the Upper Pliocene clays of Tegelen, *Muscardinus pliocaenicus* and *Glirulus pusillus*. The latter is the first record of this genus in The Netherlands. *Muscardinus pliocaenicus* shows derived characteristics and is close to the Recent hazelmouse *M. avellanarius*. The record of *Glirulus pusillus* is one of the last in Europe. Like the flying squirrel *Hylopetes debruijni*, also known from Tegelen, *G. pussilus* ranks among a group of Pliocene animals with its living relatives in Asia. Thus, there is an analogy with the Tertiary flora, which also has relicts in the same area.

Contents

Introduction

Gliridae are not very common in the fossil record of The Netherlands. Indeed, glirids are not that common in the Pliocene and Pleistocene record anyway, having had their heyday in the Oligocene and Miocene. For The Netherlands, these warmth-loving rodents can only be expected in those periods in which the climate was at least as warm as the present, since the dormice presently occur in the southernmost part of The Netherlands only as part of their northern limit. The Late Tiglian was such a warm period. The fossil seed flora from Tegelen indicates that warmth-loving plants like grapes were native to the area and the presence of the European pond turtle *Emys orbicularis* shows that temperatures were high enough to hatch its eggs. Freudenthal *et al*. (1976) have already demonstrated the presence of a dormouse, *Muscardinus* cf. *avellanarius*, in the fauna of Tegelen. Reumer (2001) described two species of glirid, *Eliomys brielliensis* and *Muscardinus pliocaenicus,* from the Late Tiglian of the Zuurland boreholes. He indicated that the Tegelen *Muscardinus* probably should also be assigned to the latter species.

From younger strata, Pleistocene dormice are only known from the localities of Wageningen Franse Kamp and Belvédère 4. Both localities, which are assigned to a warm period within the Saalian, yielded fossils of *Eliomys quercinus* (van Kolfschoten, 1985, 1990).

Since the publication of the preliminary report on the campaign in the Tegelen clay pits (Freudenthal *et al*., 1976), sampling has continued and the vast amounts of residue of the earlier campaigns were screened. This task was completed only a couple of years ago, when all of the Tegelen microvertebrate collection was registered. The entire collection comprises of *c.* 5000 dental elements of micromammals. Meanwhile, several specialists have published on the micromammals from Tegelen. Reumer (1984) included the shrews from the Limburg locality in his thesis, as did Rümke (1985) with the desmans. The mole *Talpa minor* was the subject of an unpublished student thesis (Roders, 1987). The voles from Tegelen were described by Tesakov (1998). With all of the material now sorted, it is time to finish the taxonomical work on the remaining groups. The first of these were the Petauristidae, published by Reumer & van den Hoek Ostende (2003). The current paper discusses the dormice from Tegelen. The lagomorphs are currently under study by J. Reumer (Natuurmuseum Rotterdam), which leaves the murids and bats for future work.

Material and methods

The collection of micromammal fossils from the Tegelen Clay were collected from sediments in a stream gully in the pit Russel-Tiglia-Egypte (Freudenthal *et al*., 1976). Between 1970 and 1977 a huge amount of sediments were washed in a series of campaigns. The material is stored in the National Museum of Natural History, Naturalis, in Leiden. The glirids bear the registration numbers RGM 179057-179059, 235670, 257752-257801 and 257814-257818.

The terminology for parts of molars follows Mayr (1979), with 'vorderer Centroloph' and 'hinterer Centroloph' translated as precentroloph and postcentroloph, respectively. In *Muscardinus*, where the basal glirid pattern is simplified to a series of parallel ridges, the more practical method of counting them from front to back is used. The number in brackets in the description of each element denotes the number of specimens available. Measurements were taken using a Leica Ortholux measuring microscope. All measurements are in mm. Specimens have been illustrated as coming from the left jaw to facilitate comparison. Specimens illustrated in inverse have been indicated by underlining the number in the plate caption.

Systematic palaeontology

Order Rodentia
Family Gliridae Thomas, 1897
Genus *Muscardinus* Kaup, 1829
Muscardinus pliocaenicus Kowalski, 1963

Pl. 1, Figs. 1-7.

Description — *p4* (1). The premolar is a simple, one-rooted tooth with a sub-triangular occlusal outline. It bears two equally long ridges with a much shorter ridge in front of them. The ridges are not interconnected.

m1 (17). The occlusal surface is sub-rectangular, the posterior part of the molar being a little wider than the front. The front is somewhat rounded. The chewing surface consists of six low, parallel ridges. Usually the hindmost ridge (posterolophid) is connected lingually to the one in front. Rarely there is also a labial connection between the two ridges. A similar situation occurs with the frontmost two ridges, between which a labial connection is more common, creating an encircled anterior basin. In one specimen there is a small circular elevation between the fifth and sixth ridges, in another this elevation is a connection to the fifth ridge. This feature is absent in all the other specimens. The posterior side is sometimes indented in the middle, forming an indistinct patch of cingulum.

The anterior root is plank-shaped, with a small groove indicating it consists of a fusion of two roots. There are two posterior roots, with a circular circumference.

m2 (11). The occlusal surface is sub-rectangular. The molar is far less elongated than the m1, being only somewhat longer than wide, and has a less rounded anterior side. The chewing surface consists of six low, parallel ridges which, with the exception of the posterolophid, are slightly arched towards the front. Particularly the frontmost and hindmost two ridges may be connected at the lingual side. The m2 has four roots.

m3 (6). The occlusal surface forms an irregular quadrangle. The front of the molar is wider than the back. The front side is straight; the back is slanting. There are six low ridges, which arch towards the front of the molar. The frontmost and hindmost two ridges tend to connect on both the lingual and the labial side.

There are three roots, two anteriorly and a very stout posterior root. The latter is clearly a fusion of two roots as can been seen from the grooves on the anterior and posterior side.

M1 (8). The molar is much longer than wide. Usually here are five low ridges, which are much coarser than in the other elements of this species. One specimen (RGM 257780) bears six ridges, the additional ridge apparently being intercalated between the third and fourth ridges as found in the other molars. The first two ridges show a regular curve. The third and fourth have a strong backward arch in their lingual parts. The first two valleys between the ridges, and particularly the second one, are somewhat deeper than the others. An endoloph connects all ridges except for the anterior one. Short vestigial lophs may spring from the endoloph in the second or third valley. Except for having a sixth ridge, RGM 257780 is also aberrant in having a short longitudinal extension in the middle of the third ridge and a short elongated elevation in front of the first ridge. The M1 has four strong roots underneath each corner of the molar and an additional, smaller one between the lingual roots.

M2 (3). The outline of the occlusal surface is sub-square in two of the three specimens; the other specimen is somewhat longer than wide. The occlusal surface consists of six low ridges, with a slight curve towards the front of the molar. The third ridge is interrupted at two points in two of the three specimens. Two small vestigial ridges spring from the endoloph in one specimen, viz. between the fourth and fifth, and the fifth and last transverse ridge. The other two specimens have a vestigial ridge between the fourth and fifth transverse ridge only. The molar has four roots.

M3 (3). The molar is sub-trapezoidal. The lingual is shorter than the labial side. The anterior side is rather straight; the posterior side is slanted. The M3 has the most complicated ridge pattern of all the molars. This pattern can only be observed in two out of the three available specimens, since the third is too worn. There are six transverse ridges. The fourth ridge is interrupted in one of the specimens. All ridges are connected by an endoloph. In one of the two specimens there is also a continuous ectoloph, which is less well developed in the other M3. In the specimen with the interrupted fourth ridge, vestigial lophs spring from the ectoloph in front and behind the fourth ridge. In the other specimen a somewhat longer, albeit discontinuous loph occurs intermittingly between the fourth and fifth ridge. This specimen also has a vestigial loph between the first and the second ridges, connected to the endoloph and a patch of isolated ridge in the same valley. The wide space between the fifth and the sixth lophs in this specimen is occupied by a complicated pattern of enamel islands, which merge lingually into a partial ridge connected to the endoloph. There are four roots. The two lingual roots stand closer together than the labial ones.

Measurements — The measurements are listed in Table 1.

Table 1. Measurements of *Muscardinus pliocaenicus* from Tegelen. Comparative measurements have been added from Zuurland (Z2; Z5/6), (Reumer, 2001) and Podlesice (PO), Weze 1 (We 1), Kozi Grzbiet (KG, *M. avellanarius*) and the recent Hazelmouse (REC) (Daoud, 1993).

			length		width	
		N	range	average	range	average
p4	Teg	1		0.53		0.58
	We 1	1		0.49		0.67
m1	Teg	12	1.39-1.56	1.46	1.01-1.20	1.10
	Z5/6	2	1.40-1.40	1.40	1.02-1.05	1.04
	PO	29	1.27-1.52	1.39	0.98-1.16	1.08
	We 1	1		1.40		1.03
	KG	11	1.50-1.62	1.56	1.06-1.28	1.20
	REC	56	1.52-1.66	1.61	1.10-1.30	1.25
m2	Teg	11	1.20-1.39	1.32	1.13-1.29	1.19
	PO	18	1.17-1.35	1.26	0.98-1.25	1.08
	We 1	4	1.16-1.27	1.24	0.95-1.20	1.06
	KG	13	1.21-1.40	1.34	1.16-1.34	1.23
	REC	50	1.26-1.44	1.36	1.18-1.31	1.26
m3	Teg	6	0.96-1.10	1.04	0.92-1.14	1.06
	PO	5	0.95-1.19	1.05	0.96-1.10	1.04
	REC	66	0.99-1.31	1.16	1.00-1.22	1.16
M1	Teg	8	1.60-1.84	1.70	1.06-1.29	1.15
	PO	17	1.36-1.69	1.60	0.94-1.18	1.10
	We1	1		1.62		1.10
	KG	25	1.61-1.86	1.76	1.08-1.28	1.18
	REC	60	1.70-1.94	1.80	1.20-1.37	1.30
M2	Teg	3	1.20-1.31	1.25	1.25-1.32	1.28
	Z2	1		1.35		1.23
	PO	6	1.17-1.33	1.23	1.23-1.36	1.27
	We1	1		1.19		1.22
	KG	7	1.24-1.44	1.35	1.25-1.39	1.32
	REC	50	1.24-1.46	1.36	1.25-1.40	1.33
M3	Teg	3	0.96-1.05	1.00	1.13-1.17	1.15
	PO	1		1.04		1.14
	KG	2	1.02-1.07	1.04	1.27-1.29	1.28
	REC	50	0.98-1.13	1.08	1.21-1.33	1.28

Remarks — With 51 molars *Muscardinus* is by far the commonest of the two glirid genera found in the Tegelen fauna.

In their overview of fossil and recent glirids, Daams and De Bruijn (1995) recognised four species of *Muscardinus* for the Pliocene and Pleistocene; *M. avellanarius*, *M. pliocaenicus*, *M. dacicus* and *M. helleri*. According to Daoud (1993), the small-sized *M. pliocaenicus* and *M. avellanarius* form one evolutionary lineage. The two larger Pliocene species, *M. dacicus* and *M. helleri*, are sometimes present in the same locality as representatives of this lineage. *Muscardinus dacicus* is found together with *M. pliocaenicus* in the Polish localities Podlesice and Pańska Góra (Daoud, 1993), and *M. helleri* and *M. pliocaenicus* both occur in the German locality of Gundersheim (Fejfar & Storch, 1990).

The Tegelen *Muscardinus* is too small to be placed in either *M. helleri* or *M. dacicus*. It further differs from both species in having five roots underneath the M1, whereas *M. helleri* has four and *M. dacicus* has six. Daoud (1993) considered unconnected ridges on the p4 characteristic for *M. dacicus*. However, the single p4 found in the Tegelen assemblage also displays this character.

Daoud (1993) monitored morphological and metrical changes in various glirid lineages based on Polish Pliocene and Pleistocene assemblages. One of the changes in the *M. pliocaenicus – M. avellanarius* lineage is the gradual replacement of M1 with six ridges (Morphotype 2) by M1 bearing five ridges (Morphotype 1). According to Daoud (1993), the morphotype 2 is characteristic for *M. pliocaenicus*. However, the species was described by Kowalski (1963) as having five ridges on the M1. The type series from Weze 1 contains four M1, three of which were figured by Kowalski (1963). Only one of these three bears six ridges, showing that in the type locality of *M. pliocaenicus* both morphotypes were present. Apparently the type series was not available to Daoud, since he listed one M1 only. Because the type locality of *M. pliocaenicus* contains both morphotypes, the morphotype with six ridges cannot be said to be characteristic for that species. Nevertheless, the evolutionary trend from six to five ridges is undeniable. In the Tegelen assemblage the modern morphotype is predominant, with seven out of eight M1 having five ridges only. With respect to the root formation, the Tegelen assemblage is primitive. All specimens in which the roots are preserved clearly show a fifth root. In *M. avellanarius* a fifth root may be present, but is weakly developed.

Another trend in the *M. pliocaenicus - M. avellanarius* lineage is an increase in size. In this respect the Tegelen assemblage seems to take an intermediate position between the *M. pliocaenicus* assemblages from Podlesice and Weze 1, and the Recent species (Table 1), showing an overlap with both. The notable exception is the m1, which overlaps with *M. avellanarius* only.

Using the Polish Pliocene/Pleistocene sequence, Daoud (1993) clearly demonstrated that *Muscardinus pliocaenicus* and *M. avellanarius* indeed form a single lineage. This lineage is further corroborated by the Tegelen assemblage. Since there are no off-shoots of this lineage known, in a phylogenetical species concept all material should be assigned to *M. avellanarius*. However, since the evolutionary stage within the lineage has some stratigraphical meaning, it is preferred to retain *M. pliocaenicus* as a chronospecies. Given the intermediary position of the Tegelen assemblage, it can be considered either as a primitive *M. avellanarius* or as an advanced *M. pliocaenicus*. The choice for the latter is based on the presence of the primitive morphotype of the M1 (though in small numbers), the presence of a fifth root on that element, and the relatively small m1.

Genus *Glirulus* Thomas, 1906
Glirulus pusillus (Heller, 1936)
Pl. 1, figs. 8-11.

Description — *m2* (1). The outline of the occlusal surface is sub-rectangular. The ectolophid is very prominent and forms the highest part of the molar. The anterolophid is straight and reaches the lingual side. The metalophid runs obliquely and is interrupted in the labial half of the molar. At the lingual side it touches the anterolophid. The mesolophid and posterolophid are strongly curved, and run along the lingual side at their ends, touching the metalophid and the mesolophid, respectively. A centrolophid appears to be missing. There is a clear additional ridge between the mesolophid and posterolophid, which touches the ectolophid without being connected to it. A string of enamel islands lies between the anterolophid and the metalophid. The roots have not been preserved.

m3 (1). The front of the molar is clearly wider than the posterior side. The front is straight; the posterior side is rounded. The ectolophid is high at the position of the metaconid, much lower at the back. With the exception of the posterolophid, the transverse ridges are rather straight. The posterolophid follows the contours of the back of the molar and is rounded. The metalophid joins with the anterolophid at the lingual side. Between the two lophids there is a well-defined additional ridge. The centrolophid ends at about $^3/_4$ of the width of the molar. The posterolophid and the mesolophid join at the lingual side, forming a loop at the back of the m3. Inside this loop there is a second additional ridge. The lingual conjunction of the posterolophid and mesolophid forms the starting point of a lingual ridge, which ends just short of the metalophid and is separated from it by a narrow valley. The molar has two roots. The anterior root is clearly a fusion of two roots.

M1, M2 (1, 5). The outline of the occlusal surface is (sub-)rectangular. In the element interpreted as an M1 the lingual and labial sides are equally as long, and the anterior and posterior sides are straight. In the M2 the lingual side is slightly longer than the labial side. The anterior side of the molar is straight, the posterior side slightly slanted. The occlusal surface is concave. The strong endoloph is continuous. It shows a string of indentations along its lingual flank. The paracone and metacone form high labial ridges, separated by a valley. There are five transverse ridges connecting the lingual and labial side. The anteroloph, protoloph and precentroloph forms connections between the paracone and the endoloph; the metaloph and posteroloph connect the metacone to the endoloph. The metaloph may show an abrupt bend just before reaching the endoloph. The postcentroloph is weak and ends short of the endoloph. In development it equals the three additional ridges. These are situated between the anteroloph and the protoloph, the protoloph and the precentroloph, and the metaloph and the posteroloph. These ridges touch the labial ridges without being truly connected to them and end well short off the endoloph. There are three roots; a plank-shaped lingual one and two labial roots with a circular circumference.

Measurements — The measurements are listed in Table 2.

Remarks — *Glirulus pusillus* is quite regularly encountered in European Pliocene faunas, though never in great numbers. It was originally described on the basis of a single m2 from a fissure filling at Gundersheim (Germany, Heller, 1936). More material from the same area was described by Fejfar & Storch (1990), who obtained a Pliocene fauna from a loose block of sediment from one of the Gundersheim quarries, which was designated Gundersheim 4. Fejfar & Storch (1990) tentatively suggested that *G. gemulla*, described by Kretzoi (1962) from the Hungarian locality Csarnota 2, was a junior synonym of *G. pusillus*. The material derived from various Polish localities was discussed by Daoud (1993) and Bednarczyk (1993), and Michaux (1970) noted the presence of *G. pusillus* in the Italian locality of Arondelli. In Germany the species was described from the localities of Wölfersheim (Dahlmann, 2001) and Schernfeld (Dehm, 1962). The Reuver Clay in the Lower Rhine Embayment yielded *G. pusillus* from two different localities, Frechen (Van Kolfschoten *et al*., 1998) and Hambach (Mörs *et al*., 1998). The species survived into the Early Pleistocene as is evident from finds in the Austrian locality of Deutsch Altenburg 4B (Mais & Rabeder, 1984), the French locality of Les Valerots (Chaline, 1972), and the Italian locality of Monte Peglia (Van der Meulen, 1973). The finds of this species in Tegelen comprise the first record of the species for The Netherlands.

According to Daoud (1993), there are no great differences in size and morphology between the various *Glirulus* assemblages in Poland. Other assemblages of *G. pusillus* show no large differences either, with the exception of that from Frechen (Van Kolfschoten *et al*., 1998). The m2 from this locality agree well with that of other assemblages (assuming that the length and width have been reversed in the measurements given by Van Kolfschoten *et al*.), but the M1-2 (*op. cit*., fig. 4.1, here interpreted as an M1) is aberrant. Whereas commonly five continuous ridges are present in the upper molars, in this element only the anteroloph, precentroloph and posteroloph connect to

Table 2. Measurements of *Glirulus pusillus* from Tegelen. Comparative measurements have been added from Frechen (Fr) (Van Kolfschoten *et al*., 1998), Hambach (Har) (Mörs *et al*., 1998), and Podlesice (PO) and Pańska Góra (PN) (Daoud, 1993).

			Length		Width	
		N	range	average	range	average
m2	Teg	1		1.02		0.94
	PO	8	0.98-1.06	1.01	0.96-1.02	0.98
	PN	4	0.99-1.08	1.03	0.96-1.03	1.00
	Fr	2	1.01-1.04	1.03	0.91-0.96	0.94
m3	Teg	1		0.96		0.92
	PO	1		1.02		0.95
	PN	1		1.03		0.96
	Fr	1		0.96		0.89
M1	Teg	1		1.01		0.94
	PO	6	0.90-0.97	0.95	0.92-0.98	0.96
	PN	3	0.93-0.99	0.96	0.94-0.99	0.97
	Fr	1		1.02		0.95
M2	Teg	5	0.90-1.01	0.96	0.88-0.93	0.91
	PO	6	0.96-1.01	0.99	0.96-1.03	1.00
	PN	2	0.98-1.00	0.99	0.99-1.01	1.00
	Har	1		0.96		0.92

both the endoloph and the labial ridges. The protoloph is not connected to the paracone and is cut off by a loop formed by the additional ridges between the anteroloph and protoloph, and protoloph and precentroloph, respectively. Three ridge-shaped enamel isles are found between the various ridges. Determining the homologies of the various ridges in the posterior part of the Frechen molar is difficult. There are three ridges connected to the metacone. The frontmost (?postcentroloph) is very short; the second (?metaloph) nearly reaches the endoloph; the third, somewhat shorter ridge might be homologous with the additional ridge between metaloph and posteroloph. However, there is also a ridge reaching from the endoloph to halfway along the molar between the second and third ridge from the labial side, for which no homology can be found in the typical *G. pusillus* molar. Near the end of this ridge another enamel island is present. Despite the considerable differences between the Frechen M1 and the upper molars of *Glirulus pusillus* of other localities (Tegelen, Gundersheim 4, Wölfersheim), it is best considered an aberrant specimen of the same species. The presence of additional ridges in some specimens of *G. japonicus* was documented by Kawamura (1989). However, it is noteworthy that the single *Sciurus* m2 from Frechen is also aberrant in having a connection between the mesoconid and the entoconid (van Kolfschoten *et al*., 1998). This opens the way for speculation that local circumstances (nutrition?) may have had an influence on molar morphology.

Discussion

With 59 molars, the dormice take up only a minor fraction of the entire Tegelen collection of microvertebrates. This is the usual situation in Upper Pliocene/Lower Pleistocene faunas, where the Gliridae play a minor role in rodent assemblages only. Nevertheless, as such the assemblages of both *Muscardinus pliocaenicus* and *Glirulus pusillus* are large with respect to those of other, contemporary faunas. In fact, though only consisting of eight molars, the *Glirulus pusillus* assemblage is one of the largest known from a single locality.

From a stratigraphical point of view, the presence of *Muscardinus pliocaenicus* nor *Glirulus pusillus* is surprising. Tegelen is placed in the Late Villanyian (Tesakov, 1998). Compared to the series of Polish localities used by Daoud (1993) in his analysis of the changes in the *M. pliocaenicus*-*M. avellanarius* lineage, the Tegelen assemblage falls between the youngest occurrence of *M. pliocaenicus* (Rebielice Królewskie) and the oldest assemblage assigned to *M. avellanarius* (Kozi Grzbiet). The intermediate character of the Tegelen *Muscardinus*-assemblage is thus as we would expect it for its stratigraphical position. Although *Glirulus pusillus* is primarily known from the Pliocene, it is present in Early Pleistocene faunas throughout Europe (Deutsch Altenburg 4B, Les Valerots, and Monte Peglia; see above). Tegelen is one of the younger, though not the youngest, occurrence of the species.

Reumer & van den Hoek Ostende (2003) already commented on the differences in faunal composition between microvertebrates of the Late Tiglian of the Zuurland boreholes and those from Tegelen. Both localities have yielded *Muscardinus pliocaenicus*, but in the Zuurland boreholes this species is accompanied by *Eliomys briellensis*, whereas the second dormouse in Tegelen is *Glirulus pusillus*. In combination with the presence of a flying squirrel in Tegelen, whereas a ground squirrel was found at Zuurland, and the far higher percentage of the wood mouse *Apodemus* in the Tegelen fauna, this indicates a more wooded environment for the east of The Netherlands during Late Tiglian times.

With the description of *Glirulus pusillus* in the Tegelen fauna, a second species with its closest relatives in Asia is included in the faunal list. Reumer & van den Hoek Ostende (2003) described a species of *Hylopetes*, a genus of flying squirrels that nowadays lives in southeastern Asia. *Glirulus pusillus* is believed to be the direct ancestor of *G. japonicus*, a Japanese dormouse (Kawamura, 1989).

The connection between the floras of the European Upper Pliocene and the Recent of southeast Asia is well documented. Reid and Reid (1915) defined the Tiglian on the basis of the percentage of so-called Tertiary relicts in the seed flora of the Tegelen Clay. These plants, which have their nearest living relatives in Asia and the southeastern United States, make up a major part of the flora in the Reuverian Clay, become more rare in the Tiglian Clay, and finally disappear from the European flora. A similar pattern seems to exist for some mammals. *Hylopetes debruijni* from Tegelen is the youngest record of its genus in Europe. *Glirulus pusillus* is primarily known from Pliocene localities, surviving into the Early Pleistocene. Though known from localities younger than Tegelen, it too becomes extinct shortly after the Tiglian. Both *Hylopetes* and *Glirulus* are arboreal and their disappearance from Europe may be related to the changes in the flora described above. A third species from the Tiglian with its living relatives in southeastern Asia is *Tapirus arvernensis*. Fossils of this animal were retrieved from the Pit Maalbeek just south of Tegelen, although the exact location of the find is not known (Kortenbout van der Sluijs, 1960). Westerhoff *et al*. (1998) assigned an Early Tiglian age to the sediments in the Pit Maalbeek. *Tapirus* is not known in the extensive collection of the younger Tegelen Clay pits. Thus, this genus to have disappeared earlier than did *Glirulus* and *Hylopetes*, indicating that, like in the flora, there was in the Late Pliocene/ Early Pleistocene a stepwise extinction of taxa which survived in Asia.

Acknowledgements

The SEM-photographs were made by Jeroen Goud, and the plate was assembled by Niko Korenhof. John de Vos (Leiden) commented on the manuscript, as did the referees Dr. Gudrun Daxner-Höck (Vienna) and Prof. Dr. Adam Nadachowski (Krakow). The work of Georgia Hodge and Willem Kakebeke in registering the Tegelen collection is gratefully acknowledged.

References

Bednarczyk, A. 1993. Early Pliocene terrestrial fauna with *Glirulus* (Mammalia) from Pańska Góra (Czestochowa Upland, Poland). *Acta zoologica cracoviensia*, **36** (2): 233-240.

Chaline, J. 1972. Les rongeurs du Pleistocène moyen et supérieur de France. (Systématique, biostratigraphie, paléoclimatologie). *Cahiers de Paléontologie, CNRS, Paris*, 1-410.

Daams, R. & H. de Bruijn 1995. A classification of the Gliridae (Mammalia) on the basis of dental morphology. *Hystrix (N.S.)*, **6** (1-2): 3-50.

Dahlmann, T. 2001. Die Kleinsäuger der unter-pliozänen Fundstelle Wölfersheim in der Wetterau (Mammalia: Lipotyphla, Chiroptera, Rodentia). *Courier Forschungsinstitut Senckenberg*, **227** : 1-129.

Daoud, A. 1993. Evolution of Gliridae (Rodentia, Mammalia) in the Pliocene and Quaternary of Poland. *Acta zoologica cracoviensia*, **36** (2): 199-231.

Dehm, R. 1962. Altpleistocäne Säuger von Schernfeld bei Eichstätt in Bayern. *Mitteilungen Bayerische Staatssammlung für Paläontologie und historische Geologie*, **2**: 17-61.

Fejfar, O. & G. Storch 1990. Eine pliozaene (ober-ruscinische) Kleinsäugerfauna aus Gundersheim, Rheinhessen; 1, Nagetiere; Mammalia, Rodentia. *Senckenbergiana Lethaea*, **71** (1-2) : 139-184.

Freudenthal, M., T. Meijer & A.J. van der Meulen 1976. Preliminary report on a field campaign in the continental Pleistocene of Tegelen (The Netherlands). *Scripta Geologica*, **34**: 1-23.

Heller, F. 1936, Eine oberpliocäne Wirbeltierfauna aus Rheinhessen. *Neues Jahrbuch fuer Mineralogie, Geologie und Palaeontologie. Abhandlungen. Abteilung B*, **76**: 99-160.

Kawamura, Y. 1989. Quaternary rodent faunas in the Japanese islands; Part 2. *Memoirs of the Faculty of Science. Kyoto University. Series of Geology and Mineralogy*, **54** (1-2): 1-235.

Kolfschoten, T. van 1985. The Middle Pleistocene (Saalian) and Late Pleistocene (Weichselian) mammal faunas from Maastricht-Belvédère (Southern Limburg, The Netherlands). *In:* T. van Kolfschoten, W. Roebroeks (eds.) *Maastricht-Belvédère: stratigraphy, palaeoenvironment and archaeology of the Middle and Late Pleistocene deposits. Mededelingen Rijks Geologische Dienst*, **39** (1): 45-74.

Kolfschoten, T. van 1990. The evolution of the mammal fauna in the Netherlands and the Middle Rhine area (western Germany) during the late middle Pleistocene. *Mededelingen Rijks Geologische Dienst*, **43** (3): 1-69.

Kolfschoten, T. van, A.J. van der Meulen & W. Boeningk 1998. The Late Pliocene Rodents (Mammalia) from Frechen (Lower Rhine Basin, Germany). *In:* T. van Kolfschoten, P.L. Gibbard (eds.), *The Dawn of the Quaternary. Proceedings of the SEQS-EuroMam symposium 1996. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, **60**: 161-172.

Kortenbout van der Sluijs 1960. The fossil tapir of Maalbeek, Netherlands. *Publicaties van het Natuurhistorisch Genootschap in Limburg*, **12**: 12-18.

Kowalski, K. 1963. The Pliocene and Pleistocene Gliridae (Mammalia, Rodentia) from Poland. *Acta zoologica cracoviensia*, **8** (14): 532-567.

Kretzoi, M. 1962. Fauna und Faunahorizont von Csarnóta. *Magyar Allami Földtani Intezet Evi Jelentese*: 297-395.

Mais, K. & G. Rabeder 1984. Das große Höhlensystem im Pfaffenberg bie Bad Deutsch-Altenburg (Niederösterreich) und seine fossile Faunen. *Höhle*, **35** (3/4): 213-230.

Mayr, H. 1979. Gebißmorphologische Untersuchungen an miozänen Gliriden Süddeutschlands. *Thesis Ludwig-Maximilians-Universität München*: 1-378.

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*, **17**: 1-144.

Michaux, J. 1970. Les Rongeurs (Arvicolides, Murides et Glirides) de la localite Arondelli a Villafranca d'Asti (Italie). *Palaeontographia Italica*, **66**: 67-80.

Mörs, T, W. von Koenigswald & F. von der Hocht 1998. Rodents (Mammalia) from the late Pliocene Reuver Clay of Hambach (Lower Rhine Embayment, Germany). *In:* T. van Kolfschoten, P.L. Gibbard (eds.), *The Dawn of the Quaternary. Proceedings of the SEQS-EuroMam symposium 1996. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, **60**: 135-160.

Reid, C. & E.M. Reid 1915. The Pliocene flora of the Dutch-Prussian border. *Mededelingen van de Rijksopsporingdienst van Delfstoffen*, **6**: 1-178.

Reumer, J.W.F. 1984. Ruscinian and Early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (the Netherlands) and Hungary. *Scripta Geologica*, **73**: 1-173

Reumer, J.W.F. 2001**.** Gliridae (Mammalia, Rodentia) from the Zuurland boreholes near Rotterdam, the Netherlands. *Deinsea*, **8**: 41-48.

Reumer, J.W.F. & L.W. van den Hoek Ostende 2003 (in press). Petauristidae and Sciuridae (Mammalia, Rodentia) from Tegelen, Zuurland, and the Maasvlakte (the Netherlands). *In:* J.W.F. Reumer, W. Wessels, (eds.), *Migration and distribution of Neogene mammals in Eurasia. Deinsea*, **10**.

Roders, J.T. 1987. Een vergelijking van twee recente populaties van *Talpa europaea* uit Nederland en de beschrijving van een *Talpa*-soort uit Tegelen. *Unpublished thesis Instituut voor Aardwetenschappen, Universiteit Utrecht*: 1-209.

Rümke, C.G. 1985. A review of fossil and recent Desmaninae (Talpidae, Insectivora). *Utrecht Micropaleontological Bulletin, Special Publication.* **4**: 1-241.

Tesakov, A.S. 1998. Voles of the Tegelen fauna. *In:* T. van Kolfschoten, P.L. Gibbard (eds.), *The Dawn of the Quaternary. Proceedings of the SEQS-EuroMam symposium 1996. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO.* **60**: 71-134.

Westerhoff, W.E., P. Cleveringa, T. Meijer, T. van Kolfschoten & W.H. Zagwijn 1998. The Lower Pleistocene fluvial (clay) deposits in the Maalbeek pit near Tegelen, The Netherlands. *In:* T. van Kolfschoten, P.L. Gibbard (eds.) *The Dawn of the Quaternary. Proceedings of the SEQS-EuroMam symposium 1996. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO.* **60**: 35-70.

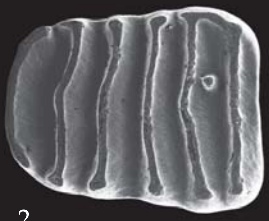
Plate 1

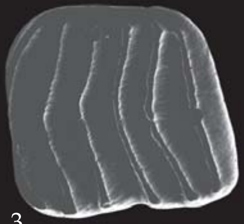
Figs. 1-7. *Muscardinus pliocaenicus* Kowalski, 1963 from the Upper Pliocene of the Russel-Tiglia-Egypte clay pit at Tegelen.
Fig. 1: p4 sin. (RGM 257818)
Fig. 2: m1 sin. (RGM 257754)
Fig. 3: m2 sin. (RGM 257771)
Fig. 4: m3 sin. (RGM 257779)
Fig. 5: M1 sin (RGM 257785)
Fig. 6: M2 dext. (RGM 257788)
Fig. 7: M3 sin (RGM 257789)

Fig. 8-11. *Glirulus pusillus* (Heller, 1936) from the Upper Pliocene of the Russel-Tiglia-Egypte clay pit at Tegelen.
Fig. 8: m2 dext. (RGM 257792)
Fig. 9: m3 dext. (RGM 257793)
Fig. 10: M1 sin. (RGM 257796)
Fig. 11: M2 sin. (RGM 257794)

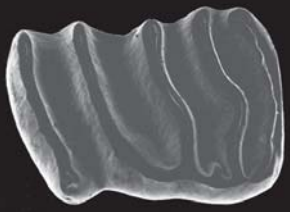
All figure *c.* 20 ×, underlined numbers indicate specimens illustrated in inverse.


1


2


3


4


5


6


7


8


9


10


11

1 mm