

Jelle W.F. Reumer¹ & Lars W. van den Hoek Ostende²

¹ Natuur museum Rotterdam

² Naturalis Leiden

Petauristidae and Sciuridae (Mammalia, Rodentia) from Tegelen, Zuurland, and the Maasvlakte (the Netherlands)

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The number of known sciurid and petauristid fossils from The Netherlands is nearly doubled with the description of material from the Zuurland boreholes, the Maasvlakte, and the Tegelen claypit. The material from Tegelen is assigned to a new species of flying squirrel, *Hylopetes debruijni* nov. sp. One molar from the late Early Pleistocene of the Zuurland borehole is assigned to *Sciurus* cf. *S. vulgaris*. The remaining finds from the Tiglian of the Zuurland boreholes, as well as the single molar from the Maasvlakte, are all assigned to *Spermophilus primigenius*; this name is preferred over the suggestive use of names of recent ground squirrels for fossil material. The presence, during roughly the same stratigraphic interval, of a flying squirrel in Tegelen and of ground squirrels in Zuurland confirms marked differences in the Late Tiglian environments between the east and the west of the Netherlands.

Correspondence: JWFR: Natuur museum Rotterdam, P.O.Box 23452, 3001 KL Rotterdam, the Netherlands, e-mail: reumer@nrmr.nl; LWvdHO: Naturalis, National Museum of Natural History, P.O.Box 9517, 2300 RA Leiden, the Netherlands, e-mail: hoek@naturalis.nmm.nl

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INTRODUCTION

Squirrels are relatively rare in the fossil record of the Plio/Pleistocene of Western Europe. Of course, they are much rarer in the living fauna than are voles or mice, which produce massive offspring each year. Furthermore, as Chaline (1972) suggested, these nimble creatures make a difficult prey to raptors, which limits their chance of being preserved in the fossil record. The first fossil squirrel in The Netherlands was published by Husson & Kortenbout van der Sluijs (1954). They described *Marmota marmota primigenia* from the Weichselian of Cadier en Keer

(province of Limburg). Freudenthal *et al.* (1976) mentioned the presence of *Sciurus* cf. *vulgaris* in the classical Tiglian (Late Pliocene) locality of Tegelen. The other published sciurid finds in The Netherlands all pertain to ground squirrels assigned to *Spermophilus* cf. *undulatus*. The loess and gravel pit of Maastricht Belvédère yielded ground squirrels in two different levels. Two molars were found in the faunal association Belvédère 3, which is assigned to the Saalian, whereas the Weichselian association Belvédère 5 yielded eight molars (van Kolfschoten 1985). The find of a ground

squirrel in Bavel is of a much older age, and is assigned to the Bavelian by van Kolfschoten (1990). The find of *Spermophilus cf. undulatus* on the Maasvlakte was mentioned twice (Vervoort-Kerkhoff & van Kolfschoten 1988, van Kolfschoten & Vervoort-Kerkhoff 1999) but this find has never been adequately described nor illustrated, which renders it unverifiable. In these publications, the ground squirrel is assigned to the Weichselian faunal assemblage of the Maasvlakte. Van Kolfschoten (1988) mentions the presence of *Spermophilus* sp. in the Zuurland-2 borehole at a depth of 62-64 m, again without any description.

The material described in this paper greatly expands the fossil record of the squirrels in The Netherlands. Since the first mentioning of a sciurid in the Zuurland borehole, sampling has continued. Nowadays the Zuurland collections are, next to Tegelen, the largest collection of small mammals from the Netherlands. In this vast collection (>4000 teeth) a total of only six squirrel molars is present, showing the extreme rarity of this group of rodents. Sampling also continued in Tegelen after the publication of the preliminary report by Freudenthal *et al.* (1976). Recently, all of the material from the locality was sorted, which resulted in the find of seventeen squirrel molars. Thus, although the teeth described in this paper are indeed an expansion of the fossil record, the finds from Zuurland and Tegelen also demonstrate the rarity of squirrel fossils. Whereas the collections together hold over 10.000 small mammal fossils, the squirrels comprise less than 0.5 % of these collections.

MATERIAL AND METHODS

Localities

The material described in this paper originates from three localities. One tooth was found by Mr. Andries Schoneveld. It originates from the Maasvlakte, an artificially made extension of the Rotterdam port system, made of suction-dredged sands coming from the

adjacent North Sea; see van Kolfschoten & Vervoort-Kerkhoff (1999). All other teeth come from the Zuurland boreholes and from Tegelen. Although these are the two most important Dutch localities for fossil small mammals, neither fauna has yet been completely described. The Zuurland sites are a series of boreholes set in the Zuurland polder near the city of Brielle, province of South Holland, some 30 km W. of Rotterdam. They are performed by Mr. Leen Hordijk as a private project out of scientific curiosity. By now, nine borings have been set at close range to one another, and sampling still continues. These borings proved extremely successful for retrieving small mammal molars, as well as other fossils such as molluscs and seeds.

As far as the small mammals are concerned, papers have appeared on *Allophaiomys* (van Kolfschoten 1998), *Mimomys hordijkii* (van Kolfschoten & Tesakov 1998), the Insectivora (Reumer & Hordijk 1999), the Gliridae (Reumer 2001), and the Muridae (Reumer 2003). The voles, which make up the major part of the collection, have only been published from borehole Zuurland-1 and part of Zuurland-2 (van Kolfschoten 1988). The reader is referred to Reumer & Hordijk (1999) for general information on the boreholes. In the present paper, the provenance of the material is indicated by the letter Z for Zuurland, the number of the borehole, followed by the depth in metres. E.g., Z4/62.85-64 means that the material originates from borehole Zuurland-4, at a depth of 62.85 to 64 m.

The material from Tegelen was collected in the 1970's in a series of campaigns performed by the former Rijksmuseum of Geologie en Mineralogie (RGM), now part of Naturalis. A preliminary faunal list was published by Freudenthal *et al.* (1976), where also general information on the locality can be found. Publications about the small mammals from Tegelen have appeared on the Soricidae (Reumer 1984), the Desmaninae (Rümke 1985), and the Arvicolidae (Tesakov 1998). Only recently, in 2001, all of the mate-

rial from the Tegelen campaigns has been sorted out.

Methodology

The terminology for parts of molars follows Cuenca Bescos (1988). The molars were measured based on the method indicated by van de Weerd (1976). Unfortunately, van de Weerd presented drawings from his method of measuring only. This leaves room for interpretation, particularly when measuring molars from another genus (Van de Weerd used *Spermophilinus* to demonstrate his method). Therefore a method of measuring should also include a description of the criteria according to which a molar was orientated. We have interpreted the measurement method of van de Weerd as follows:

- m1, m2, and m3 were orientated using the slightly undulating front of the molar, by lining up the two outermost points of the molar;
- P4, M1 and M2 were orientated using the undulating buccal side, by lining up the

flank of the paracone and metacone. Note that these are not always the outermost points of the molars, the mesostyle may protrude further.

- p4 (not indicated by van de Weerd) and M3 are not orientated as readily. The elements were orientated using a tangent along the hindmost (p4) or frontmost (M3) part of the (pre)molar. This method is more imprecise in that there is room for interpretation when determining the point along which to place the tangent. After the element has been orientated, length and width were taken at right angles.

All measurements in this paper are given in millimetres.

TAXONOMY

Order Rodentia

Family Petauristidae

Genus *Hylopetes* THOMAS, 1908

Hylopetes debrijni nov. sp. (Plate I)

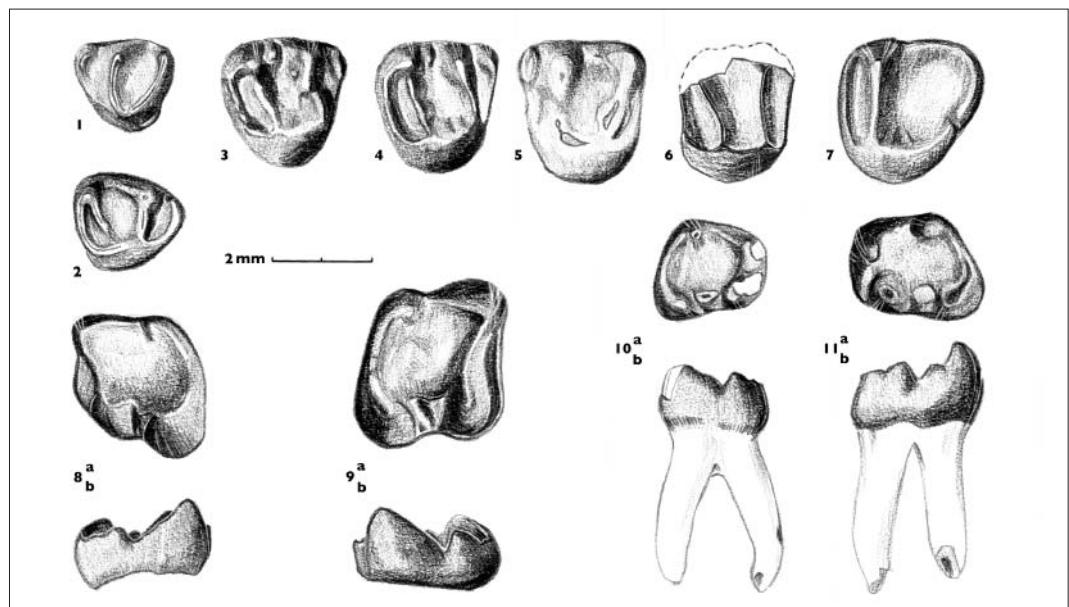


Plate I *Hylopetes debrijni* nov. sp., Tegelen, in **a**: occlusal views, **b**: lingual views. **1**: dP4 sin., RGM 257805; **2**: dP4 dex., RGM 257806; **3**: P4 dex., RGM 257804; **4**: P4 dex., RGM 179055; **5**: P4 sin., RGM 257803; **6**: M2 dex., RGM 235669, buccal contour restored; **7**: M3 sin., RGM 257808; **8ab**: m1 sin., RGM 257810; **9ab**: m2 dex., RGM 257813; **10ab**: p4 dex., RGM 235667; **11ab**: p4 sin., RGM 235668. Bar = 2 mm.

Synonymy *Sciurus cf. vulgaris* from Tegelen, in: Freudenthal *et al.* 1976, plate 2, fig. 1. *Sciurus warthae* from Wölfersheim, in: Dahlmann 2001, plate 7, figs 20-27. Sciuridae indet. 1 from Wölfersheim, in: Dahlmann 2001, plate 10, fig. 4.

Derivatio nominis The species is named in honour of Dr. Hans de Bruijn, who contributed greatly to the knowledge of fossil Petauristidae.

Diagnosis A large species of *Hylopites*, upper premolars with a well individualized mesostyle, no accessory ridges in the upper (pre)molars, lower molars with a well developed anterolophid, enamel at most only slightly wrinkled.

Differential diagnosis From *H. hungaricus*, *H. macedoniensis*, and *H. hoeckearum* our new species differs by being considerably larger, and by having almost no enamel wrinkling.

Holotype m2 dex. RGM 257813, Plate 1, figure 9ab; L= 2.92; W= 3.26

Type locality Russel-Tiglia-Egypte clay pit, Tegelen, Province of Limburg, The Netherlands (Tiglian, MN17).

Other known occurrence Wölfersheim (Wetterau, Germany, Late MN15)

Known stratigraphic range MN 15- MN 17

Description of the holotype The molar is somewhat wider than it is long. The enamel is slightly crenulated, particularly in the central basin. The metaconid is the highest cusp. Protoconid, entoconid and hypoconid are clearly lower, and are all of about similar height. The metaconid and protoconid are connected by a slightly curved metalophid. A small and low mesoconid lies between the protoconid and hypoconid. The buccal side is emarginated off the position of the mesoconid. The

anterior cingulum is conspicuous and bears a low anterolophid. At the buccal side the cingulum becomes thinner as it rounds the base of the protoconid. Metaconid and entoconid are separated by a sharp notch. The anterior face of the entoconid is round. The hypoconid is sub-equal in size to the metaconid. The hypoconid and entoconid are connected by a continuous posterolophid.

Material and measurements

DP4 dex. RGM 257806; L= 2.12, W= 1.99
 (Plate 1, fig. 2)
 DP4 sin. RGM 257805; L= 1.88, W= 1.85
 (Plate 1, fig. 1)
 DP4 sin. RGM 257807; L= 1.75, W= 1.67
 P4 dex. RGM 179055; L= 2.39, W= 2.58
 (Plate 1, fig. 4, also depicted in Freudenthal *et al.* 1976, plate 2, fig. 1)
 P4 dex. RGM 257804; L= 2.43, W= 2.46
 (Plate 1, fig. 3)
 P4 sin. RGM 257803; L= 2.42, W= 2.75
 (Plate 1, fig. 5)
 M2 dex. RGM 235669; L= -, W= - (Plate 1, fig. 6)
 M3 dex. RGM 257809; L= 2.85, W= 2.69
 M3 sin. RGM 257808; L= 2.86, W= 2.80
 (Plate 1, fig. 7)
 p4 sin. RGM 257802; L= 2.21, W= 2.25
 p4 sin. RGM 235668; L= 2.48, W= 2.21
 (Plate 1, fig. 11ab)
 p4 dex. RGM 235667; L= 2.06, W= 2.11
 (Plate 1, fig. 10ab)
 m1 sin. RGM 257.810; L= 2.56, W= 2.89
 (Plate 1, fig. 8ab)
 m1 sin. RGM 257.812; L= -, W= -
 m1 dex. RGM 257811; L= -, W= -
 m2 dex. RGM 257813; L= 2.92, W= 3.26
 (Plate 1, fig. 9ab, holotype)
 m3 dex. RGM 179056; L= -, W= -

Description

DP4 Two of the three available DP4 are somewhat abraded through acid and/or resorption. The milk molar has a triangular occlusal outline. The protocone is the largest cusp. The parastyle is a low cusp at the end

of a large anterior shelf. It is connected to the protocone by a low anteroloph. The buccal cusps are of similar size, the paracone being slightly larger. Halfway between the paracone and the metacone lies a tiny mesostyle, with spurs from the two main buccal cusps running towards it. The protoloph and metaloph converge towards the protocone, even leading to a marked V-shaped pattern in one of the specimens (Plate 1, fig. 1). The protoloph is continuous; the metaloph is interrupted just before reaching the protocone in two out of the three specimens. The least abraded specimen (Plate 1, fig. 2) shows a low but distinct posteroloph bordering the posterior basin. In the abraded specimens the posteroloph is very faint.

P4 The three P4 found of this species show considerable morphological variation. The premolar is molariform, so much so that the largest, heavily abraded specimen (Plate 1, fig. 5) was first mistaken for an M1. The protocone is the largest cusp. The parastyle is transversely elongated. It is separated from the paracone by a deep valley. The anteroloph is sharp in one specimen, faint in the other two, in which the parastyle is more or less individualised. The paracone and the metacone are of the same height, but the latter cusp is smaller than the paracone. Between the paracone and the metacone lies a small, conical mesostyle, closer to the metacone than to the paracone. Deep and narrow valleys separate the mesostyle from the paracone and the metacone. The protoloph and metaloph stand far apart and are parallel to each other. The metaloph is clearly thicker than the protoloph, with thinner sections where it connects to the metacone and protocone respectively. In one specimen (Plate 1, fig. 3) the protoloph consists of two parts, starting at the protocone and paracone respectively. These two ridges meet at the middle of the premolar and touch at their edges only, as if the protoloph had been broken with one part displaced laterally. This constricted protoloph is also observed in *H. macedoniensis* (see e.g. de Bruijn,

1995, Plate 3, fig. 14). The specimen with a well-developed anteroloph (Plate 1, fig. 4) also has a well-developed posteroloph. In the other two specimens the posteroloph is weaker.

M2 The molar (Plate 1, fig. 6) is heavily damaged, lacking the area around the metacone, part of the paracone, and the parastyle. The lingual side is relatively straight. It is completely occupied by the protocone. The protoloph and metaloph are rather sharp. The protoloph is straight and slopes up to the tip of the paracone. The first part of the metaloph runs parallel to the protoloph. After that, the metaloph bends in the direction of the posterobuccal corner of the molar and becomes somewhat thicker. The anteroloph and posteroloph are lower than the central ridges. The anterior basin is about half the length of the central basin. The posterior basin is about the same width near the protocone, but becomes narrower due to the bending of the metaloph.

M3 The protocone is very large, occupying the lingual part of the molar. The only other cusp is the paracone, which is somewhat elongated. The protocone and paracone are connected by a well-developed protoloph. In front of the protoloph lies a shelf, bearing an anteroloph which is thickest near the paracone. The largest part of the molar consists of the central basin, which is bordered by a posterior rim, which is highest in the posterobuccal corner of the M3. The rim is weakly interrupted at the buccal side behind the paracone. There is a notch in the rim at the posterolinguinal side of the molar.

p4 Two of the three p4's are preserved with the two sturdy roots intact. The posterior root is only slightly thicker than the anterior one. The anterior side of the premolar is somewhat narrower than the posterior side. The enamel in the central basin is slightly wrinkled in RGM 235667 (Plate 1, fig. 10ab). In the other two, more worn specimens, these cre-

nulations can no longer be observed. The metaconid is the highest cuspid. Its tip is slightly inclined towards the central basin. A low and elongated mesoconid lies between the protoconid and the hypoconid. In one specimen the protoconid lies directly adjacent to the metaconid. The other two specimens have a very short metalophid. These two specimens have an anterior cingulum, which is completely occupied by the rather thick anterolophid. The anterior cingulum is lacking in the third specimen. In RGM 235668 (Plate 1, fig. 11ab) the mesolophid has developed like a cuspid directly adjacent to the metaconid rather than a loph; in RGM 235667 it is more ridge-shaped. This area is damaged in the third specimen (RGM 257802, not depicted). There is a narrow valley just in front of the entoconid. The anterior face of the entoconid, which is much smaller than the other main cusps, is rounded. The continuous posterolophid borders the central basin at the back.

m1 Only one of the three m1's (RGM 257810, Plate 1, fig. 8ab) has been preserved intact. RGM 257812 is very much abraded due to acid, whereas RGM 257811 is damaged, with the metaconid and hypoconid lacking a large part of their lingual side and buccal side, respectively. The latter, unworn, m1 is the only specimen that shows extensive crenulations in the central basin. The anterior side of the molar is narrower than the posterior side. The metaconid is the highest cuspid. The protoconid, the hypoconid and the entoconid are somewhat lower, and all of about the same height. The mesoconid is low and elongated, and is separated from the protoconid and hypoconid by two notches at the buccal side. The metaconid and protoconid are connected by a curved metalophid. The anterior cingulum is wide and bears a low anterolophid. The metaconid and the entoconid are separated by a clear notch just in front of the latter cusp. The mesolophid is completely incorporated in the posterior arm of the metaconid. The anterior side of the entoconid is rounded. The hypoconid and entoconid are

connected by a continuous posterolophid.

m2 See description of the holotype. Only one m2 of this species was found.

m3 The only available m3 is damaged, lacking the area around the metaconid. The cusps are low. The protoconid is conical. A low metalophid runs from the protoconid in the direction of the metaconid. In front of the protoconid is a very narrow and faint anterior cingulum. The mesoconid is elongated and very low. The hypoconid and entoconid are completely incorporated in the thick posterolophid. Just in front of the entoconid, and separated from it by a shallow valley, a remnant of the mesolophid is preserved.

Remarks

Pliocene and Pleistocene flying squirrels are rare. So far no Pleistocene flying squirrels have been reported from the Netherlands, and only very few from the adjacent regions.

There are some Pliocene finds from the region though. Flying squirrels are known for the Upper Pliocene Reuver clay. An m3 of *Blackia* was found in the locality of Frechen (van Kolfschoten *et al.* 1998) and the locality of Hambach even yielded four species of flying squirrel, *Plionpetaurista plioacaenica*, *Blackia* aff. *woelfersheimensis*, *Hylopites hungaricus* and *Petauristinae* gen. et sp. indet. (Mörs *et al.* 1998; possibly three species only as we suspect that their

Petauristinae gen. et sp. indet. in fact also belongs to the *Hylopites*; Mörs 2002 gives a slightly different list comprising four species from Frechen and Hambach combined).

Morphologically, the species from Tegelen is closest to genera like *Blackia* and *Hylopites*. However, these are always very small species, much smaller than our material. *Blackia* is moreover provided with heavily wrinkled teeth. Although much larger than any known fossil *Hylopites*, comparison with photographs like the ones of *H. macedoniensis* given by de Bruijn (1995; pl 3, figs. 12-21) leave little doubt that our species

should be assigned to that genus. It shares with the other *Hylopotes* species the molariform P4 and the relatively small milk molar. Moreover, Recent *Hylopetes* from Asia are considerably larger than the fossil European representatives of this genus (we here follow the congruity proposed by Bouwens & de Bruijn 1986), suggesting that size does not really matter here. Molars of the larger flying squirrels, like those of the genera *Pliopetaurista* and *Petauria*, all have dental patterns which are far more complicated than found in the Tegelen species.

In the literature (Dahlmann 2001) we came across a published series of sciuroid molars from Wölfersheim (Wetterau, Germany). Dahlmann (2001) identified most of these molars as *Sciurus warthae* SULIMSKI 1964. The similarity with our Tegelen *Hylopetes* is so striking, that we cannot but consider the Wölfersheim material to belong to the same species of flying squirrel. Dahlmann's sample apparently lacked a P4, but the other elements (Dahlmann 2001, plate 7, figs 20-27) are morphologically identical to our Tegelen material. Also the sizes are similar (provided that the measurements given for his DP4: L= 1.14 mm, W= 1.04 mm are mistaken and should read L= 2.14 mm and W= 2.04 mm, respectively; this conforms the depicted DP4 in Dahlmann's plate 7 fig. 20 and the 1 mm reference bar in the same plate). The P4 missing from Dahlmann's sample is found in his plate 10 fig. 4. This tooth was published as an M1 of "Sciuridae indet. 1"; it is however a P4 and comparison of this tooth with our P4's (Plate 1, figs 3-5) shows the striking resemblance. This also applies to the sizes. We are therefore quite certain that *Hylopetes debruijni* nov. sp. also occurs in the Late Ruscinian (Late MN15) of Wölfersheim.

This discovery (a *Hylopetes* published as *Sciurus warthae*; i.e. a petauristid published as a sciurid) suggests that it is not impossible that more often flying squirrels are overlooked. The recognition and hence the taxonomy of fossil sciurids and petauristids is quite complicated and probably many correc-

tions should be made, which is however beyond the scope of the present paper.

Family Sciuridae
Genus *Sciurus* LINNAEUS, 1758

***Sciurus* sp. indet.** (Plate 2, fig. 1ab)

Material and measurements

1 m3 dex., Z6/38-39; L= 2.95, W= 2.53.

Description

The available m3 is moderately worn. Its roots are broken off except for the anterolinguinal root; the posterior root appears to have been divided in a larger posterobuccal one and a smaller posterolingual one. The metaconid is the highest cuspid, between it and the poorly individualised entoconid there is a narrow valley dividing the lingual rim. Between the protoconid and the hypoconid there is a lower mesoconid, separated from the two cuspids by valleys forming a V-shaped pattern on the buccal side of the tooth. A small sulcus anteriorly of the metalophid is the remnant of the trigonid basin.

Remarks

The m3 from Z6/38-39 is the only *Sciurus* thus far discovered from the rich Zuurland small mammal collection. It is from the 38-39 m levels, tentatively assigned to the Eburonian or Early Waalian (Reumer 2003). The fossil record of the genus *Sciurus* is not extremely abundant. Faunal assemblages rarely contain more than one or two molars. Few species of fossil *Sciurus* have been described from Europe. One of these, *S. whitei*, should be regarded with caution. This rather enigmatic species was described on the basis of a single P4 from the Upper Freshwater-Bed at West Runton, England by Hinton (1914). Hinton comments on this P4: "It differs importantly from the P4 of *S. vulgaris*, and indicates a species which, when more fully known, will probably not be able to find a place within the genus *Sciurus* as restricted by modern mammalogists."

Sciurus whitei is ill-defined. Nevertheless the name is sometimes used to indicate small-sized squirrels from the Early Pleistocene of e.g. Tarkö and Untermassfeld (Jánossy 1962; Maul 2001).

Another fossil species placed in *Sciurus* is *S. warthae*, described by Sulimski (1964) from the Pliocene locality of Weze 1 (Poland). Comparison of the measurements of *S. vulgaris* (from own observation) with those from *S. warthae* (Sulimski 1964, table 4) show that the sizes of the lower dentition largely overlap. The only exception is the m3, which shows a relatively larger length for *S. warthae*, and a smaller width. The likely presence of a small posterolingual root could favour an allocation to *S. warthae*. Such a root is rare in the recent species of *Sciurus*, but was described for the fossil species by Sulimski (1964). Comparison (own observation) with the measurements for *Sciurus vulgaris* shows that the length for the Zuurland m3 falls in the uppermost reaches of the range of that spe-

cies. Because we have only one tooth, identification down to species level does not seem justified, so we decided to identify our late Early Pleistocene tooth from Zuurland as *Sciurus* sp. indet.

Genus *Spermophilus* CUVIER, 1825

***Spermophilus primigenius* (KORMOS, 1934)** (Plate 2, figs 2-5)

Material and measurements

- 1 DP4 sin. from Z2/63-64; L= 2.17, W= 2.08
- 1 M1/2 dex. from Z2/64-65; L= 2.73, W= 3.17
- 1 M1/2 sin. from Z5/62.9-64; L= 2.75, W= - (Plate 2, fig. 5)
- 1 m2 sin. from Z2/65-66; L= 2.95, W= 3.97 (Plate 2, fig. 4ab)
- 1 m2 sin. from Z5/64-65; L= 3.04, W = 3.64 (Plate 2, fig. 3ab)
- 1 m3 sin. from the Maasvlakte; L= 3.95, W= 3.29 (Plate 2, fig. 2ab)

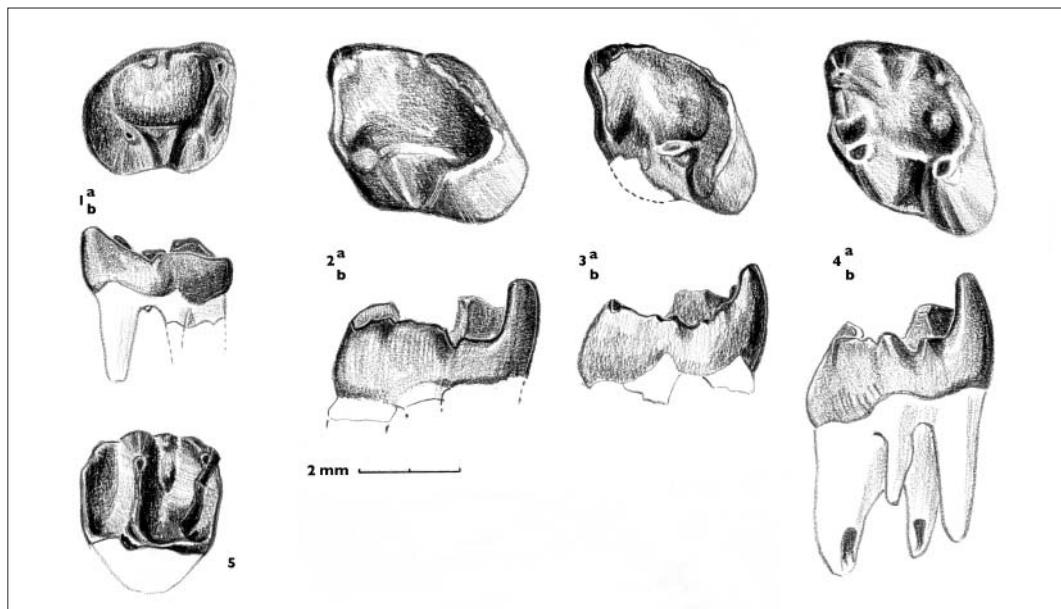


Plate 2. *Sciurus* sp. indet. 1: m3 dex., Zuurland 6/38-39. 1a: occlusal view, 1b: lingual view. *Spermophilus primigenius*. 2: m3 sin., Maasvlakte; 3: m2 sin., Zuurland 5/64-65; 4: m2 sin., Zuurland 2/65-66; all same views as 1; 5: M1/2 sin., Zuurland 5/62.90-64, occlusal view, lingual contour restored. Bar = 2 mm.

Description

DP4 The tooth has partly lost its enamel as a result of (postsedimentary?) solution. The protocone is the highest cusp; it is connected by a V-shaped loph-pattern to both paracone and metacone. The anterior flange shows a valley that is wider than the trigon basin, hence the distance parastyle-paracone is slightly larger than the distance paracone-metacone. Behind the metaloph a low cingulum is present. There are no other cuspules present.

M1/2 There are two teeth that can be identified as M1/2. One is a heavily worn right molar, the other is a left molar that has its lingual part broken off, but that is otherwise unworn, apparently of a juvenile or semi-adult specimen, and showing great morphological detail (Plate 2, fig. 5). The protocone is the highest point of the U-shaped structure joining the paracone, the protocone and the posterior cingulum. The metacone is connected to the protocone by a sharp ridge bearing a secondary cuspule (metaconule) that is, however, poorly individualised. On the bottom of the trigon basin we find two tiny cuspules; the buccalmost of which can be considered the mesostyle. Anterior of the protoloph there is a pronounced cingular ridge ending in the parastyle. This ridge is separated from the protoloph by a wide valley and in fact forms a third transverse ridge. A small cuspule with a size like that of the mesostyle is situated at its buccal end. The other, complete but worn, M1/2 has similar morphology, only the anterior cingular ridge is less pronounced. A small mesostyle was present between paracone and metacone.

m2 The metaconid is the highest cusp of this -in occlusal view- lozenge-shaped tooth, followed by protoconid, hypoconid and entoconid. In lingual view the metaconid is high and hook-like (Plate 2, figs. 3b, 4b). Protoconid and hypoconid are connected by a low but conspicuous ridge, that has acquires a cusp-

like swelling in one of the teeth (Plate 2, fig. 3). The posterolophid, enclosing the tooth basin at its posterior end, has a pearl-chain like rim. Between entoconid and metaconid there is a conspicuous cuspid, separated by a valley from the entoconid in one of the teeth (Plate 2, fig. 4), this situation is not developed in the other one. Another cuspid is present between the metaconid and protoconid on the anterior rim of the molar of one tooth (Plate 2, fig. 4), this is what Kormos (1934) calls the paraconid.

m3 The only available m3 (from the Maasvlakte, Plate 2, fig. 2ab) shows a morphology that is principally identical to that of the m2. The tooth is somewhat more elongate, has a longer ridge between protoconid and hypoconid and has no paraconid-like cusp between metaconid and protoconid. Like in m2, the posterior margin (hypolophid) shows a pearl-chain like rim.

Remarks

When comparing our Zuurland and Maasvlakte *Spermophilus* to recent Eurasian ground squirrel material, it can be concluded that it is of about equal size as middle-sized species such as *S. undulatus* (PALLAS, 1778) or *S. xanthoprymnus* (BENNETT, 1835), and considerably smaller than e.g. *S. fulvus* (LICHENSTEIN, 1823). When studying the dentition of recent *Spermophilus* species it can be noted that the morphology of the teeth is highly variable, within certain limits of course, but such features as absence/presence of small cuspules or the development of the rudimentary trigonid basin in lower molars varies considerably within species. Between species there is a great overlap in sizes. It is therefore extremely difficult, if not impossible, to unambiguously distinguish between recent species on the basis of molars only. A detached M1/2 from - for example - *S. undulatus* or *S. xanthoprymnus* can not be identified down to the species level with absolute certainty.

Earlier finds of *Spermophilus* in The

Netherlands from the Middle and Late Pleistocene of Maastricht Belvédère (van Kolfschoten 1985) and the late Early Pleistocene of Bavel (van Kolfschoten 1990) were all published as *S. cf. undulatus*. It is, however, not advisable to designate an Early Pleistocene ground squirrel from The Netherlands with the name of a Recent species from Kazakhstan, Transbaikalia, Northern Mongolia and Northern China, since this would falsely suggest conspecificity of the two. From the European Early Pleistocene the species *S. primigenius* was described by Kormos (1934). His description (Kormos, 1934: 315) comes close to our material, although in the Hungarian material the paraconid seems better developed. *S. primigenius* has since been reported from quite a number of Late Pliocene and Early Pleistocene (Villányian, Biharian) localities, especially in Central Europe. Jánossy (1986) mentions Villány 3, Osztramos 3, Villány 5, Nagyharsányhegy 2 (type locality), Somssichhegy 2, Villány 6, Villány 8. Of these, Villány 3 and 5 and Osztramos 3 are considered more or less contemporaneous with the classic Tegelen locality (Freudenthal et al. 1976), which in its turn has been correlated with the Zuurland interval 62–66 m by Tesakov (1998). Nagyharsányhegy 2 is only slightly younger (Jánossy 1986).

S. primigenius has furthermore been found in such Early Pleistocene localities as Izvoru 2 (Romania; Radulesco & Samson 1986) and Betfia 8 (Romania; Terzea & Jurcsák 1976). It has also been reported from Middle and Late Pleistocene localities in England (Sutcliffe & Kowalski 1976). The Middle and Late Pleistocene *S. cf. undulatus* from Belvédère 3 and 5 are possibly also better assigned to *S. primigenius*; the sizes are identical to our material as can be judged from the measurements given by van Kolfschoten (1985: 50). The Belvédère M1/2's are lacking the small mesostyles but otherwise closely resemble the Zuurland squirrels. The same reasoning applies to the P4 from Bavel (van Kolfschoten 1990).

It is, summarising, in our opinion unwarranted to synonymise a fossil Dutch tooth with a Recent species from Eastern Siberia. Thus the denomination *S. primigenius* for the Tiglian squirrels from Zuurland and for the material from the Maasvlakte and other Pleistocene localities seems the best choice.

DISCUSSION

With the exception of the *Sciurus* m3, all sciurid molars from the Zuurland boreholes were retrieved from the 62–66 m trajectory. This part of the section has been correlated with Tegelen by Tesakov (1998). However, in this trajectory *Allophaiomys* has also been found (van Kolfschoten 1988; 1998). Van Kolfschoten considered the presence of *Allophaiomys* in a Late Villányian assemblage ‘remarkable if not improbable’ and ‘does not exclude that these came from a higher level’. Although van Kolfschoten (1998) states that ‘a few molars referred to *Allophaiomys* have been found at a depth between 62 and 66 m’, he ten years earlier (van Kolfschoten 1988) already identified 26 molars of *Allophaiomys* from this level in the Zuurland 2 borehole alone. Contamination or reworking is, however, unlikely in the Zuurland sampling method. It seems strange to publish 26 molars in 1988, and call this number ‘a few’ in 1998, followed by the suggestion that they ‘should be discarded’. Nevertheless, the presence of *Allophaiomys* in the 62–66 trajectory is problematic. However, since a Late Tiglian age for this trajectory is confirmed by the pollen record (De Jong 1988), the mollusc record (Meijer 1988), and by the arvicolidids (Tesakov 1998), there seems no reason to doubt the correlation to the Late Tiglian.

The sciurid assemblages from the Late Tiglian of Zuurland and Tegelen are remarkably different. In Zuurland only ground squirrels have been found, whereas the Tegelen assemblage consists of a flying squirrel only! This would suggest a rather different environment for the two localities, in which Tegelen represents a forested paleoenvironment whe-

reas the landscape was far more open near Zuurland. In other rodent groups we also find differences. Tegelen and Zuurland share the glirid *Muscardinus pliocaenicus*. Apart from this, in Zuurland *Eliomys briellensis* was found (Reumer 2001), whereas Tegelen has a *Glirulus* as second glirid species (own observation). *Apodemus*, which makes up more than 20 % of the Tegelen collection, is extremely rare in the Zuurland 62-66 m levels (Reumer 2003). Unfortunately, the vole assemblages of Tegelen and Zuurland cannot be compared, since the latter has yet to be fully published. There are, however, already some differences apparent from the preliminary result of the Zuurland 2 borehole (Van Kolfschoten 1988). Here *Mimomys pitymyoides* was found in a relatively small sample, whereas the species is extremely rare in the Tegelen fauna. This opens the possibility that the distribution of *Allophaiomys* too is partly environmentally controlled.

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