Cour. Forsch.-Inst. Senckenberg | 256 | 291–304 | 4 Figs, 1 Tab. | Frankfurt a. M., 15. 11. 2006

A century of research on the classical locality of Tegelen (province of Limburg, The Netherlands)

With 4 figs, 1 tab.

Lars W. van den Hoek Ostende & John de Vos

Abstract

In 1904 Eugène Dubois published the first report on fossil mammals from the vicinity of Tegelen. After a century of research the clay-pits from the area are known as a classical locality for Villafranchian mammals. Antje Schreuder's work was particularly important for making the fossils from Tegelen known. Her papers, however, also indicate some problems. The large mammal fossils were gathered by clay-workers in the local ceramic industry, and the fragmentary nature of the fossils is partly caused by injudicious handling while extracting the bones from the clay. Because the Tegelen fossils are chance finds rather than the results of careful excavations, their exact provenance is not established. The only exception is the collection of micromammals, which was gathered by Thijs Freudenthal during expeditions in the 1970s. Large size variation in the cats and hyenas, and the presumed presence of *Stephanorhinus kirchbergensis* cast doubt on to whether the fossils from Tegelen represent a single time frame.

Key words: Tegelen, Villafranchian, fossil mammals, faunal list

Introduction

The locality is the most important entity in mammal palaeontology. A species is a concept, subject to the interpretation of scholars, and can often change as the available material is revised. A locality, in contrast, is real. It is a place where you can get your hands dirty while unearthing fossil bones. To the palaeontologist it also represents a window to the past, a stage in evolution, allowing a glimpse to a particular time frame.

By placing the localities of a particular area in stratigraphical order, we obtain a picture of the regional development. Comparing localities from different areas, particularly if supplemented with radiometric dates and/or palaeomagnetic sequences, we can come to interregional correlations. Thousands of localities of different time frames are known all over the world by now. Ideally, a palaeontologist should take as many localities as possible into account when reconstructing the history of life. This raises, however, many practical problems, particularly when dealing with localities outside ones area of study. Therefore, interregional correlations are often based on the comparison with classical localities. This is, for instance, the basis for the subdivision of the Neogene and Paleogene into MN-zones (Mein 1975, de Bruijn et al. 1992) and MP-zones (Schmidt-Kittler 1987), respectively. The reference localities for these zones are the ones best studied and most cited in the literature, and which are believed to be best known to all the scholars interested in that particular time frame.

There are clear advantages in choosing well-known localities in schemes for interregional correlations. However, there are drawbacks as well. Many of these classical localities were excavated in earlier times without the scrutiny and sophistication used in modern excavations. Material from neighbouring sites, but from different levels, may have been entered in museum collections under the same locality name. Herein lies the importance of re-excavating

Authors' address: Dr. Lars van den Hoek Ostende & Dr. John de Vos, Nationaal Natuurhistorisch Museum Naturalis, P.O. Box 9517, 2300 RA Leiden, The Netherlands, <Hoek@Naturalis.nl>, <Vos@Naturalis.nl>

classical sites such as Senèze (Delson et al. 2004) and St. Vallier (Debard et al. 1994, Valli 2001). However, many classical localities are no longer accessible or have been exhausted. They can still be studied from the material saved in (museum) collections. In these cases knowing the history of the collection is essential. The method of excavation, the material's original state of preservation, the way of processing the finds, and even what has happened with the material after it has been stored, they can all influence our interpretation of a fossil collection.

In this article we discuss such a classical locality that is no longer available for further excavations. The clay pits near the Dutch village of Tegelen (province of Limburg) are known for over a century to yield fossil remains of mammals (Dubois 1904). When Reid & Reid (1915) established the Tiglian on the basis of the seed flora from the locality, the pits became a type locality for a chronostratigraphic unit that is still widely used. Its reputation as a classical locality was strengthened when, next to the large mammals and seeds, also the pollen (Zagwijn 1963) and micromammals (Freudenthal et al. 1976) were studied. Although the Tegelen fauna has been the subject of numerous studies over the years (e.g. Reumer 1984, Spaan 1992, Tesakov 1998, Reumer & van den Hoek Ostende 2003, van den Hoek Ostende 2003, O'Regan & Turner 2004), no recent overview of the entire fauna has been given, with the exception of an exhibition guide (van den Hoek Ostende 1990) and a popular article (Vervoort-Kerkhoff & van Kolfschoten 1987), both in Dutch and therefore not widely accessible to the scientific community.

In this paper we give a review of the results of a hundred years of palaeontological research in the Tegelen clay pits, to show how we reached our present state of knowledge. The history of the research has been extensively dealt with elsewhere (Zagwijn 1998, van den Hoek Ostende 2004), but since knowledge of the history of the collections is vital for understanding the fauna, it is shortly reiterated here.

The Tegelen Clay

The clay-beds near Tegelen are known since Roman times. The village even owns its name to the Latin word for tile, *tegula*. Tegelen had a flourishing ceramic industry. Till the end of the 19th century its main products were household pottery, but as the pottery shops were out-competed by cheaper alternatives, the industry shifted to the production of tiles and (chimney) bricks. Because the clay from the Tegelen region proved very suitable for these high-quality products, it was extensively exploited. During these excavations, which in the first part of the 20th century were done by manual labour, bones were regularly encountered by the clay-workers. Hence, Tegelen owns its reputation as a fossil mammal locality to the exploitation for the ceramic industry.

Not all of the clay-beds in the region are of the same age. A bluish clay with intercalated lignite beds outcrops near Reuver, a few kilometres to the south of Tegelen. Based on the seed flora, Reid & Reid (1915) showed that this clay is clearly older than that near Tegelen. The Reuver Clay lies in the upper part of the Kieseloolite Formation, which is constituted by Upper Pliocene fluvial sediments. The Kieseloolite Formation is overlain by the recently introduced Waalre Formation, which includes the former Tegelen Formation together with the 'Rhine'part of the former Kedichem Formation (Weerts et al. 2003). The Waalre Formation, which in the vicinity of Tegelen consists of fluvial sediments, was deposited in the Late Pliocene[1] and Early Pleistocene by the Rhine-Meuse system. The basis of the formation in the region consists of gravels and sands, while it is capped by clay layers that seem to be a mixture of channel fills and laterally extending floodplain clays (Westerhoff et al. 1998). These clays are certainly not all of the same age. The exposures in the Maalbeek pit were shown to be older than those in the former pits in the direct vicinity of Tegelen (Westerhoff et al. 1998), an age difference that had already been assumed from the presence of tapir and mastodont remains in the pit. An array of northwest to southeast-ranging major and minor faults complicates the geology of the region (fig. 1). One of these structures, called the Tegelen fault, runs between the Maalbeek pit and the other Tegelen pits. Also, the clay beds in the pits near Tegelen itself belong to different sedimentary cycles. This is most apparent in the pit Russel-Tiglia-Egypte, where a stream gully cuts through the underlying clay beds. Although Kortenbout van der Sluijs & Zagwijn (1962: 32) admitted that "a certain stratigraphic gap between the two cycles may be present", it is clear that they did not consider this gap to be very large. The basis of the stream gully infilling consists of sandy clay with a high amount of plant remains. According to Kortenbout van der Sluijs & Zagwijn (1962), similar sandy beds were found at the base of the clay in the Canoy-Herfskens pits, formerly called the Russel-Tiglia-pit, and the Russell-Tiglia-Wambach-pit, indicating that the clay in these pits would be of the same age as the gully infilling in the Russel-Tiglia-Egypte pit. This, of course, is a very rough correlation of the clay beds and should be regarded as a preliminary assessment. Kortenbout van der Sluijs intended to study the various clay-beds for his PhD-thesis, which, however, never appeared. That the method is prone to error is shown by the correlation of the Maalbeek pit, the sediments of which Kortenbout van der Sluijs & Zagwijn (1962) believed to be younger than those in the Russel-Tiglia-Egypte pit, whereas they are in fact older (Westerhoff et al. 1998). Nevertheless, Kortenbout van der Sluijs & Zagwijn's (1962) descrip-

[1]The Plio-Pleistocene boundary used in this article follows the GTS. This may account for some differences with particularly Dutch literature, in which this boundary is placed earlier.

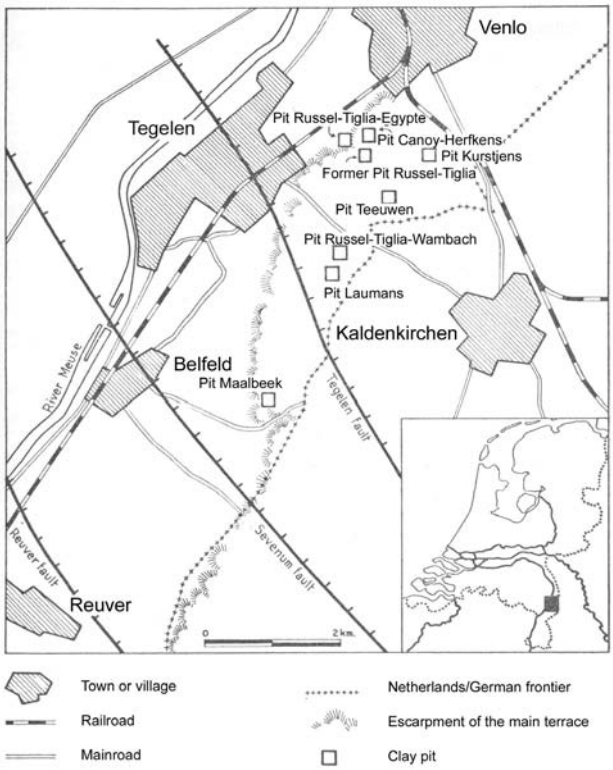

Fig. 1: The location of the various clay pits near Tegelen (reproduced from KORTENBOUT VAN DER SLUIJS & ZAGWIJN 1962).

Fig. 2: Much of our knowledge on the Tegelen fauna and the way it was excavated we owe to the work of ANTJE SCHREUDER (1887–1952).

tions clearly show that the beds near Tegelen belong to *at least* two sedimentary cycles.

Taphonomy

The great paradox of Tegelen is that although it is known as a classic fossil mammal locality, no excavations were ever organised (VAN DEN HOEK OSTENDE 2004). Instead, chance finds of clay workers were gathered and palaeontologists periodically collected these up during visits to the various clay pits. Hence, all the Tegelen fossils are of uncertain stratigraphic provenance. Most of our knowledge on how the bones were gathered we owe to ANTJE SCHREUDER (fig. 2). In her articles, particularly those written in Dutch, she gave little anecdotes on how the fossils had been recovered. Thus, she related about the important role of the clay-workers, who even retrieved fossils of small mammals.

"Notwithstanding the fact that the clay-layers worked 35 year ago, when Dubois, Krause and Weingärtner brought together the rich collections now preserved in Haarlem (Teylers Museum), Berlin (Preuss. Geol. Anst.) and in Amsterdam (Zoolog. Museum of the Univ.), we owe it to the spade-digging by the firm of 'Canoy-Herfkens' that in the last decennium new mammals, such as *Desmana tegelensis*, *Hypolagus brachygnathus* and *Pannonictis pliocaenica* have been recorded" (SCHREUDER 1945: 158).

The fossil material from Tegelen is very fragmented, with only a few favourable exceptions. This seems mostly due to preservation of the material and the fact that it was pulled out of the clay by laymen.

"Quite undamaged specimens are rare in the collections, as in the clay they are wet and often so soft, that they become injured by the spade of the workmen; they break still more when pulled out of the clay. Moreover, when dried, they are often so burst, that they must be glued immediately on the spot, or the loss of some fragments would make a restoration impossible (SCHREUDER 1945: 158)."

"The bones of the elephant, when wet, are so little resistant that the spade cleaves them without the workman observing this" (SCHREUDER 1945: 158).

The point is well illustrated in SCHREUDER (1949) by fossils of the hyena that were obtained by the Maastricht museum in 1943, and by bear fossils which were collected for the Leiden museum in 1949. In the case of the hyena, a skull fragment had been found with part of the P4 associated with some isolated lower molars. The bear material consisted of some isolated upper and lower molars. SCHREUDER (1949) assumed in both cases that the skull and mandible must have been present, but were destroyed during the extraction from the clay. She wrote:

"Collecting without expertise ever so often lead to only the very dark and conspicuous teeth and molars being noticed by the clay workers and them being – as it were – plucked from the jawbone, and even then just some, and certainly not the entire dentition. The fossil bone cannot be distinguished that easily, and is furthermore soft, as long as it is still in the clay. If one were to bring the clay workers to collect such a group of molars and teeth together with the embedding sediment, so bone and clay together, and store it, one would certainly obtain considerable pieces of the skull and mandible, provided the preparation would be done in a laboratory. Preferably, of course, osteologists should be found willing to come to Tegelen and to collect there, because they know what can be expected in the direct vicinity once a molar or bone has been found" (Schreuder 1949: 115, translated from Dutch).

And even if fossils were found, it was sometimes a matter of easy gain, easy loss, as is clear from the first finds of *Leptobos* in the clay.

"How little notion there is about the value of the fossils may be shown by the fact that we owe the first fossils of the ox of Tegelen, viz. three upper molars, only to the circumstance that the hole in the trousers of the finder, a clay-worker, wasn't larger still; all the smaller elements of the dentition had fallen through on the way from the pit to his home" (Schreuder 1936a: 207, translated from Dutch).

Thus, it is clear that the conditions in which the fossils were found were far from perfect. Another aspect that from Schreuder's articles is that the fossiliferous beds varied in richness. It is ironical that during the period she did most of her work, finds were relatively few.

"That the clay-layers now in working are much poorer in fossils than those of former years is due to the fact that the fossils are heaped up in a certain region of the deposit, from which the working has shifted more and more. The proprietors expect that within ten years the rich spots will come into working again, and it is to be hoped that there will be some scientific authority to prevent the destruction of the majority of these highly valuable fossils, which most of them have undergone during the clay digging of the past years" (Schreuder 1945: 158–159).

These quotations show that later in life Schreuder became more cynical about the way the collections were formed, emphasising as she did the unprofessional way in which the material was retrieved from the clay. This certainly explains why such a large number of Tegelen in the various collections is so fragmentary. After her death, collecting continued in exactly the same fashion as before. Probably, there were no alternatives. Although much material has been collected, the various Tegelen collections are not very large, if one considers that they represent seventy years of collecting, and that during that period tremendous amounts of clay were excavated for the ceramic industry. This probably reflects the fact that the clays were not so very rich in fossils. From Schreuder's papers we know that concentrations did occur, but whether these would have been rich enough to organise a proper excavation is very much open to doubt. Nevertheless, sizable collections are preserved in Teylers Museum in Haarlem, in The Zoological Museum Amsterdam, in the Natuurhistorisch Museum Maastricht, and in the Rijksmuseum voor Geologie en Mineralogie (now Naturalis) in Leiden.

The collections

The Teylers collection, which was formed in the years 1904–1933, contains the first fossil mammalian finds from the Tegelen clay-pits. These were collected by a young medical student called Laurens Stijns. This amateur palaeontologist contacted Eugène Dubois, whose fame was rapidly rising after the find of *Pithecanthropus* in Java. Among his other positions, Dubois was the curator of the Paleontological-Mineralogical Cabinet of Teylers Museum in Haarlem. Dubois was slow in responding to Stijns' first request for assistance, but his interest grew after he visited the clay-pits in 1902. He obtained Stijns' collection 'for study' and set up a deal with one of the pit-owners, August Canoy. Fossils found by the clay-workers were regularly sent to Haarlem. The Teylers Museum provided handsome compensation for the finds. Thus, Dubois, and later workers as well, never excavated bones himself, but simply gathered the specimens incidentally found by others.

Dubois published very little on the Tegelen palaeontology. He introduced the locality, publishing the first faunal list (Dubois 1904). A year later, Dubois (1905) described the deer fossils. At the same time he enticed others to work on Tegelen. The bear fossils (*Ursus etruscus*) were described by Newton (1913). Several years before Newton (1907) had also described the first micromammal from Tegelen, *Mimomys pliocaenicus*, which had been found while sieving the clay for fossil seeds. This study of the seed flora was undertaken by Clement Reid, a palaeobotanist who had worked on the seed flora from the Cromer Forest Beds. As Dubois (1904) claimed that the Tegelen Clay was an equivalent of the Cromer Forest Beds, the interest of Reid in the flora was obvious. Reid did not concur with Dubois that Tegelen was coeval to the Cromer Forest Beds. He published his finding together with his wife Eleanor (Reid & Reid 1915). They showed, on the basis of the percentage of Tertiary floral elements, that Tegelen is older than the British localities. Furthermore, they also demonstrated that the clay just south of the village of Tegelen contains a higher number of exotic elements, indicating an even older age. Dubois (1904) had assumed a similar age for all the clay beds in the region. Reid & Reid (1915) created the Teglian (= Tiglian) for the clay beds near Tegelen, and the Reuverian for the beds that outcrop south of the village.

By the time Reid & Reid (1915) had created the Tiglian, Dubois had lost interest in the Tegelen Clay beds. When van Regteren Altena (1951) catalogued the Tegelen collection kept in Teylers, he found a box sent in 1913 that

had never been opened. Others continued collecting in the clay pits. Some collections were sent to Germany (Zagwijn 1998), others to the Amsterdam museum and still others to the mission museum in Steyl. The latter collection is now part of the Tegelen collection in Naturalis. Dubois did supervise two PhD theses on the Tegelen fauna. The first was by a Jesuit priest called father Bernsen, who was Dubois' assistant in the collection of 'Indian fossils' (from Java and Sumatra) in the Leiden museum. His thesis dealt with the rhinoceros fossils from the Tegelen clay (Bernsen 1927). Dubois also held a position at the University of Amsterdam and his assistant there, Antje Schreuder, wrote her thesis on the beavers from Tegelen (Schreuder 1928). After his thesis, Bernsen set out to describe the entire Tegelen fauna in a series of articles in the 'Natuurhistorisch Maandblad' (Bernsen 1930b, 1931a–d, 1932a, b, 1933/34). His untimely death prevented him from finishing this task, and Antje Schreuder completed the last paper in the series.

The Amsterdam and Maastricht collections were formed in the years 1933–1950. After Dubois retired, Antje Schreuder found herself without a formal position. She was allowed to continue her studies at the Zoological Museum in Amsterdam. Because of her fragile health, she focused on the study of small mammals (van Det & van den Hoek Ostende 2003). Her second interest was Tegelen, on which she published a series of papers (Schreuder 1928, 1929, 1935, 1936a, b, 1945, 1946, 1949). The Amsterdam museum already held a small collection of fossils from the clay pits, which consisted of material collected by father Weingärter between 1909 and 1912, and the Böhmers and van Bemmel collection, gathered between 1928 and 1934. Schreuder was recognised as a specialist both in The Netherlands and abroad. New fossils were therefore sent to the Amsterdam museum and formed a small but important collection.

The collection in the Natuurhistorisch Museum Maastricht was likely gathered in the same period. In the catalogue entries date (but the years of acquisition are registered only for a relatively small part of the collection) between 1930 and 1946. Many of the fossils were determined by Antje Schreuder, which places them in the same time frame.

Macro- and micromammals of the Leiden collection in the years 1948–1977: In one of her last articles on the Tegelen mammals, Schreuder (1949) ended with the sentence "May 'Leiden' as well as 'Groningen' succeed in adding valuable fossils to the Tegelen collections, now that the clay layers in exploitation are again richer in fossils than they have been for years." It was Leiden that took up the challenge. However, as before no true excavations were organised, but material was still collected from the clay-workers during visits to the various pits. The trips were initially organized by van der Vlerk and Brouwer. Van der Vlerk was building a stratigraphical framework for The Netherlands, in which the Tegelen clay pits played an important role. When Brouwer left the museum for a post at Leiden University, his position as curator was taken over by Kortenbout van der Sluijs, who also participated in the collecting trips. Apparently the more fossiliferous beds mentioned by Schreuder were now being exploited. Although mechanical digging had replaced the handwork in many of the pits, the Leiden team succeeded in gathering the largest Tegelen collection. This should have been a tremendous boost for the research, but things turned out differently. Van der Vlerk intended the study of the Tegelen Clay, including its fossil remains, as a PhD thesis for Kortenbout van der Sluijs (Zagwijn in litt. 2003). His student, however, proved to be not much of a writer. He did co-author an article on the stratigraphy of the Tegelen Clay Pits (Kortenbout van der Sluijs & Zagwijn 1962), and gave a description of the tapir fossils from Maalbeek (Kortenbout van der Sluijs 1960), but other than that produced no papers on the fauna. The research, however, was claimed and would remain so until the beginning of the 1980s.

At the beginning of the 1960s micromammal research got a tremendous boost through the work of among others Volkert Fahlbusch, Pierre Mein, Hans de Bruijn and Thijs Freudenthal. The latter was contacted by Waldo Zagwijn of the Dutch Geological Survey. At the time the former clay-pits near Tegelen were flooded, but Zagwijn had received word that the pit Russel-Tiglia-Egypte would be temporarily drained. During a visit to the pit Tom Meijer, a malacologist of the Geological Survey, had taken samples from a filled-in stream gully in which he found a number of rodent molars.

Freudenthal started collecting at the Russel-Tiglia-Egypte pit in 1970. For seven years collecting continued during campaigns, which lasted about three weeks each (fig. 3). The goal of the campaigns was two-fold. Of course, they were aimed at building a good collection of Tegelen microvertebrates. Freudenthal's personal interest, however, lay with developing a method for processing fossiliferous sediment, which he then could use in microvertebrate research on Miocene deposits in Spain.

Freudenthal et al. (1976) published a preliminary report on the field campaigns. In this article Albert van der Meulen from Utrecht University presented the first overview of the micromammal fauna. Van der Meulen had finished his PhD on Pleistocene faunas some years earlier and therefore had a much better background for working on the fauna than Freudenthal, whose experiences lay with Miocene faunas. Thus, part of the material from the campaigns was sent to Utrecht, both in sorted and unsorted samples, whereas the rest was stored in Leiden. Only in 2001 were all of the micromammals from Tegelen registered. This involved not only the return of the Utrecht collection to Leiden, but also the washing and sorting of unprocessed sediments still in the museum. Only then did the overall results of the campaigns become clear. Freudenthal and his team had collected c. 5000 dental elements of micromammals from the pit Russel-Tiglia-Egypte. In order to do so, they had sieved c. 192 m^3 of sediment in a

Fig. 3: In the 1970s nearly 200 m³ of clay from the pit Russel-Tiglia-Egypte was sieved in search of micromammals.

clay bed, which was about two metres high. On average, 24 micromammal fossils per m³ were collected, which suggests that the clay was poor in fossils. However, from the quadrant system used by Freudenthal, it can be calculated that the majority of the molars come from the lowermost part of the section, where the concentrations are well over one hundred molars per m³. In contrast, some of the uppermost quadrants proved to be sterile.

The fauna

Non-mammalian vertebrates: Most of the papers on the Tegelen fauna deal with the mammals, but these are not the only vertebrates found in the Limburg locality. Gaudant (1979) distinguished eleven species of fish in the Tegelen fauna. The assemblage consisted of species still found in The Netherlands and was indicative for slow moving to stagnant waters. The only reptile to be described from Tegelen thus far is the European pond turtle, *Emys orbicularis*, already noted by Dubois (1904). Schreuder (1946) gave a description of a beautifully preserved carapace of this turtle. Preliminary identifications made by Massimo Delfino of Florence University show that Tegelen had a rich herpetofauna, with at least thirteen different species.

Fig. 4: The first reconstruction of the Tegelen landscape as made by Dubois. Note the presence of a hippopotamus, based on the false identification of *Sus strozzii*.

The only bird described from Tegelen is *Haliaaetus albicilla*. Van Regteren Altena had found in the Tegelen collection in Teylers museum several bones, which had been found close together and presumably belonged to one individual. The fossils were described by Junge (1953). The Leiden collection harbours several unidentified bird remains.

The large rodents: Remains of the extinct beaver *Trogontherium cuvieri* are so abundant in the Tegelen Clay that in the German literature these beds are often referred to as the "*Trogontherium*-Tone". Apart from this beaver, *Castor fiber* was also found at Tegelen, but it is far more rare. The full description of the Tegelen beaver fossils was given by Schreuder (1928, 1929, 1931). She used the name *Trogontherium boisvilletti*, as she made a difference between a western and an eastern species of *Trogontherium*, *T. boisvilletti* and *T. cuvieri*, respectively. Mayhew (1978) used the same names, but as chronosubspecies. Pre-Elsterian find (thus including Tegelen) were attributed to *T. c. boisvilletti*, the younger representative to *T. c. cuvieri*. Heinrich (1998) did not make any distinctions between subspecies, but showed the evolutionary developments within *T. cuvieri*. His paper shows that the assemblage from Tegelen is not only the most primitive one, but also by far the oldest.

Another large rodent, *Hystrix refossa*, is represented only by the articulated distal end of a humerus and proximal part of the ulna. Bernsen (1932b) had described the fossil as *H.* cf. *etrusca*, a junior synonym of *H. refossa* (van Weers 1994). The presence of a porcupine in Tegelen is remarkable. Present *Hystrix* favours dry and open biotopes, whereas Tegelen represents a wet, forested environment.

Primates: The presence of a monkey was first noted by Bernsen (1930a). *Macaca sylvanus* is a rare element in the fauna, but is represented by one of the best preserved fossils from Tegelen, a lower mandible with almost a complete dentition. The mandible was preserved in a concretion of clay, a mode of fossilisation not uncommon in Tegelen. Originally Bernsen described it as *Macaca florentina*, but nowadays the Pleistocene monkeys of Europe are considered to belong *M. sylvanus* (Szalay & Delson 1979). Schreuder (1945, 1949) described some additional material. A deciduous molar of the monkey was found on the sieve during the micromammal expeditions of the 1970s. Thus, the macaque is one of the few larger mammals found in conjunction with the micromammal fauna.

Artiodactyles: The deer were the first fossil mammals to be described from Tegelen. Apart from *Trogontherium cuvieri,* they are the most common large mammals in the fauna. Dubois (1905) recognised three species. As was usual in those days, small differences with fossils from other localities were emphasised and Tegelen got its 'own' species of deer, *Cervus teguliensis* and *Cervus rhenanus*, the latter being named after the river Rhine, which deposited the clay-beds. The third species present according to Dubois was *Cervus dicranius*. The revision of Bernsen (1933/34), which was finished after his death by Schreuder, made the situation even more complex, since *Cervus* cf. *ctenoides* was added to the list. Kunst (1937), however, assumed that only one large species of deer was present in Tegelen, which she called *Cervus* (*Eucladoceros*) *teguliensis.*

By the end of the 1980s it was clear that there was a wild growth in the taxonomy of the Villafranchian deer. The material from Tegelen was restudied, particularly in comparison to the French Villafranchian species, which had been extensively described by Heintz (1970). Spaan (1992) concluded that the French *Cervus philisi* was a junior synonym of *C. rhenanus*, and that *Eucladoceros teguliensis* and *E. senezensis* were also conspecific. Later, a revision of the genus *Eucladoceros* showed that *E. ctenoides* was the oldest available name for this species (de Vos et al. 1995).

The first fauna lists from Tegelen (Dubois 1904, 1905) featured *Hippopotamus*, and the animal also appears on a reconstruction he made of the Tegelen environment (fig. 4). The presumed presence of hippos in Tegelen was based on the misidentification of a canine of the pig *Sus strozzii. Hippopotamus* was also listed for Tegelen by Guérin (1980), but hippos have never been found in the Tegelen Clay.

The presence of *Sus strozzii* was first noted by Richarz (1921), who gave a short description of nine molars. Bernsen (1931c) described the finds in more detail. The best fossil of the Tegelen pig can be found in the Amsterdam collection, to which it was donated in 1935. It is an almost complete mandible of a young individual and was described by Schreuder (1936a, 1945).

Leptobos is a rare element in the Tegelen fauna. Schreuder (1936a) described some molars, a horn pit and a scapula. Hooijer (1947) described a radius and Kortenbout van der Sluijs (1960) mentioned the presence in the Maalbeek pit. The finds from Tegelen are attributed to *Leptobos elatus*.

Perissodactyles: Bernsen (1927) wrote a PhD on the rhinoceroses of the Tegelen Clay. He concluded that there were two species of rhino represented in the fauna, viz. '*Rhinoceros' etruscus* and '*Rhinoceros' Mercki*. It is noteworthy that all of the material assigned to the second species by Bernsen came from the same collection, that from the Mission Museum at Steyl (now included in the Naturalis collection). Some of the rhinoceros remains in the Natuurhistorisch Museum Maastricht were identified by Schreuder as 'merkii'. Loose (1975) did not concur with Bernsen, and believed that all of the material should be assigned to a single species, *Dicerorhinus etruscus.* But Guérin (1980) also recognised the two species found by Bernsen, nowadays known as *Stephonorhinus etruscus* and *S. kirchbergensis*.

So it is a matter of debate whether or not two species of rhinoceros are represented. This is partly due to the nature of the material, which is fragmented and not very

rich. Therefore, it seems open to different interpretations. On the other hand, one would not expect *Stephanorhinus kirchbergensis*, a Middle Pleistocene species, in the Tegelen fauna. As Guérin interpreted the fauna to be much younger than is commonly assumed, this was not as much a problem for him. However, this interpretation of the age was partly based on the false assumption that the hippopotamus was present in the Tegelen fauna.

Horse fossils are rare in Tegelen, but the presence of equids was already noted by Dubois (1904). He classified the horse as *E. stenonis* Cocchi race *major* Boule. The same classification was used by Bernsen (1931a). When Raven (1935) described large metapodials from Tegelen, he preferred the name *Equus robustus*. The use of different names is indicative of the confusion in horse taxonomy at the time. Viret (1954) introduced the name *E. bressanus*, with which he specifically indicated not only the finds from Chagny and Sénèze, but also the remains from Tegelen.

In 1930 some peculiar molars were found near Maalbeek by A. Bloemers, a clay worker for the N.V. Nederlandse Gresbuizenindustrie. He took the fossils home, where they lay for several decades. In the 1950s, when he was nearly 90 years old, he donated the fossils to a psychologist in Belfeld, Dr. Verkooijen, for whom he was a gardener. Verkooijen took the fossils to the Natuurhistorisch Museum Maastricht for identification, where the curator E. M. Kruytzer identified them as the dentition of a tapir. The exact locality where the molars had been found is not clear. Bloemers was asked to indicate the place he had excavated the molars. Unfortunately, the account given by Kruytzer (1957) in his preliminary note differs from the one given by Kortenbout van der Sluijs (1960), who gave a full description of the fossils. Both authors agree, however, that the find was made in the top layer of a blue clay, just below a brown bank.

Carnivores: The carnivore guild of Tegelen consists of one bear, one hyena, one cat and two mustelids. No species of dog were found and other unexpected absentees are the sabre-toothed cats. The bear *Ursus etruscus* was the first carnivore to be described (Newton 1913). Bernsen (1932a) also described canines from the bear from the collection of the Natuurhistorisch Museum Maastricht. Schreuder (1935) described a second dentition of *U. etruscus*, and gave a description of a third dentition in 1949. That year, two mandibles were found. It is clear from notes in the registration books in Naturalis that Schreuder had seen these specimens, but they were never described. No post-cranial elements of the bear have been collected at Tegelen.

The hyena is represented both by coprolites and skeletal elements. The first description of the hyenid fossils was given by Bernsen (1931d). Schreuder (1949) noted a peculiarity about the hyena fossils from Tegelen. There is a large variation in the sizes and, particularly, a dentition in the Maastricht museum stands out by being very small. Schreuder explained this by assuming sexual dimorphism. This provides, however, a problem, since recent hyenas show only a limited size difference between males and females. According to Holekamp & Smale (2000) females of *Crocuta crocuta* are only 10% larger than the males, a difference which would be unnoticeable in fossil assemblages. Bernsen (1931d) and Schreuder (1949) classified the species as *Hyaena perrieri*. Werdelin & Soulanias (1991) listed the Tegelen assemblage under the name *Pliocrocuta perrieri*.

Schreuder (1935) indicated the presence of two mustelid species in Tegelen. However, the material she described all belongs to a single species, *Enhydrictis ardea*. Nevertheless, a second mustelid is present. Willemsen (1988) described, apart from the *Enhydrictis* fossils, a mandible of the pole-cat *Mustela palerminea*. This mandible had been obtained during one of the collecting trips of the curators from the Leiden Museum and is now in the collection of Naturalis.

The pantherine fossils from Tegelen were described for the first time by von Koenigswald (1961), who named the panther *Panthera schreuderi* (sic). Hemmer & Schütt (1969) synonymized *Panthera schreuderi* with *P. gombaszoegensis*. However, according to Hemmer (1965), one of the specimens from Tegelen represented *P. schaubi*, a rather enigmatic species from Séneze, which was later synonymised with *Puma pardoides* (Hemmer 2001). Hemmer et al. (2004) explicitly included part of the Tegelen material in this species.

O'Regan & Turner (2004) gave full descriptions of all available specimens, including a cast made from a natural mould formed by a concretion. They concluded that all of the material could be attributed to one species. However, like in the hyenas, there is a remarkable variation in size. O'Regan & Turner provided several possible explanations for this, including the possibility that the material represented different time frames (*P. gombaszoegensis* shows an increase in size over time). In the end, they decided the best explanation for the differences in size was assuming sexual dimorphism.

Proboscideans: Remains of elephants from the Tegelen Clay are rare. Only eleven fossils have been found, all of which can be attributed to *Mammuthus meridionalis* (Guenther 1986). In what is generally referred to as 'the main fauna', that is the finds from the direct vicinity of Tegelen, only one proboscidean species has been found. However, in 1960 a molar of the mastodont *Ananacus arvernensis* was found in the Maalbeek pit, somewhat more to the south. Originally the find was dated as Eburonian, based on the pollen analysis of the clay adhered to the molar (Kortenbout van der Sluijs & Zagwijn 1962). The pollen spectrum from this clay clearly represented a cold period. Westerhoff et al. (1998), however, showed that the find layer was probably deposited in a colder period within the Tiglian, older than the main fauna.

Micromammals: The presence of micromammals in the Tegelen Clay was first noted by Newton (1907), who described finds of the vole *Mimomys pliocaenicus*.

As we noted earlier, no palaeontological excavations were organised at Tegelen and thus for over half a century nobody took to sieving the clay in search of micromammals. Nevertheless, chance finds did occur, and Antje Schreuder (1945: 18) praised the clay workers that had found fossils of hares and desmans. She extensively discussed the find of the hare *Hypolagus brachygnathus* (Schreuder 1936b) and described the desmans from Tegelen in her review of this subfamily of Talpidae (Schreuder 1940).

Systematic study of the micromammals only became possible after the expeditions of Freudenthal in the 1970s. The first large paper dealing with small mammals from the Limburg locality was the PhD thesis of Reumer (1984), in which he compared the Tegelen shrews to those from various Hungarian localities. Reumer noted the presence of four shrew species: *Beremendia fissidens*, *Petenyia hungarica*, *Sorex minutus* and *Drepanosorex praearaneaus*. The latter species is nowadays generally placed in *Sorex*, of which *Drepanosorex* is considered a subgenus (Reumer 1985). Rümke (1985) included the desmans from Tegelen in her review on the Neogene Desmaninae. Two desman species are present in the fauna, *Desmana thermalis* and *Galemys kormosi*. A student of Rümke, Jolanda Roders, wrote an unpublished MSc thesis on the talpine mole from the locality and concluded that the assemblage is referable to *Talpa minor* (Roders 1987).

The vole fauna was studied by Tesakov (1998). The voles are represented by six species, *Mimomys pliocaenicus*, *M. tigliensis*, *M. reidi*, *Pitymimomys pitymyoides*, *Clethrionomys kretzoii* and *Ungaromys nanus*. The studies of Reumer, Rümke and Tesakov were all done before all of the material had been sorted. Since then, the material has nearly been doubled. Among the material found there were five molars of the lemming *Dicrostonyx*. Unfortunately, it is unclear from which quadrant these fossils came. The find of *Dicrostonyx* in a fauna otherwise dominated by elements typical for a forest environment is surprising, and as yet not understood.

The recently screened sediment harboured another surprise in the glirids, viz. the first record for The Netherlands of *Glirulus pusillus*. This small dormouse was, together with the far more numerous *Muscardinus pliocaenicus*, described by van den Hoek Ostende (2003). The sciurid from Tegelen presented even a bigger surprise; the species identified as *Sciurus* cf. *vulgaris* by Freudenthal et al. (1976) turned out to be a new, large species of *Hylopetes*, *H. debruijni* (Reumer & van den Hoek Ostende 2003). Freudenthal et al. (1976) already noted the presence of the murids *Apodemus* and *Micromys* in Tegelen. *Apodemus* is the most numerous micromammal in the Tegelen fauna. The bats from Tegelen are as yet undescribed.

Micromammals were also collected from the pit Maalbeek (Westerhoff et al. 1998). This assemblage is older than the one collected from the pit Russel-Tiglia-Egypte, but contains the same species. The studies in the Maalbeek pit are still continuing under the direction of Thijs van Kolfschoten of the Archaeological Institute of the Leiden University.

Table 1 gives a full overview of the Tegelen fauna. The finds from Maalbeek have not been included in this table, since it has been clearly established that they are older than the main fauna (Westerhoff et al. 1998).

The age of the Tegelen fauna

The age of the Tegelen fauna seems easily enough determined. It is, of course, Tiglian. However, that answer is a bit too easy. We first have to determine that there is indeed one Tegelen fauna and secondly, since the Tiglian and its boundaries are not defined by fossil mammals, the stage as such cannot be used for interregional correlations in mammal palaeontology.

As to the question whether or not there is one Tegelen fauna, it is obvious that not all of the finds from the Tegelen area are of the same age. The fossils of the tapir and mastodont f ound in the pit Maalbeek are generally considered to be older than the fauna found in the pits nearer to the village of Tegelen itself (Westerhoff et al. 1998). Of course, these rare species attract attention, but they are certainly not the only large mammals found in Maalbeek. Kortenbout van der Sluijs (1960) also mentioned the presence in Maalbeek of *Eucladoceros ctenoides*, *Cervus rhenanus*, *Leptobos* cf. *elatus* and *Stephanorhinus etruscus*, species that are also known from other Tegelen pits.

Another obvious difference in age lies with the micromammals. These were collected from the filled in stream gully in the pit Russel-Tiglia-Egypte and are thus per definition separated from the main clay beds in that pit. However, the hiatus between the deposition of the two is of unknown duration. The Tiglian substages TC5 and TC6 were defined on the basis of pollen spectra in the stream gully from which the micromammals were collected. Most of the material was, together with a rich seed flora, collected from the base of this gully. The recognised evolutionary stages of all recorded arvicolid species and the lack of remains of *Microtus* place the fauna in the Late Villanyian (Tesakov 1998). This age is corroborated by, for example, the stage of evolution of the glirid *Muscardinus pliocaenicus* (van den Hoek Ostende 2004). However, its relation to the larger mammal fauna from the region is unclear. Furthermore, after Tesakov published his findings on the voles from Tegelen, five molars of the lemming *Dicrostonyx* were found in the collection. This suggests that even in the small mammal assemblage some contamination may be present, since a lemming does not seem to fit the remainder of the micromammal assemblage, which consists primarily of wood-inhabitants and/or semi-aquatic species.

Apart from the older age for the fauna from the Maalbeek pit, and the (somewhat) younger age of the micromammal fauna, the homogeneity of the other fossils is also open to doubt. The reason for this lies with the

Table 1: Faunal list of Tegelen. The second column gives the last description. If the classification used in this paper deviates from the one in the last description, the reference to the classification is added in the third column. Species exclusively found in the Maalbeek pit (*Anancus arvernensis*, *Tapirus arvernensis*) have not bee included in the list.

	Description	Classification according to
PISCES		
Esox lucius	Gaudant 1979	
Anguilla anguilla	Gaudant 1979	
Carassius carassius	Gaudant 1979	
Tinca tinca	Gaudant 1979	
Abramis brama	Gaudant 1979	
Alburnus alburnus	Gaudant 1979	
Scardinus erythophthalmus	Gaudant 1979	
Rutilus rutilus	Gaudant 1979	
Cyprinidae gen. et sp. indet.	Gaudant 1979	
Perca fluviatilis	Gaudant 1979	
Lucioperca lucioperca	Gaudant 1979	
Gasterosteus aculeatus	Gaudant 1979	
AMPHIBIA		
Triturus cristatus	det. M. Delfino	
Triturus sp.	det. M. Delfino	
Palaeobatrachidae indet.	det. M. Delfino	
Bufonidae indet.	det. M. Delfino	
Rana gr. *R. ridibunda*	det. M. Delfino	
Hyla gr. *H. arborea*	det. M. Delfino	
Pelobates sp.	det. M. Delfino	
Bombina sp.	det. M. Delfino	
REPTILIA		
Emys orbicularis	Schreuder 1945	
Anguis fragilis	det. M. Delfino	
Lacerta sp.	det. M. Delfino	
Colubrines indet.	det. M. Delfino	
Natrix natrix	det. M. Delfino	
AVES		
Haliaaetus albicilla	Junge 1953	
MAMMALIA		
Soricomorpha		
Desmana thermalis	Rümke 1985	
Galemys kormosi	Rümke 1985	
Talpa minor	Roders 1987	
Petenyia hungarica	Reumer 1984	
Beremendia fissidens	Reumer 1984	
Sorex (Drepanosorex) praearaneus	Reumer 1984	Reumer 1985
Sorex minutus	Reumer 1984	
Rodentia		
Trogontherium cuvieri	Schreuder 1928	Mayhew 1978
Castor fiber	Schreuder 1928	

	Description	Classification according to
Hylopetes debruijni	Reumer & Van den Hoek Ostende 2003	
Muscardinus pliocaenicus	Van den Hoek Ostende 2003	
Glirulus pusillus	Van den Hoek Ostende 2003	
Micromys sp.	Freudenthal et al. 1976	
Apodemus cf. *sylvaticus*	Freudenthal et al. 1976	
Mimomys pliocaenicus	Tesakov 1998	
Mimomys tigliensis	Tesakov 1998	
Mimomys reidi	Tesakov 1998	
Pitymimomys pitymyoides	Tesakov 1998	
Clethrionomys kretzoii	Tesakov 1998	
Ungaromys nanus	Tesakov 1998	
Dicrostonyx sp.	Unpublished	
Hystrix refossa	Bernsen, 1932b	Van Weers 1994
Lagomorpha		
Hypolagus brachygnathus	Schreuder 1936b	
Chiroptera		
Chiroptera undet. 1	Unpublished	
Chiroptera undet. 2	Unpublished	
Primates		
Macaca sylvana	Schreuder 1945, 1949	Szalay & Delson 1979
Proboscidea		
Mammuthus meridionalis	Guenther 1986	
Artiodactyla		
Sus strozii		
Eucladoceros ctenoides	Spaan 1992	De Vos et al. 1995
Cervus rhenanus	Spaan 1992	
Leptobos cf. *elatus*	Scheuder 1936a, Hooijer 1947	
Perissodactyla		
Stephanorhinus etruscus	Guérin 1980	
?*Stephanorhinus kirchbergensis*	Guérin 1980	
Equus robustus	Bernsen 1931a, Raven 1935	Viret 1954
Carnivora		
Mustela palerminea	Willemsen 1988	
Enhydrictis ardea	Willemsen 1988	
Ursus etruscus	Schreuder 1945, 1949	
Panthera gombaszoegensis	O'Reagan & Turner 2004	
Pliocrocuta perrieri	Schreuder 1949	Werdelin & Soulanias 1991

carnivores and the rhinoceroses. In the case of the rhinos, it is the assumed presence of *Stephanorhinus kirchbergensis* (Bernsen 1927, Guérin 1980) that presents a problem. This species is otherwise known from the Middle Pleistocene and Tegelen would be by far the oldest occurrence. Such a very early occurrence seems unlikely. One possible explanation would be that a part of the fossils from Tegelen is indeed much younger than the rest. In favour of this hypothesis would be that almost all of the *S. kirchbergensis* fossils are from one collection (viz. Mission Museum Steijl), and thus likely to have been collected at the same locality. The alternative explanation would be that the presence of *S. kirchbergensis* is based on the misidentification of *S. etruscus* fossils, as assumed by Loose (1975).

The large carnivores from Tegelen all show a large variation in size. Schreuder (1949) explained this variation in the bears and hyenas by assuming sexual dimorphism, and the same explanation was coined for the panther by O'Regan & Turner (2004). In the case of the bears, sexual dimorphism is well documented. However, for hyenas the very limited dimorphism found in recent forms makes it an unlikely explanation for the large variation found in the small fossil assemblage. In our opinion, the same holds true for the panther. O'Regan & Turner (2004) found the amount of variation acceptable, since it is only somewhat larger than the differences between males and females in lions. However, the sample they compared with was much larger than the few fossils available from Tegelen. Furthermore, the lion may not be the best felid to compare with, since it is the only pack hunter in its family, with different roles for males and females. O'Regan & Turner (2004) did consider the possibility of different ages in the Tegelen fauna, since *Panthera gombaszoegensis* shows an increase over time. However, they rejected this on the basis of Tegelen being a classical locality. Given the uncertainty about the provenance of the material, we feel that assuming a different age for various parts of the fauna is at least as good an explanation as sexual dimorphism.

Another peculiarity about the Tegelen fauna is the presence of *Trogontherium cuvieri*. This extinct beaver has its first occurrence in the Limburg locality and the assemblage is also clearly the most primitive one (Heinrich 1998). The age difference with the next occurrence discussed by Heinrich is, however, remarkably large. The assemblage from the Maasvlakte is about one million years younger than the assumed age of Tegelen. In other words, like *Stephanorhinus kirchbergensis*, *T. cuvieri* is a species otherwise known from the Middle Pleistocene.

Thus, there are several indications that the fossils from Tegelen come from different time frames. The evidence is somewhat circumstantial, but this is logical given the relatively stability of the Villafranchian ecosystem. If for example, the pit Maalbeek had not yielded remains of mastodont and tapir, the remainder of the fauna would not have given any reason to assume an older age of the sediments in that particular pit. By the same token, younger sediments in the area would yield a very similar fauna. Only evolutionary changes within lineages, such as the increase in size of various carnivores, would reveal a difference in age.

To complicate things further, the mammal sequence in the Netherlands is very incomplete. There appears to be a hole of one million years between Tegelen and the next faunas, which are assigned to the Bavelian, viz. the Maasvlakte (van Kolfschoten & Vervoort-Kerkhoff 1999) and Het Gat (Mol et al. 2003). These faunas are not even *in situ*, but have been found washed up on the beach (Maasvlakte) or have been collected by fishermen from the bottom of the North Sea (Het Gat). There are, however, some Bavelian fossils that have been found in situ in The Netherlands. Two different locations near Bavel yielded a small mammal assemblage and some macrofossils (van Kolfschoten 1990). Even in the Zuurland boreholes this gap of a million years seems present, as the 'Tiglian' faunas are immediately followed by 'Cromerian' faunas (Reumer & Hordijk 1999).

The presumed one million year gap is relevant for the interpretation of the Tegelen fauna. So far the fauna has always been interpreted as a single fauna, its upper limit set by the upper boundary of the Tiglian. Thus, the possibility that part of the material was derived from younger sediments in the upper part of the Waalre formation was never taken into account. Such an explanation would explain the peculiarities in the mammal record. This would imply that in fact the one million year gap has been partly filled, but that this has never been recognised. Given the stability of the Villafranchian mammal community over time, we would even not expect to be able to recognise 'Tiglian' mammal fauna from younger ones. The main argument against the presence of younger sediments is provided by palaeomagnetism. Van Montfrans (1971) found a normal polarity in various pits in which mammal fossils have been found. Drees (2005) noted that the presumed reversal to reversed polarity on the Tiglian-Eburonian boundary is based on sequences, the age of which had been reinterpreted since the publication of Montfrans' thesis. Nevertheless, it is most likely that the sediments in the pits Egypte, Kurstjens, Wambach, and Laumans were deposited during the Olduvai Chron (Chron C2n), providing an upper age limit of 1.77 My for the mammals from these pits.

Conclusions

A century of research on the clay-pits near Tegelen has yielded extensive collections of Villafranchian mammals in various Dutch museums (Teylers Museum, Naturalis, Zoological Museum Amsterdam, Natuurhistorisch Museum Maastricht). We owe these collections to the ceramic industry in the region, as clay workers regularly gathered chance finds of bones and teeth. No scientific excavations have ever taken place and, therefore, the exact provenance of the material is not known (although usually the pit

where it has been collected is indicated). Comparing the number of fossils retrieved to the huge amount of sediment excavated during the 20th century suggests that the clay beds near Tegelen may not have been very rich in fossils. From notes by Schreuder we know that some of the clay beds had a much richer fossil contents than others. Her writings also provide an explanation for the fragmentary nature of most of the Tegelen fossils. The bones were often waterlogged and as they were pulled out of the clay by laymen, they were often damaged during excavation. Therefore it is certainly no coincidence that some of the finest fossils from Tegelen were encrusted in concretions, protecting them from harm by injudicious handling by clay-workers.

The only scientific excavations that did take place near Tegelen were the expeditions in search of smaller mammals in the pit Russel-Tiglia-Egypte (Freudenthal et al. 1976) and the Maalbeek pit (Westerhoff et al. 1998). The assemblage from Russel-Tiglia-Egypte was sampled from a 2 m clay bed in a filled-in stream gully. Most of the assemblage springs from the bottom of this in-fill. The age of the assemblage was determined as Upper Villanyian on the basis of the state of evolution of *Mimomys pliocaenicus* (Tesakov 1998). The recent discovery of five *Dicrostonyx* molars in the assemblage is a puzzle that is as yet unsolved.

As we do not know the exact location in which the various large mammal fossils were found, the question whether or not they are all of similar age is justified. The presumed presence of *Stephanorhinus kirchbergensis* (Guérin 1980), and interpreting the large variations in size within the panther and hyena as a state of evolution rather than the result of sexual dimorphism, would suggest that indeed material of different ages is mixed. Although the evidence of mixture of ages is circumstantial, we suggest that there are enough doubts to be cautious about the age of Tegelen, when using it for interregional correlations.

Acknowledgements

Various people helped us with our research and with finishing our manuscript. Anne Schulp provided us with a copy of the registration data on Tegelen of the Natuurhistorisch Museum Maastricht. Massimo Delfino kindly allowed us to use his identifications of the herpetofauna. Willem Kakebeeke reconstructed the micromammal excavation from Freudenthal's notes, and calculated the fossil richness of the various quadrants. Tom Meijer critically read the manuscript, and provided us with some useful comments. Doris Nagel suggested and provided copies of literature on hyenas, and helped formulate the German abstract. Steve Donovan made some linguistic improvements; additional linguistic remarks were made by Paul Mazza. Ralf-Dietrich Kahlke and Lutz Maul acted as reviewers, and suggested a number of improvements to the text. The help of all these colleagues was greatly appreciated.

References

Bernsen, J. J. A. (1927): The Geology of the Tiglian Clay and its fossil remains of Rhinoceros. — Dissertation, University of Amsterdam: 1–108; Amsterdam.

Bernsen, J. J. A. (1930a): On a Fossil Monkey found in the Netherlands (*Macacus* cf. *florentinus* Cocchi). — Proceedings of the Koninklijke Akademie van Wetenschappen, **33** (7): 771–777; Amsterdam.

Bernsen J. J. A. (1930b): Eine Revision der Fossilen Säugetierfauna aus den Tonen von Tegelen. (I) *Elephas meridionalis.* — Natuurhistorisch Maandblad, **19** (12): 146–152; Maastricht.

Bernsen, J. J. A. (1931a): Eine Revision der Fossilen Säugetierfauna aus den Tonen von Tegelen. (II) *Equus stenonis*. — Natuurhistorisch Maandblad, **20** (2): 25–31; Maastricht.

Bernsen, J. J. A. (1931b): Eine Revision der Fossilen Säugetierfauna aus den Tonen von Tegelen. (III) *Macacus* cf. *florentinus*. — Natuurhistorisch Maandblad, **20** (5): 67–71; Maastricht.

Bernsen, J. J. A. (1931c): Eine Revision der Fossilen Säugetierfauna aus den Tonen von Tegelen. (IV) *Sus strozzii.* — Natuurhistorisch Maandblad, **20** (7): 104–108; Maastricht.

Bernsen, J. J. A. (1931d): Eine Revision der Fossilen Säugetierfauna aus den Tonen von Tegelen. (V) *Hyaena perrieri*. — Natuurhistorisch Maandblad, **20** (11): 153–158; Maastricht.

Bernsen, J. J. A. (1932a): Eine Revision der Fossilen Säugetierfauna aus den Tonen von Tegelen. (VI & VII) *Ursus etruscus* & *Mustela* sp. — Natuurhistorisch Maandblad, **21** (2): 20–26; Maastricht.

Bernsen, J. J. A. (1932b): Eine Revision der Fossilen Säugetierfauna aus den Tonen von Tegelen. (VIII) *Hystrix* cf. *etrusca*. — Natuurhistorisch Maandblad, **21** (6): 78–81; Maastricht.

Bernsen J. J. A. (1933/34): Eine Revision der Fossilen Säugetierfauna aus den Tonen von Tegelen. (IX) Cervidae. — Natuurhistorisch Maandblad, **22** (11): 136–138, **23** (4,6 & 7): 38–46, 71–77, 82–86, Maastricht.

De Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., & Morales, J. (1992): Report of the RCMNS working group on fossil mammals, Reisensburg 1990. — Newsletter on Stratigraphy, **26** (2/3): 65–118; Stuttgart.

Debard, E., Faure, M., & Guérin, C. 1994. Estratigraphie du gisement villafranchien moyen de Saint-Vallier (Drôme). — Compte Rendu de l'Academie des Sciences, **318** (II): 1283–1286; Paris.

Delson, E., Faure, M., Guérin, C., Aprile, L., Argant, J., Blackwell, B., Debard, E., Martin-Suarez, E., Monguillon, A., Parenti, F., Pastre, J.-F., Sen, S., Swisher III, C.C., & Valli, A. (2004): Franco-American research at the Villafranchian locality of Senèze (Haute-Loire, France): why are new enquiries needed? — In: Maul, L. C., & Kahlke, R.-D. (Eds.). 18th International Senckenberg Conference/VI International Palaeontological Colloquium in Weimar. Late Neogene and Quaternary biodiversity and evolution: regional developments and interregional correlations. — Terra Nostra 2004/2: 96–97; Berlin.

Det, M. E. van, & Hoek Ostende, L. W. van den (2002): Antje Schreuder (1887–1952): een bescheiden pionier. **—** Cranium, **19** (2): 123–129; Leiden.

Drees, M. (2005): An evaluation of the Early Pleistocene chronology of The Netherlands. — www.Palarch.nl, vertebrate palaeontology, **1** (1): 1–46.

Dubois, E. (1904): Over een equivalent van het Cromer Forest-Bed in Nederland. — Verslagen van de Gewone Vergadering Wisen Natuurkunde, Afdeling van de Koninklijke Akademie van Wetenschappen, **13**: 243–251; Amsterdam.

Dubois, E. (1905): L'age de l'argile de Tegelen et les espèces cervidés qu'elle contient. — Archives du Musée de Teyler, Series II, **9**: 605–615; H aarlem.

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

Gaudant, J. (1979): L'ichtyofaune tiglienne de Tegelen (Pays-Bas):

signification paléoécologique et paléoclimatique. — Scripta Geologica, **50**: 1–16; Leiden.

Guenther, E. W. (1986): Funde von *Archidiskodon meridionalis* und *Trogontherium cuvieri* aus den interglazialen Tegelen-Schichten. — Quartärpaläontologie**, 6**: 53–65; Berlin.

Guérin, C. (1980): Les Rhinoceros (Mammalia, Perissodactyla) du Miocene supèreur au Pleistocène terminal en Europe occidentale; Comparaison avec les espèces actuelles. — Thèse Doctorat d'Etat et Sciences Université Lyon I, Documents des Laboratoire de Géologie, Lyon, **79** (1–3): 1–1185; Villeurbanne.

Heinrich, W.-D. (1998): Evolutionary trends in *Trogontherium cuvieri* (Mammalia, Rodentia: Castoridae) and their implications. — In: Kolfschoten, T. van, & Gibbard, P. L. (Eds.), The Dawn of the Quaternary. Proceedings of the SEQS-EuroMam symposium 1996. — Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, **60**: 573–578; Haarlem.

Heintz, E. (1970): Les Cervides Villafranchiens de France et d'Espagne. — Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Serie C, **22** (I): 1–303 + pl. 1–40, (II): 1–206; Paris.

Hemmer, H. (1965): Studien an "*Panthera*" *schaubi* Viret aus dem Villafranchien von Saint-Vallier (Drôme). — Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **122** (3): 324–336; Stuttgart.

Hemmer, H. (2001): Die Feliden aus dem Epivillafranchium von Untermassfeld. — In: Kahlke, R.-D. (Ed.): Das Pleistozän von Untermassfeld bei Meiningen (Thüringen). — Monographien des Römisch-Germanischen Zentralmuseums Mainz, **40** (3): 699–782 + pl. 132–143; Bonn (Dr. Rudolf Habelt GmbH).

Hemmer, H., Kahlke, R.-D., & Vekua, A. K. (2004): The Old World puma – *Puma pardoides* (Owen, 1946) (Carnivora: Felidae) – in the Lower Villafranchian (Upper Pliocene) of Kvabebi (East Georgia, Transcaucasia) and its evolutionary and biogeographical significance. — Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **233** (2): 197–231; St uttgart.

Hemmer, H., & Schütt, G. (1969): Ein Unterkiefer von *Panthera gombaszoegensis* (Kretzoi, 1938) aus den Mosbacher Sanden. — Mainzer Naturwissenschaftliches Archiv, **8**: 90–101; Mainz.

Hoek Ostende, L. W. van den (1990): Tegelen, ons land 2 miljoen jaar geleden. — 1–48; Haarlem (Teylers Museum).

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

Hoek Ostende, L. W. van den (2004): The Tegelen clay-pits: a hundred year old classical locality. **—** In: Winkler Prins, C. F., & Donovan, S. K. (Eds.): VII Symposium Cultural Heritage in Geosciences, Mining and Metallurgy: Libraries – Archives – Museums: "Museums and their collections", Leiden (The Netherlands), 12–23 May 2003. **—** Scripta Geologica, Special Issue, **4**: 127–141; Leiden.

Holekamp, K. E., & Smale, L. (2000): Feisty females and meek males: reproductive strategies in the spotted hyena. **—** In: Wallen, K., & Schneider, J. E. (Eds.): Reproduction in context. Social and environmental influences on reproduction: 257–285, Cambridge, Mass. & London (MIT Press).

Hooijer, D. A. (1947): Notes on some fossil mammals of the Netherlands. **—** Archives du Musée de Teyler, Serie III, **10**: 33–51; Haarlem.

Junge, G. C. A. (1953): Fossil bones of a White-tailed Eagle, *Haliaeetus albicilla* (L.) from the Tegelen clay. **—** Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen, Series B, **56** (3): 285–290; Amsterdam.

Koenigswald, G. H. R. von (1961):. Fossils cats from the Tegelen Clay. **—** Publicaties van het Natuurhistorisch Genootschap in Limburg, **12**: 19–27; Maastricht.

Kolfschoten, T. van (1990): The Early Biharian Mammal Faunas from Bavel and Dorst-Surae. **—**Quartärpaläontologie, **8**: 265–272; Berlin.

Kolfschoten, T. van, & Vervoort-Kerkhoff, Y. (1999): The Pleistocene and Holocene mammalian assemblages from the Maasvlakte near Rotterdam (the Netherlands), with special reference to the Ovibovini *Soergelia minor* and *Praeovibos* cf. *priscus*. **—** In: Reumer, J. W. F., & De Vos, J. (Eds.): Elephants have a snorkel! Papers in honour of Paul Y. Sondaar. **—** Deinsea **7**: 369–382; Rotterdam.

Kortenbout van der Sluijs, G. **(**1960): The fossil tapir of Maalbeek, Netherlands. **—** Publicaties van het Natuurhistorisch Genootschap in Limburg, **12**: 12–18; Maastricht.

Kortenbout van der Sluijs, G., & Zagwijn, W. H. (1962): An introduction to the stratigraphy and geology of the Tegelen clay-pits. **—** Mededelingen van de Geologische Stichting, N. S., **15**: 31–37; Haarlem.

Kruytzer, E. M. (1957): Fossil tapir found in the Netherlands. **—** Natuurhistorisch Maandblad, **46** (9–10): 110; Maastricht.

Kunst, C. E. (1937): Die niederländischen pleistozänen Hirsche. **—** Dissertation, Leiden University: 1–125; Leiden.

Loose, H. (1975): Pleistocene Rhinocerotidae of W. Europe with reference to the recent two-horned species of Africa and S.E. Asia. **—** Scripta Geologica **33**: 1–59; Leiden.

Mayhew, D. F. (1978): Reinterpretation of the extinct beaver *Trogontherium* (Mammalia, Rodentia). **—** Philosophical Transactions of the Royal Society London B, **281** (B 983): 407–438; London.

Mein, P. (1975): Résultats du groupé de travail des vertebras. Biozonation du Neogène méditerranéen à partir des Mammifères. — In: Senes, J. (Ed.): Report on the activity of the RCMNS Working Groups, Bratislava (1971–1975): 78–81; Bratislava.

Mol, D., Post, K, Reumer, J. W. F., De Vos, J., & Laban, C. (2003): Het Gat: preliminary note on a Bavelian fauna from the North Sea with possibly two mammoth species. — Deinsea, **9**: 253–266; Rotterdam.

Montfrans, H. M. van (1971): Paleomagnetic dating in the North Sea Basin. — PhD thesis University of Amsterdam: 1–113; Amsterdam.

Newton, E. T. (1907): Note relative à des fragments fossiles de petits vertébrés trouvés dans les dépôts pliocènes de Tegelen-sur-Meuse. **—** Bulletin Societé Belge Géologique **21**: 591–596; Bruxelles.

Newton, E. T. (1913): On the remains of *Ursus etruscus* (= *U. arvernensis*) from the pliocene deposits of Tegelen sur Meuse. **—** Verhandelingen van het Geologisch Mijnbouwkundig Genootschap voor Nederland en Koloniën, Geologische Serie, **1**: 249–254; 's Gravenhage.

O'Regan, H. J., & Turner, A. (2004): Biostratigraphic and palaeoecological implications of new fossil felid material from the Plio-Pleistocene site of Tegelen, The Netherlands. — Palaeontology, **47** (5): 1181–1193; Oxford.

Raven, T. (1935): Neue Funde quartärer Säugetiere in den Niederlanden. II. **—** Proceedings van de Koninklijke Akademie van Wetenschappen te Amsterdam **38** (3): 290–296; Amsterdam.

Regteren Altena, C. O. van (1951): Systematic catalogue of the palaeontological collection. 7th supplement. Vertebrata from the pleistocene Tegelen Clay, Netherlands. **—** Archives du Musée Teylers, Ser. III, **10**: 182–208; Haarlem.

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

Reumer, J. W. F. (1984): The Ruscinian and Early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. — Scripta Geologica, **73**: 1–173; Leiden.

Reumer, J. W. F. (1985): The generic status and species of *Drepanosorex* reconsidered (Mammalia, Soricidae). **—** Revue Paleobiologie, **4** (1): 53–58; Genève.

Reumer, J. W. F., & Hordijk, L. W. (1999): Pleistocene Insectivora (Mammalia) from the Zuurland boreholes near Rotterdam, The Netherlands. — In: Reumer, J. W. F., & De Vos, J. (Eds.): Elephants have a snorkel! Papers in honour of Paul Y. Sondaar. **—** Deinsea, **7**: 253–281; Rotterdam.

Reumer, J. W. F., & Van den Hoek Ostende, L. W. (2003): Petauristidae and Sciuridae (Mammalia, Rodentia) from Tegelen, Zuurland, and the Maasvlakte (the Netherlands). **—** In: Reumer, J. W. F., & Wessels, W. (Eds.): Migration and distribution of Neogene mammals in Eurasia. **—** Deinsea, **10**: 455–467; Rotterdam.

Richarz, S. (1921): Neue Wirbeltierfunde in den Tonen von Tegelen bei

Venlo. — Centralblatt für Mineralogie, Geologie und Paläontologie, **1921**: 664–669; Stuttgart.

Roders, J. T. (1987): Een vergelijking van twee recente populaties van *Talpa europaea* uit Nederland en de beschrijving van een *Talpa*-soort (*Talpa minor*) uit Tegelen. — Unpublished MSc. Thesis Utrecht University: 1–209; Utrecht.

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

Schmidt-Kittler, N. (Ed.) (1987): International symposium on mammalian biostratigraphy and paleoecology of the European Paleogene, Mainz, February 18th–21st 1987. — Münchner geowissenschaftliche Abhandlungen A, **10**: 1–311; München.

Schreuder, A. (1928): Bijdrage tot de kennis van *Conodontes* en *Trogontherium*. — Disserstation, University of Amsterdam: 1–49; Amsterdam.

Schreuder, A. (1929): *Conodontes* (*Trogontherium*) and *Castor* from the Teglian Clay compared with Castoridae from other localities. — Archives du Musée Teyler, Ser. III, **4**: 99–321; Haarlem.

Schreuder, A. (1931): *Conodontes, Trogontherium* and the other Castoridae. — Paläontologische Zeitschrift, **13**: 148–176; Berlin.

Schreuder, A. (1935): A note on the Carnivora of the Tegelen Clay, with some remarks on the Grisoninae. — Archives Néerlandaises de Zoologie, **2** (1): 73–94; Leiden.

Schreuder, A. (1936a): Het groote varken uit de klei van Tegelen. — De Levende Natuur **40**: 205–211; 's Graveland.

Schreuder, A. (1936b): *Hypolagus* from the Tegelen Clay; with a note on recent *Nesolagus*. — Archives Néerlandaises de Zoologie, **2**: 225–239; Leiden.

Schreuder, A. (1940): A revision of the fossil water-moles (Desmaninae). — Archives Neerlandaises de Zoologie, **4** (2/3): 201–233; Leiden.

Schreuder, A. (1945): The Tegelen Fauna, with a description of new remains of its rare components (*Leptobos, Archidiskodon meridionalis, Macaca, Sus strozzii)*. — Archives Néerlandaises de Zoologie, **7**: 153–204; Leiden.

Schreuder, A. (1946): De moerasschildpad, *Emys orbicularis* (L.), fossiel en levend in Nederland. — Natuurhistorisch Maandblad, **35**: 58–61; 72–75; Maastricht.

Schreuder, A. (1949): Nieuwe zoogdierfossielen uit de Tegelse Klei. — Geologie en Mijnbouw, **11** (3): 115–126; Den Haag.

Spaan, A. (1992): A revision of the deer from Tegelen (province of Limburg, The Netherlands). — Scripta Geologica, **98**: 1–85; Leiden.

Szalay, F. S., & Delson, E. (1979): Evolutionary History of the Primates. — 1–580; New York, London (Academic Press).

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

Valli, A. M. F. (2001): Le gisement villafranchien moyen de Saint-Vallier (Drôme): nouvelles données paléontologiques (Cervidae, Bovinae) et taphonomiques. — Documents des Laboratoires de Géologie, Lyon, **153**: 1–275; Lyon.

Vervoort-Kerkhoff, Y., & T. van Kolfschoten (1987): Tegelen. — Cranium, **4** (1): 20–23; Dieren.

Viret, J. (1954): Le loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. — Nouvelles Archives du Musée d'Histoire Naturelle Lyon, **4**: 1–200; Lyon.

Vos, J. de, Mol, D., & Reumer, J. W. F. (1995): Early Pleistocene Cervids from the Oosterschelde (the Netherlands) with a revision of the cervid genus *Eucladoceros* Falconer, 1868. — Deinsea, **2**: 95–121; Rotterdam.

Weers, D. J. van (1994): The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus *Hystrix*. — Scripta Geologica, **106**: 35–52; Leiden.

Weerts, H. J. T., Cleveringa, P., Ebbing, J. H. J., Land, F. D., & Westerhoff, W. E. (2003): De lithostratigrafische indeling van Nederland. Formaties uit het Tertiair en Kwartair. — Rapport 03–051–A. Nederlands Instituut voor Toegepast Geowetenschappen TNO; Utrecht.

Werdelin, L., & Solounias, N. (1991): The Hyaenidae: taxonomy, systematics and evolution. — Fossils and Strata, **30**: 1–104; Oslo.

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

Willemsen, G. F. (1988): *Mustela* and *Enhydrictis* (Carnivora, Mustelidae) from Tegelen (the Netherlands). — Proceedings van de Koninklijke Akademie van Wetenschappen, Series B, **91** (3): 311–320; Amsterdam.

Zagwijn, W. H. (1963): Pollen-analytic investigations in the Tiglian of the Netherlands. — Mededelingen Geologische Stichting, N. S., **16**: 49–71; Haarlem.

Zagwijn, W. H. (1998): Borders and boundaries: a century of stratigraphical research in the Tegelen-Reuver area of Limburg (The Netherlands). — In: Van Kolfschoten, T., & Gibbard, P. L. (Eds.): The Dawn of the Quaternary. Proceedings of the SEQS-EuroMam symposium 1996. — Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, **60**: 19–34; Utrecht.

Manuscript submitted 2005–10–04
Revised manuscript accepted 2006–06–12