

# A villafranchian mustelid, *Pannonictis ardea* (Gervais, 1859) (Carnivora, Mustelidae) from Langenboom (Noord-Brabant, The Netherlands)

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Among many fossils from the sandpit 'De Kuilen' at Langenboom (Noord-Brabant, The Netherlands), two specimens of a large-sized mustelid were discovered. One specimen is a fragment of a maxilla with two molars: P<sup>4</sup> and M<sup>1</sup>; the other a mandible with two premolars P<sub>3</sub> and P<sub>4</sub> and one molar M<sub>1</sub>. Both fossils are described and illustrated. A comparison with several mustelid finds from sites of Villafranchian age elsewhere in Europe revealed a close resemblance to fossil remains described under different names. We conclude that the maxillary specimen represents a male individual, the mandible specimen a female, both belonging to *Pannonictis ardea* (Gervais, 1859) Schaub, 1949.

KEY WORDS: Mammalia, Mustelidae, *Pannonictis*, Pliocene, Langenboom

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## Introduction

In the last ten years an enormous number of fossils have been collected from the artificial lake 'De Kuilen' in Langenboom (province of Noord-Brabant, The Netherlands), most of them of late Miocene or Pliocene marine origin. Yet in the last few years a growing number of fossil remains of terrestrial mammals have been discovered as well, among the rich yield of shark teeth and cetacean bone fragments. Among these fossils it was particularly some molars of several animals that drew the attention of palaeontologists and these were described recently. The species identified so far include deer *Cervus rhenanus* Dubois, 1904 (see de Vos & Wijnker, 2006), jaguar *Panthera onca gombaszoegensis* Kretzoi, 1938 (Mol *et al.*, 2011) and beaver *Castor fiber* L. 1758 (Wessels *et al.*, in prep.). Of these only a molar of *Cervus rhenanus* was found *in situ*, in a layer that, on the basis of the available stratigraphic data, is supposed to be of early Pliocene age. A more elaborate synthesis of the Langenboom stratigraphy, presented by Wijnker *et al.* (2008) seems to confirm this conclusion. But other fossils of terrestrial mammals have been found in Langenboom as well, including remains of mastodon, horse, tapir, pig, bovid, rhinoceros and a second kind of deer, at least. Many of these (*ex situ*) finds seem to indicate an origin from layers of different ages as well,

both younger and older than early Pliocene.

Many of these mammal fossils have been referred to on several occasions (Ahrens, 2003, 2004) but have not been described in detail to date. Some time ago a fragment of a mustelid maxilla with two well-preserved molars, so far unknown from the Langenboom fauna, was recognized in Dick and Dirkje Hofman's Langenboom collection. Another mustelid specimen from the same sandpit is in the collection of Frank van Esch: an incomplete mandible with three well-preserved molars.

## Systematic palaeontology

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Mustelidae Fischer von Waldheim, 1817

Subfamily Mustelinae Fischer von Waldheim, 1817

Genus *Pannonictis* Kormos, 1931

## *Pannonictis ardea* (Gervais, 1859)

Figure 1

1828 Marte - Bravard, pp. 8, 11, 13, 128.

\*1859 *Mustela ardea* Gervais, p. 252, pl. 27, fig. 5.

1949 *Pannonictis ardea* Bravard - Schaub, p. 500-503, figs 5-6.

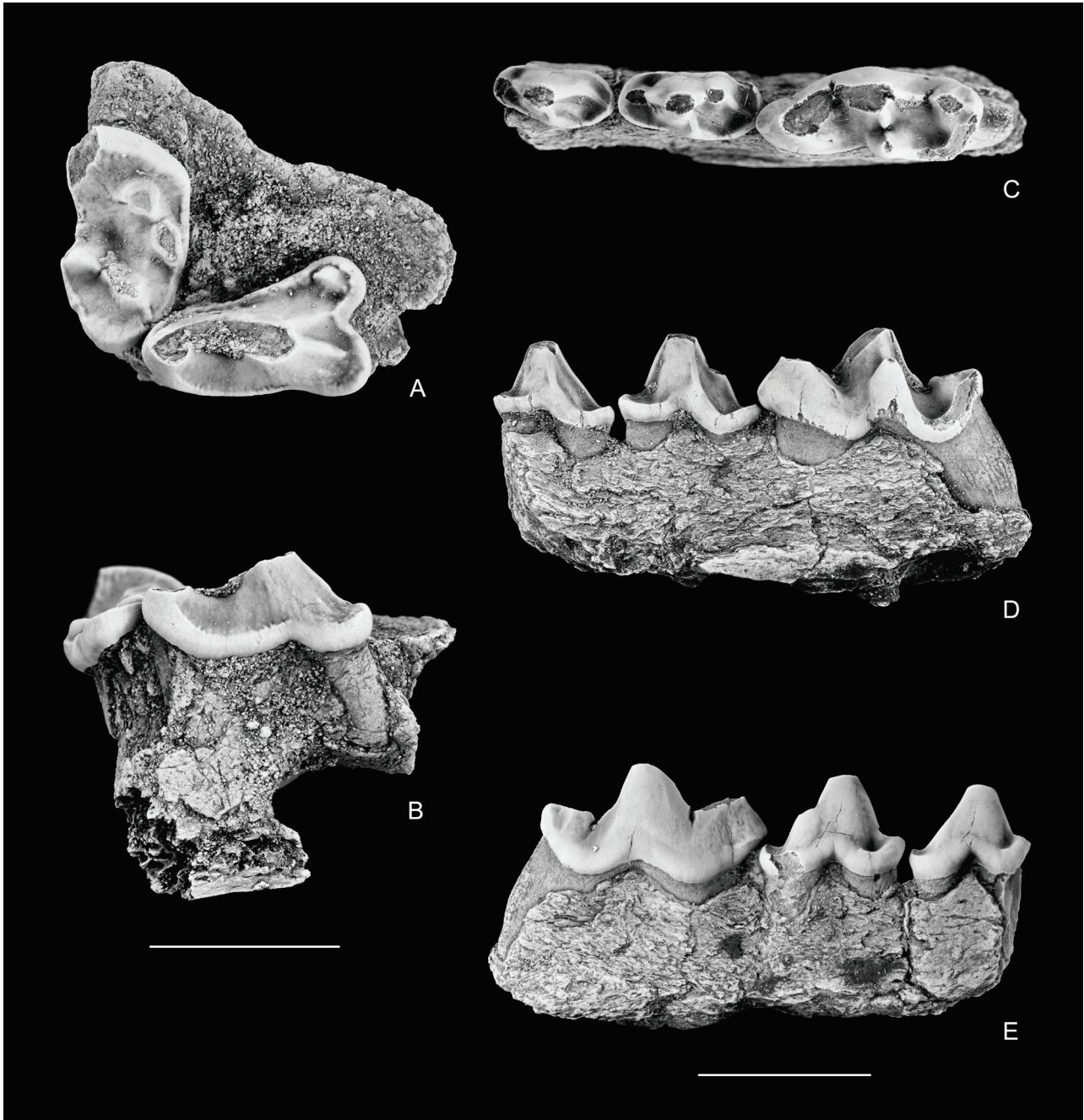
*Material* – Maxillary fragment with P<sup>4</sup> and M<sup>1</sup>, collected by Dick & Dirkje Hofman, now collection Museum De Groene Poort, Boxtel (MAB 4601); Figure 1 A-B. Mandibular fragment with P<sub>3</sub>, P<sub>4</sub> and M<sub>1</sub>, collected by Frank van Esch, collection van Esch, cast in Museum De Groene Poort, Boxtel (MAB 9001); Figure 1 C-E.

*Descriptions*

Left maxillary fragment with P<sup>4</sup> and M<sup>1</sup>.

The left P<sup>4</sup> and M<sup>1</sup> are attached to a small fragment of the maxilla, the lingual side of P<sup>4</sup> making an angle of about 60°

with the anterior side of M<sup>1</sup>. On the labial side two roots of P<sup>4</sup> and on the posterior side one root of M<sup>1</sup> are visible, all with a brownish colour. The enamel of the crown has a shining black appearance, except on the worn apices of some cusps. In the P<sup>4</sup> the paracone is the highest cusp, posteriorly it slopes down and forms a shearing blade together with the much lower metacone on the posterior end of the crown. This blade shows a large wear facet. The cingulum is well-developed all around the crown. Anterior to the paracone a small parastyle is present. The protocone is the lowest cusp of the crown. It is not worn and is surrounded anteriorly and lingually by the cingulum. The talon is narrow.



**Figure 1.** *Pannonictis ardea* (Gervais, 1859) Schaub, 1949. A-B: left maxillary fragment with P<sup>4</sup> and M<sup>1</sup> (MAB 4601); A - occlusal view, B - labial view. C-E: right mandibular fragment with P<sub>3</sub>, P<sub>4</sub> and M<sub>1</sub> (MAB 9001); C - occlusal view, D - lingual view, E - labial view; specimens whitened with ammoniumchloride. Scale bars represent 10 mm (photographs Barry van Bakel).

Location	collection nr	genus	species	from	P <sup>4</sup> length	P <sup>4</sup> width	M <sup>1</sup> length	M <sup>1</sup> width	male/ female
Villány	OB 3594	<i>Pannonictis</i>	<i>plioacaenica</i>	Rook (1995)	13.20	8.30	6.80	12.80	m
Villány- Kalkberg	UP 766	<i>Pannonictis</i>	<i>plioacaenica</i>	Rook (1995)	10.70	7.80			m
Villány- Kalkberg	UP 129	<i>Pannonictis</i>	<i>plioacaenica</i>	Rook (1995)	11.50		6.50		m
Villány- Kalkberg	UP 765	<i>Pannonictis</i>	<i>plioacaenica</i>	Rook (1995)	11.20	7.25	6.20	9.35	m
Villány- Kalkberg	UP 149	<i>Pannonictis</i>	<i>plioacaenica</i>	Rook (1995)	12.00	7.60			m
Villány- Kalkberg	UP 132	<i>Pannonictis</i>	<i>plioacaenica</i>	Rook (1995)	12.55	8.70	7.25	12.05	m
Saint Vallier	QSV 150	<i>Enhydriectis</i>	<i>ardea</i>	Viret (1954)	10.4	6.2	5.2	10.5	f
Tegelen	RGM 72.158	<i>Enhydriectis</i>	<i>ardea</i>	Willemsen (1988)	11.6	5.9			f
<b>Mill- Langenboom</b>	<b>MAB 4601</b>	<b><i>Pannonictis</i></b>	<b><i>ardea</i></b>		<b>12.7</b>	<b>7.4</b>	<b>6.5</b>	<b>12.4</b>	<b>m</b>

**Table 1.** Length and width of P<sup>4</sup> and M<sup>1</sup> (in mm) of mustelid MAB 4601 from Langenboom, compared with some European mustelids, *Pannonictis plioacaenica* from Villány and *Enhydriectis ardea* from Saint-Vallier and Tegelen. Measurements of Villány material after Rook (1995), of Saint-Vallier material after Viret (1954). RGM = NCB Naturalis, Leiden, The Netherlands; OB and UP = Geological Institute of Hungary, Budapest, Hungary; QSV = Muséum d'Histoire Naturelle de Lyon, France.

The anterior side of the M<sup>1</sup> is about parallel with the posterior side. The labial side has a bluntly rounded shape, the talon on the posterior-lingual side is slightly rounded and curved upwards with respect to the rest of the crown surface. The hindmost part of the talon is broken off. On the M<sup>1</sup> surface four cusps are exposed, the metacone on the posterior-labial side with a smooth surface on the pointed apex, the other three cusps with obvious wear facets.

Between the metacone and paracone on the labial side of the crown and the more lingually situated protocone and protoconule the surface has a longitudinal concavity. The dimensions of the molars are given in table 1 together with data of the same elements of related mustelids from other European sites.

Right mandibular fragment with P<sub>3</sub>, P<sub>4</sub> and M<sub>1</sub>.

The two lower premolars are two-rooted and monocuspid, both presenting a high and strong paraconid, that slopes down posteriorly to a shallow talonid basin surrounded by a strong cingulum. The talonid covers only the minor distal part of the teeth. The proximal part of the teeth also exhibits a strong cingulum at the base of the paraconid. Both premolars show few traces of wearing, the mandible clearly being of a rather young adult.

M<sub>1</sub> has two robust roots and exhibits a strongly developed paraconid and protoconid on its surface, both slightly worn at the top. The metaconid is much smaller and lower than the other two cusps of the trigonid. It is situated posterolingually from the protocone, from which the base of the metaconid is not free. The hypoconid forms part of the ridge that surrounds the talonid. Length and width of the molars are given in table 2.

Location	collection nr	attribution	data from	P <sub>3</sub> length	P <sub>3</sub> width	P <sub>4</sub> length	P <sub>4</sub> width	M <sub>1</sub> length	M <sub>1</sub> width	male/ female
Villány- Kalkberg	UP 135	<i>Pannonictis pilgrimi</i>	Rook (1995)					13.5	5.35	f
Villány- Kalkberg	UP 768	<i>Pannonictis pilgrimi</i>	Rook (1995)	6.2	3.85	7.25	4	13.55	5.35	f
Beremend	UP 606	<i>Pannonictis pilgrimi</i>	Rook (1995)	6.1		6.4		11.8		f
Villány- Kalkberg	OB 3596	<i>Pannonictis plioacaenica</i>	Rook (1995)	6.7	4	7.7	4.2	15.3	6.8	m
Villány- Kalkberg	OB 3600	<i>Pannonictis plioacaenica</i>	Rook (1995)	6.7	4.3	8.2	4.3	15.4	6.3	m
Villány- Kalkberg	UP 129	<i>Pannonictis plioacaenica</i>	Rook (1995)	7.15		7.35		15.9		m
Villány- Kalkberg	UP 769	<i>Pannonictis plioacaenica</i>	Rook (1995)	7	4.5			15.7	6.6	m
Villány- Kalkberg	UP 767	<i>Pannonictis plioacaenica</i>	Rook (1995)	6.65	4.75	8.9	4.75	15.95	6.55	m
Villány- Kalkberg	UP 134	<i>Pannonictis plioacaenica</i>	Rook (1995)			8.85	4.5	15.45	6.35	m
Tegelen	RGM 72.158	<i>Enhydriectis ardea</i>	Willemsen (1988)	6.1	3.4			12.7	5.2	f
<b>Mill- Langenboom</b>	<b>MAB 009001</b>	<b><i>Pannonitis ardea</i></b>		<b>6.4</b>	<b>3.4</b>	<b>7</b>	<b>4.1</b>	<b>12.7</b>	<b>5</b>	<b>f</b>

**Table 2.** Measurements of lower dentition of *Pannonictis ardea* from Langenboom MAB 009001 compared with some European *Pannonictis* finds described under different names. Data of the Langenboom fossil in bold. Measurements of Villány material after Rook (1995), of Saint-Vallier material after Viret (1954). For abbreviations see Table 1.

*Discussion* – Since the early Villafranchian the genus *Pannonictis* has been distributed in Eurasia from eastern China to western Europe. However, most of the finds of this large-sized mustelid are scant and fragmentary, resulting in a proliferation of names in the literature, like *Pannonictis ardea*, *Enhydriactis ardea* (Viret, 1954), *Pannonictis pliocaenica* (Kormos, 1931), *P. pilgrimi* (Kormos, 1933), *P. nestii* (Martelli, 1906) and unclear taxonomic history. Garcia *et al.* (2008) gave an overview of all localities where fossil remains of mustelids were found and of the species of the two genera *Pannonictis* and *Enhydriactis* to which these remains have been assigned by several authors. From this latter paper the most relevant specimens and/or data have been used herein for a comparison with the two fossils from Langenboom. These are: *Enhydriactis ardea* from Saint Vallier (Viret, 1954) and Tegelen (Willemsen, 1988), *Pannonictis pliocaenica* and *P. pilgrimi* described by Kormos (1931, 1933) from several Hungarian sites, with supplementary biometrical data from Rook (1995) and the holotype of *P. ardea* from Perrier-Etouaires. The last mentioned taxon was by several authors erroneously attributed to Bravard (1828). In Bravard's 'Monographie' of 1828, however, a fossil 'Marte' is indeed mentioned, but not illustrated or described. The taxon was first introduced by Gervais (1859) as *Mustela ardea* and transferred to the genus *Pannonictis* Kormos, 1931 by Schaub (1949), who based his opinion on the holotype, consisting of one left mandible with  $M_1$ . According to Gervais 'cette espèce a été recueillie à Ardé, près Issoire, par M. Bravard, qui lui a donné le nom spécifique sous lequel nous la citons' ['This species has been collected at Ardé near Issoire by Mr Bravard, who has given it the specific name under which we cite it'].

Schaub (1949) referring to *Pannonictis ardea* wrote: 'Le Muséum de Paris possède une mandibule gauche, qui ne porte que la carnassière. C'est le type de *Mustela ardea* Bravard. Le document provient de la Côte d'Ardé, localité du versant est de la Montagne de Perrier, située au niveau des Sables des Etouaires. *Mustela ardea* fut figurée par Gervais, Zool. et Pal. franç. Pl. 27.5. La diagnose est très courte: "Plus robuste et plus grand que le Putois. Longueur de la carnassière 0,011. Son talon est peu excavé." .... Il est évident que la carnassière ne peut pas être attribuée à une espèce du genre *Martes*. Par contre, elle possède la même structure que la carnassière inférieure de *Pannonictis pilgrimi*, espèce découverte par Kormos (1934 [sic]) dans les brèches 'préglaciales' de Villány-Mészköhegy (Hongrie). .... J'attribue donc le Mustélide de Perrier au genre *Pannonictis*. Quant à sa détermination spécifique, je propose de conserver le nom choisi par Bravard....'. ['The Paris Museum owns a left mandible, in which only the carnassial is preserved. It is the type of *Mustela ardea* Bravard. The specimen originates from the Côte d'Ardé, a locality on the eastern slope of the Montagne de Perrier situated at the level of the Sables des Etouaires. *Mustela ardea* was illustrated by Gervais, Zool. et Pal. franç. Pl. 27.5. The diagnosis is very short: "More robust and larger than the polecat. Length of the carnassial 0,011. Its talon is not much excavated." .... It is evident that the carnassial can not be attributed to a species of the genus *Martes*. On the contrary, it has the same structure as the

lower carnassial of *Pannonictis pilgrimi*, a species discovered by Kormos (1934 [sic]) in the 'pre-glacial' breccia of Villány-Mészköhegy (Hongrie). .... I therefore attribute the Mustelid of Perrier to the genus *Pannonictis*. Concerning its specific determination, I propose to preserve the name chosen by Bravard....'].]

In our study we did not aim to revise the mustelid material or the taxonomic position of specimens, but only record the *Pannonictis* finds from Langenboom. However, in deciding which name would be most appropriate for our specimens, we follow Garcia *et al.* (2008) and do so in agreement with some of their major conclusions, as discussed below.

In general appearance the morphological characters of  $P^4$  and  $M^1$  of the Langenboom maxilla MAB 4601 seem to correspond with *Enhydriactis ardea* depicted by Viret (1954) as well as with *Pannonictis pliocaenica* illustrated in Kormos (1931). *Enhydriactis ardea* is the smaller and more slender mustelid, *P. pliocaenica* is more robust. Notwithstanding the obvious affinity between these two mustelids, Viret (1954) considered them to be distinct species not so much on account of their different sizes, but rather based on a number of differences in skull morphology and - to a lesser extent - in dentition.

For the  $P^4$  of the holotype of *Pannonictis pliocaenica* Kormos (1931) mentioned the 'very peculiar shape of the carnassial' with a very strong cingulum which forms a triangular, cup-like excavation on the lingual side and extends caudally beyond the middle line of the tooth, the crown thus assuming the shape of an equilateral triangle in ventral aspect.

Viret (1954), in his comparison of the  $P^4$  of *Enhydriactis ardea* with *Pannonictis pliocaenica*, observed not only a difference in size but also a lower crown and a moderate cingulum, forming a small parastylar cushion on the anterior side of the crown in *E. ardea*. On the lingual side the low and concave talon resembles that of *P. pliocaenica*, but it is less prominent and less separated from the anterior border of the crown.

Willemsen (1988) studying some mustelid fossils from Tegelen described a right  $P^4$  from the pit Canoy Herfkens (NCB Naturalis, Leiden; RGM 72 158) also as *Enhydriactis ardea*. This fossil shows the same morphological characters as described by Viret (1954) but is relatively small and slender.

The size and morphology of the Langenboom  $P^4$  is more *Pannonictis*-like. With respect to the  $M^1$ , Kormos pointed to the rhombiform upper first molar that (together with the lower carnassials morphology) is a character in which the Villány fossil proves to be the most like the polecat- or marten-sized grison. The anterior and posterior sides of the molar are parallel. The Saint-Vallier  $M^1$  is more triangular in outline. Our Langenboom  $M^1$  corresponds better with a *Pannonictis*  $M^1$ .

As to the dimensions of the two teeth of MAB 4601, length and width of the molars fit quite well in the range of Villány molars that are presented in Table 1 and also in the more comprehensive data given by Garcia & Clark Howel (2008).

In 1933 Kormos described a second *Pannonictis* species from Villány as *P. pilgrimi*: a smaller form that according

to Kormos (1933) showed sufficient differences with *P. pliocaenica* to differentiate the two. But as Viret (1954) argued, *Enhydriactis ardea* and *Pannonictis pilgrimi* are in fact the same species, the latter being a junior synonym of the first.

Ficarelli & Torre (1967) in their description of a Sardinian mustelid *Enhydriactis galictoides* gave upper dentition patterns of a number of related mustelids. Of the mustelids shown in their fig. 7 there is one in particular (d = UP 765 = another *Pannonictis pliocaenica* from Villány) that clearly shows a very close resemblance to the two molars of the Langenboom MAB 4601 specimen presented here. The teeth in the Langenboom mandible were compared with some fossils of a mustelid from Tegelen (NCB Naturalis, Leiden: RGM 72 158) that were described by Willemsen (1988) as *Enhydriactis ardea*. The premolar P<sub>3</sub> and two molars M<sub>1</sub> from Tegelen show such a close resemblance, in morphology as well as in measurements, to the corresponding teeth from Mill-Langenboom, that in our opinion they must belong to the same species.

In the collection of the Natural History Museum in Basel (Switzerland) are housed specimens of the two *Pannonictis* species that were described and illustrated by Kormos in 1931 (*Pannonictis pliocaenica*) and 1933 (*P. pilgrimi*). Mandibles and lower dentition of both species show the same morphology as the Langenboom fossil, but the *P. pliocaenica* teeth are noticeably more robust than the corresponding teeth of *P. pilgrimi*, *Enhydriactis ardea* and the Langenboom *Pannonictis ardea*, as can be seen in table 2. Measurements of the lower dentition of the Langenboom fossil also fit quite well in the data-set provided by Garcia & Clark Howell in 2008.

Garcia et al. (2008) taxonomically revised the Eurasian occurrences of *Pannonictis*. In their analysis they included the extensive Villány-Kalkberg-collection stored at the Hungarian Geological Institute at Budapest with many *Pannonictis*-remains that had not been studied or published so far. They reached several conclusions about the different European species involved and their nomenclature. *Pannonictis pliocaenica* and *P. pilgrimi* in their opinion are probably males and females respectively of one species exhibiting sexual dimorphism, a phenomenon that can be seen in all mustelids. *Pannonictis* and *Enhydriactis* are separate genera, closely related, the latter genus being represented only by *E. galictoides* from Sardinia, a late Pleistocene relict of an old genus.

We agree with their conclusions and think that morphological differences as described by several authors are due to intraspecific variability and sexual dimorphism. The mandible MAB 9001 described herein would then have belonged to a female of this species, the maxilla MAB 4601 to a male. We suggest that *Pannonictis ardea* would be the most appropriate name for the species, as *ardea* has priority over the other names. But at the same time we realize that our assumption that all names used so far could be synonymous needs more evidence than we can produce on the base of the specimens from Langenboom.

The fauna of Saint-Vallier is an important biostratigraphic reference fauna for mammal zonation in Europe. It is considered to be the typical MN17 standard zone, often called middle Villafranchian. Guérin *et al.* (2004) published a

synthesis of biostratigraphic and palaeoecological conclusions based on new excavations between 1993 and 1999 as well as on old (and well known) data. They argue that a mammalian community of the Saint-Vallier type presents evidence of a landscape with a mosaic of steppe and open wooded areas including bodies of water or streams in a relatively humid, not very cold climate. A strictly aquatic life of *Pannonictis*, comparable to the style of otters, is not likely, but habitats close to river courses are suggested (Garcia *et al.* 2008).

*Pannonictis ardea* is represented in the Saint-Vallier-fauna and in several other European faunas of comparable or slightly younger age (Perrier, Villány-Kalkberg, Tegelen). It looks as if many of the other land mammal fossils found in Langenboom also testify to a fauna of the Villafranchian type, such as in Saint-Vallier and/or Tegelen.

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