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New record of the European jaguar, *Panthera onca gombaszoegensis* (Kretzoi, 1938), from the Plio-Pleistocene of Langenboom (The Netherlands)

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A left lower molar of the European jaguar, *Panthera onca gombaszoegensis* (Kretzoi, 1938), collected *ex situ* at the locality 'De Kuilen' near Langenboom (province of Noord-Brabant, The Netherlands), is described and illustrated. This specimen is compared to Early Pleistocene material from Untermassfeld (Thüringen, eastern Germany) and from Tegelen (province of Limburg, The Netherlands). The three other records of *P. onca gombaszoegensis* from The Netherlands are briefly reviewed. *P. onca gombaszoegensis* is a fauna element of the Late Pliocene and Early Pleistocene in The Netherlands.

KEY WORDS: Mammals, pantherine cats, North Sea Basin.

Introduction

During screen washing in 2002 of glauconitic sediments of Miocene and Pliocene age at the 'De Kuilen' locality near Langenboom (Wijnker *et al.*, 2008), Mr Jan Boes (Emmeloord), discovered a molar of a terrestrial mammal. The Langenboom marine sediments are very rich in species and famous among local fossil collectors. To date, more than 200 species of molluscs, 34 species of birds, 9 species of decapod crustaceans, more than 30 species of sharks and rays, some 30 odd species of bony fish, more than 20 species of whales and dolphins, 4 species of seal and a single walrus have been recorded from the locality.

A few terrestrial mammal species have also been noted at this locality (Ahrens, 2003, 2004), namely the mastodon of Auvergne, *Anancus arvernensis* (Croizet & Jobert, 1828), the Etruscan rhino, *Stephanorhinus etruscus* (Falconer, 1868), Strozzi's wild boar (*Sus strozzii* Forsyth Major, 1881, the Etruscan bear (*Ursus* cf. *etruscus* Cuvier, 1823), a horse (*Equus* sp.) and the Rhine deer (*Cervus rhenanus* Dubois, 1904). In general, these species are of Early Pleistocene or early Villafranchian age. However, the exact provenance and context of these specimens remain unknown, because they were amassed *ex situ* by various collectors at various times from sand dumps at Langenboom.

In recent years, more fossil terrestrial mammals have been collected. Although these specimens have only been identified preliminarily and are awaiting detailed study and description, it is clear that some further species may be added to Ahrens's (2004) list. For instance, teeth and post-crania of tapirs, *Tapirus arvernensis* (Croizet & Jobert, 1828), have been identified (J. de Vos and D. Mol, pers. obs.). In The Netherlands, the odd-toed tapir is known only from the Maalbeek clay pit south of Tegelen, of Early Pleistocene age (Mol *et al.*, 2008); for a detailed description, reference is made to Kortenbout van der Sluijs (1960). In 1961, the same locality yielded a molar of *Anancus arvernensis* (see Braber *et al.*, 1999). Recently, the Rhine deer (*Cervus rhenanus*) was recorded by de Vos & Wijnker (2006) from Langenboom, on the basis of a molar (M3 sup. dext.) collected from an *in situ* layer by a scuba diver, 14 m below the water level of the artificial lake. So far, this molar is the single terrestrial mammal fossil collected *in situ* at this locality. The molar was found in a sequence of marine sands of the Pliocene Oosterhout Formation.

The new molar (a lower first molar, m1 inf. sin.; J. Boes collection, unregistered, and an accurate cast in the collection of the NCB Naturalis at Leiden) is here attributed to the European jaguar, *Panthera onca gombaszoegensis*. It represents the first record of this subspecies from Langen-

boom. We have compared this specimen to rich material from the Early Pleistocene of Untermassfeld (Thüringen, eastern Germany), housed in the collections of the Forschungsstation für Quartärpaläontologie der Senckenbergischen Naturforschenden Gesellschaft at Weimar (IQW registration numbers), and to Early Pleistocene specimens from Tegelen in the NCB Naturalis collections at Leiden (St. and RGM registration numbers; note that O'Regan & Turner (2004) applied the abbreviation NGM for the registration of the Naturalis collection in Leiden). At present, the extinct European jaguar is known from three localities in The Netherlands: Tegelen (O'Regan & Turner, 2004), the Maasvlakte (Hemmer & Kahlke, 2005) and from Langenboom (this paper).

Panthera onca gombaszoegensis

The extinct European jaguar (Fig. 1) was first described by Miklos Kretzoi (1938), as *Leo gombaszoegensis*, from the classic Early Pleistocene site of Gombaszög, Hungary. In the literature, this species is often referred to as *Panthera gombaszoegensis* (*e.g.* O'Regan & Turner, 2004) or occasionally as *P. onca gombaszoegensis*, *e.g.* Hemmer (2001), Hemmer *et al.*, (2001, 2010), Hemmer & Kahlke (2005). Herein, we follow Hemmer (2001) and Hemmer *et al.* (2010) interpreting this as a subspecies, *P. onca gombaszoegenis*. The European jaguar was a huge pantherine felid, a heavily-built predator with a body weight range between 70 and 210 kg, which was much larger than the modern jaguar from South America, *Panthera onca* Linnaeus, 1758. The oldest fossils of the extinct taxon are those from Tegelen (2.4-1.7 Ma; see O'Regan & Turner, 2004). On the basis of the size of the dentition, O'Regan & Turner (2004) concluded that the Tegelen fossils represent the smallest individuals of *P. onca gombaszoegensis* known.

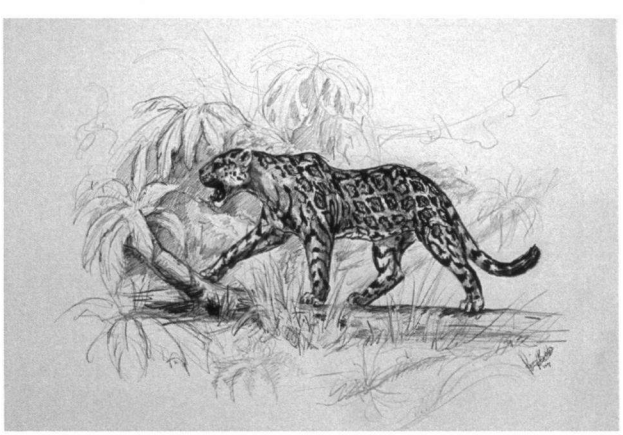

Figure 1. Artist's impression of *Panthera onca gombaszoegensis* (drawing by Remie Bakker, Rotterdam, 2009).

The locality of Untermassfeld (Thüringen), dated at *c.* 1 Ma, has yielded a rich late Early Pleistocene fauna with two machairodonts and four pantherine felids, including *P. onca gombaszoegenis* which was studied in detail by Hemmer (2001). The European jaguar co-occurred in Early and Middle Pleistocene assemblages with machairodont competitors such as *Homotherium* and *Megantereon* and pantherine felids such as *Acinonyx pardinensis* Croizet & Jobert, 1828 and *Lynx issiodorensis* Croizet & Jobert, 1828 (see Turner, 1995). During the Early Pleistocene, *P. onca gombaszoegensis* was the sole representative of the genus *Panthera* in Europe. Other records of this species are from Middle Pleistocene localities such as Westbury-sub-Mendip (England), Mosbach (Germany), Atapuerca (Spain) and L'Escale (France). At the start of the Middle Pleistocene (*c.* 0.9 Ma), *P. pardus* Linnaeus, 1758 and some 300,000 years later, *P. leo fossilis* (von Reichenau, 1906) made their first appearance as competitors of *P. onca gombaszoegensis*. Approximately 500,000 BP, the European jaguar went extinct (O'Regan & Turner, 2004).

Material and description

A single m1 sin. (original, not registered, J. Boes collection, Emmeloord; see Figs 2 A, 2 B; an artificial cast is in coll.RGM 592802).

Figure 2 A, B. The Langenboom m1 sin. of *Panthera onca gombaszoegensis* (J. Boes collection, unregistered), in buccal and lingual views, respectively. Length = 21.0 mm.

This near-complete specimen is well-preserved; only a part of the posterior root is missing. It is attributed to a mature, yet not too old individual based on the wear of the molar. In comparison with other specimens of this subspecies from localities such as Tegelen, Untermassfeld and elsewhere, it is clear that the present specimen is relatively small and probably belonged to a female. It is well known that there is a quite marked sexual dimorphism in large felids, the males being larger than the females. Another hypothesis is that stratigraphically older members of this species were of smaller size. For measurements of the Langenboom specimen, see Table 1.

Site	Specimen	Side	Length	Width
Langenboom	J. Boes unregistered	sin.	21,0	9,6
Tegelen	AM A3	dex.	20,2	9,7
Tegelen	NGM unregistered	sin.	20,9	9,6
Tegelen	NGM 102738	sin.	26,0	11,0
Tegelen	NGM 103142	sin.	n.a.	9,9
Halykes	AL 7	sin.	22,8	11,0
Sammezzano	IGF 853	sin.	21,1	10,4
Castelfranco	IGF 852	sin.	21,3	10,0
S. Maria nr II Tasso	IGF 851	dex.	22,4	10,4
Upper Valdarno	IGF 12458	dex.	n.a.	9,9
Untermassfeld	1995/25343 (Mei. 24872)	dex.	23,0	11,2
Untermassfeld	1983/19169 (Mei. 18689)	sin.	22,5	11,2
Untermassfeld	1980/17157 (Mei. 16678)	dex.	25,4	12,2
Untermassfeld	1986/21780 (Mei. 21298)	dex.	27,7	13,2
L'Escale	FSM 1048	dex.	25,2	11,8
L'Escale	CD 614	dex.	26,3	13,6
L'Escale	CD 613	dex.	25,8	11,3
L'Escale	CD 763	dex.	25,4	11,8
L'Escale	CD 762	sin.	25,8	12,3
Atapuerca	Sabadell	sin.	22,6	10,8
Atapuerca	Sabadell	dex.	23,6	11,4
Westbury-sub-Mendip	M47598	sin.	26,2	12,0
Westbury-sub-Mendip	M47340	sin.	22,9	11,5
Westbury-sub-Mendip	F74 (M33678)	dex.	23,9	11,8
Westbury-sub-Mendip	F75 (M33679)	dex.	22,9	11,3
Westbury-sub-Mendip	F56 (probably M33684)	dex.	25,2	11,2
Gombasek	GIH unregistered	sin.	24,2	11,6
Gombasek	8915 (V59/1085)	sin.	20,0	9,9
Gombasek	M9 (V59/1084)	sin.	22,3	10,9
Koneprusy	IGF 851 V	sin.	23,3	11,5
Mosbach 2	1968-398	dex.	24,2	12,5

Table 1. Measurements (in mm) of m1 of European *Panthera onca gombaszoegensis* (see references) and the Langenboom specimen described herein.

The crown is undamaged; the buccal side being convex and barely worn and the enamel strongly wrinkled. Such wrinkled structure of crown enamel is also seen in molars of extant cheetah (*Acinonyx jubatis* Schreber, 1775), but this large felid has very high-crowned m1 and can thus be excluded from consideration. There is a pronounced cingulum at the base of the entire crown. The lingual side is near-straight, with a slight swelling; this does not represent a true lingual bulge. A similar slight swelling has been noted in a lower m1 from the Russel-Tiglia-Egypte quarry at Tegelen (NCB Naturalis, Leiden coll., St.103142), as described by O'Regan & Turner (2004). Some examples of m1 of *P. onca gombaszoegensis* show a small metaconid, *e.g.* IQW 1986/21780 (Mei. 21299) from Untermassfeld. Such a metaconid is missing from the Langenboom m1; we do not consider this feature to be diagnostic for *P. onca gombaszoegensis*.

The length of the protoconid exceeds that of the paraconid, a feature typical of *P. onca gombaszoegensis* (see O'Regan & Turner, 2004). The same holds true for the length of the cutting edge of the protoconid. The V-shaped notch between the conids measures more than 90 degrees and the depth equals half the height of the protoconid.

The top of the anterior root is less wide towards the base of the crown in comparison to specimens from Untermassfeld (*e.g.* left mandible with c and p3-m1 [IQW 1983/19169

(Mei. 18689)], right mandible with i2, c and p3-m1 [IQW 1995/25343 (Mei. 24872)], m1 dex. [IQW 1986/21780 (Mei. 21299)] and m1 dex. [IQW 1980/17157 (Mei. 16678)]).

Records of the European jaguar from The Netherlands and adjacent North Sea area

1. Maasvlakte

Hemmer & Kahlke (2005) described and illustrated a fragmentary right mandible of a female P. *onca gombaszoegensis* from the Maasvlakte. The locality is famous amongst fossil collectors who have amassed extensive collections of vertebrate remains of a mixed Early Pleistocene to Holocene age, in which four faunas (numbered 0 to III) are distinguished. The morphology of the Maasvlakte specimen suggests it to be of a late Early or early Middle Pleistocene age and was attributed by Hemmer & Kahlke (2005) to Fauna I. That fauna is characterised by an assemblage of large mammals such as muskox [*Praeovibos* cf. *priscus* Staudinger, 1908), steppe goat (*Soergelia* sp.), moose [*Alces latifrons* (Johnson, 1874)], fallow deer (*Dama* sp.), giant deer [*Praemegaceros verticornis* (Dawkins, 1872)] and *Megaloceros* sp., hippopotamus (*Hippopotamus amphibius antiquus* Desmarest, 1822), wild boar (*Sus scrofa* cf. *mosbachensis* Küthe, 1932), Etruscan rhinoceros (*Stephanorhinus etruscus*), horse (*Equus* sp.), southern mammoth [*Mammuthus meridionalis* (Nesti, 1825)], lynx (*Lynx* sp.), otter [*Aonyx antiqua* (Blainville, 1841)] and bear (*Ursus* cf. *deningeri* von Reichenau, 1904), a fauna assemblage characteristic for the late Early Pleistocene of NW Europe.

2. Tegelen

Staff members of the Rijksmuseum van Geologie en Mineralogie (now Netherlands Centre for Biodiversity Naturalis, Leiden) collected (August 16, 1960) at the Russel-Tiglia claypit (Tegelen) a deformed felid mandible in a clay concretion, together with some isolated dental elements (amongst others a p4 inf. sin and a m1 inf. sin.) of one individual. These specimens, catalogued as St. 102738, were identified as *Felis (Panthera) schreuderi* von Koenigswald, 1960. That taxon is a junior synonym of *P. onca gombaszoegensis* as noted by Hemmer & Schütt (1969) and confirmed by O'Regan & Turner (2004).
All material from Tegelen attributed to *P. onca gombaszoegensis* was studied by O'Regan & Turner (2004), inclusive of specimen St. 102738, a concretion which contains the natural mould of a deformed left and right mandible of the same individual. The original label with St 102738 reads (in Dutch), '*Felis (Panthera) schreuderi* Von Koenigswald. Concretie met afdrukken van mandibula sin. en mandibula dext.: fragmenten van mandibula sin.; p/4 sin.; m1 sin. Tiglien. Limburg, gebied ten Noorden van Geleen tot Mook, Tegelen. Groeve Russel-Tiglia, Egypte. Coll.: Prof. v.d. Vlerk & Kortenbout v/d Sluijs, 16 aug. 1960' [translated: '*Felis (Panthera) schreuderi* von Koenigswald. Concretion with imprints of mandible sin. and mandible dext.: fragments of mandible sin.; p/4 sin.; m1 sin. Tiglian. Limburg, area North of Geleen to Mook, Tegelen. Quarry Russel-Tiglia, Egypte. Coll.: Prof. v.d. Vlerk & Kortenbout v/d Sluijs, 16 Aug. 1960']. This indicates that all the dental elements associated with the concretion bear the same catalogue number.
A rubber cast of the natural mould was produced, and based on the size of this it was concluded that the specimen was substantially larger than other individuals of the species. However, O'Regan & Turner, 2004, did not realize then that the clay of the concretion would have compacted and formed shrinkage cracks, the expansion causing a wider space for the molars, explaining why measurements of the rubber cast exceeded those of the original molar. Subsequently of that study it turned out that the left unnumbered m1 which they referred to as RGM 102738, fits the natural mould of the left mandible in the concretion (St. 102738). As would be expected, the m1 is too small for the hole left by the m1 in the clay concretion and is also smaller than the m1 of the rubber cast.
In our study of the Langenboom specimen, we have compared it to an individual from Tegelen (NGM, no number in O'Regan & Turner, 2004; see Table 1 herein). The measurements of the crowns in both specimens are near-equal (length/width 21,0/9,6 mm *vs* 20,9/9,6 mm). The abrasion of the Tegelen m1 is stronger, which indicates it to have belonged to a slightly older individual. The enamel of the crown of the Tegelen specimen is also strongly wrinkled.

3.Yerseke (North Sea)?

Another record of the European jaguar has been published quite recently by Probst (2009, pp. 260-261), on the basis of a calcaneum from Yerseke (Kees van Hooijdonk collection, Rucphen, The Netherlands, no. Y.1661) from sediments dredged from the bottom of the North Sea off the Zeeland coast. This specimen was briefly described by van Hooijdonk (2003) and identified as *Homotherium* on the basis of similarities with a typical *Homotherium* calcaneum. However, van Hooijdonk (2003) did note that Y.1661 was considerably smaller than that of *Homotherium* and badly weathered.
In an attempt to confirm or reject that identification, sample Y.1661 was studied by experts on large felids and one of the options considered was that this calcaneum could also be attributed to the European jaguar; a thorough description and discussion have never been presented. According to van Hooijdonk (D. Mol, pers. comm., June 26, 2009), it is unclear to him why this calcaneum was placed in *P. onca gombaszoegensis* by Probst (2009). For now, we list Y.1661 herein as Felidae indet.

Evolutionary trends

The scatter diagram (Fig. 3), based on measurements of the m1 of *P. onca gombaszoegensis* listed in Table 1, illustrates a trend in the evolution of this subspecies towards larger size. Specimens from Tegelen (*c.* 2.4-1.7 Ma) and Gombasek (Gombaszög) are small, while individuals from Untermassfeld, Westbury-sub-Mendip, Mosbach, Atapuerca and L'Escale (all dated at approximately 1 Ma) are considerably larger.
Specimen RGM 103142 (rubber cast) is too large and appears isolated in the diagram (the square at point 26/11) by the fact that it is situated between the late early and early middle Pleistocene specimens.
The scatter diagram does not allow conclusions on male and female clustering.

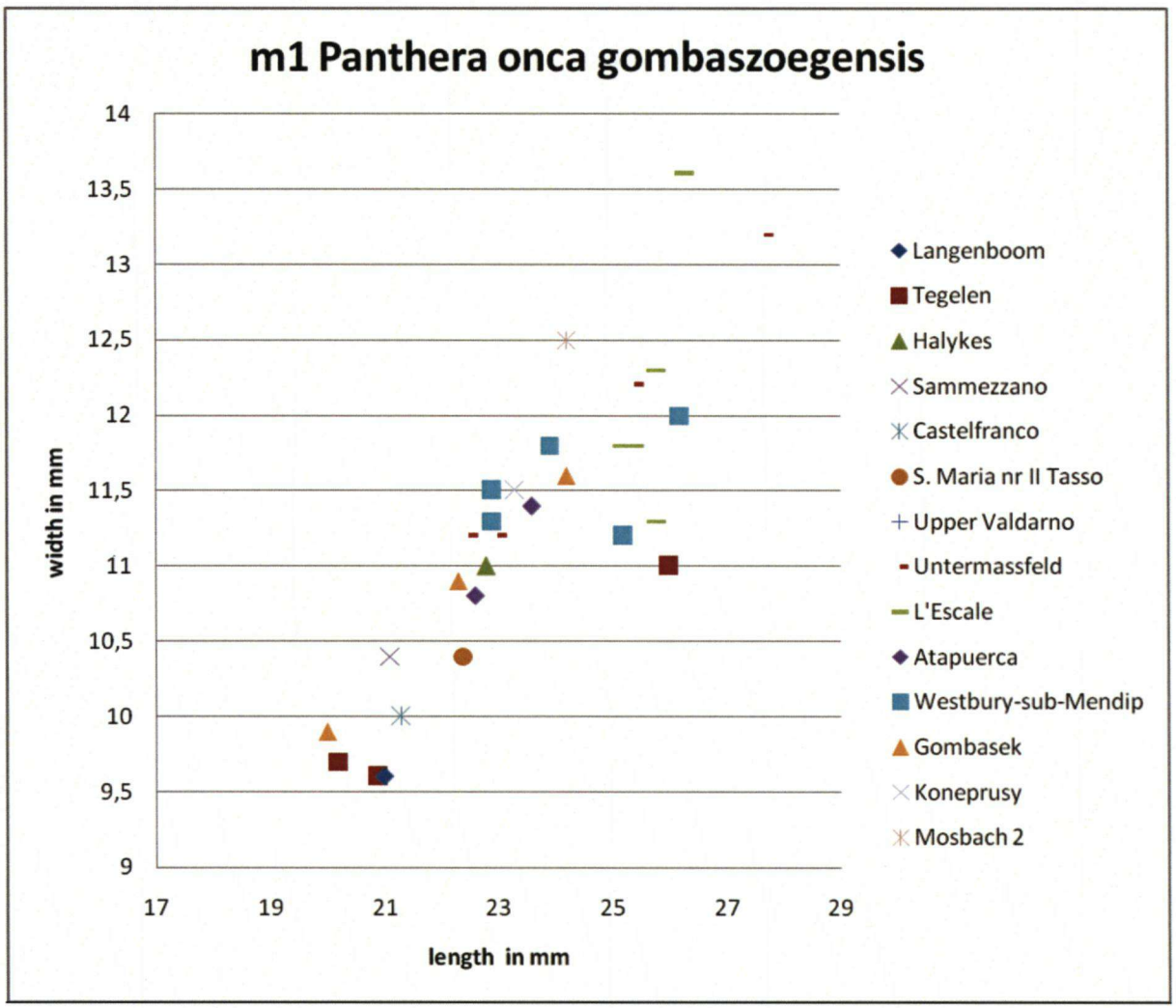

Figure 3. Scatter diagram of length and width of m1 of the European jaguar, *Panthera onca gombaszoegensis* (modified from O'Regan & Turner, 2004).

Discussion

Our comparative study allows attribution of the m1 from Langenboom to *P. onca gombaszoegensis*. Unfortunately, the exact stratigraphical provenance remains unclear. Based on the state of preservation, this find might prove that this subspecies belonged to a fauna which included *Tapirus arvernensis* and thus is older than 2.7 Ma (Sardella *et al.*, 1998), possibly deriving from the Oosterhout Formation interval from which also *Cervus rhenanus* was recorded (de Vos & Wijnker, 2008). If this is correct, *P. onca gombaszoegensis* must be placed in the Early Pliocene or early Villafranchian. However, a date of >2.7 Ma contradicts data supplied by Sardella *et al.* (1998), indicating that this subspecies ranged in age between 1.9 and 0.8 Ma. The uncertainty about the stratigraphic provenance of the Langenboom specimen does not allow to extend its stratigraphic range, so we can only assume a Pliocene to Early Pleistocene age for the present material.

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