The first record of a beaver – *Trogontherium (Euroxenomys) minutum* – in the Höwenegg fauna (Miocene, southern Germany)

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Abstract

The fist record of a beaver from the Late Miocene (MN 9) Höwenegg fauna, a dentary fragment with all teeth, is described in detail. It likely represents *Trogontherium (Euroxenomys) minutum*. The taxonomic affinities of the species are discussed. The Late Miocene fauna correlates with the Neogene mammal unit MN 9.

Keywords: Beaver, systematics, Höwenegg, Late Miocene, MN 9.

Zusammenfassung

Der Erstnachweis eines Bibers in der obermiozänen (MN 9) Höwenegg-Fauna wird detailliert beschrieben. Er gehört wahrscheinlich zu *Trogontherium* (*Euroxenomys*) *minutum*. Die taxonomischen Probleme werden diskutiert.

1. Introduction

The Upper Miocene fossil site at the Höwenegg (northern Hegau district, Southwest Germany) was discovered in the 1930s and elaborately excavated for several decades (Tobien 1986, Jörg & Rothausen 1991, Heizmann et al. 2003). The site is renowned for its excellently preserved complete mammalian skeletons, including females with foetuses. The tridactyl horse *Hippotherium primigenium*, the rhinoceros *Aceratherium incisivum*, and the archaic antelope *Miotragocerus pannoniae* are known from multiple skeletons. Muntiacine and tragulid deers are represented by partial skeletons. However, remains of small mammals are extremely rare. The few finds sampled in the last appr. 50 years will be published elsewhere. So far 9 specimens have been found, and only the lagmomorphs can be determined to species level. The ongoing excavation at the Höwenegg site by the SMNK staff yielded a dentary fragment of a small beaver in April 2009. This is the first record of a castorid in the Höwenegg fauna. The discovery of fossil beaver remains at Höwenegg is not unexpected, given that the fauna was deposited in a lacustrine environment. The lacustrine deposits of the Höwenegg-Formation are a sequence of white or grey marl-layers alternating with reddish-brown layers that are interpreted to be tuffaceous mudflows. A $^{40}Ar/^{39}Ar$ dating of the deposits indicates an age of 10.3 ± 0.19 Ma. The Höwenegg-Fauna is biostratigraphically correlative with the European Mammal Unit MN 9 (Lower Pannonian) (Munk et al. 2007).

The castorid dentary described herein was extracted from the layer Höw 03/I, 12-top, which represents a tuffaceous mudflow. Here, we present a description of the specimen, discuss its taxonomic attribution, and compare it with other records of the species from localities in the wider vicinity, older and younger.

The dentary is housed in the Staatliches Museum für Naturkunde Karlsruhe (SMNK) under the catalogue number SMNK-Pal. 6601. All measurements were taken on the occlusal surface and are given in mm. The terminology of the dental elements follows Stirton (1935).

Acknowledgements

We would like to thank the Revealing Hominid Origins Initiative (NSF grant BCS-0321893 awarded to R.L. Bernor by the project directors F.C. Howell and T.D. White, University of California, Berkeley) for funding the excavations at Höwenegg 2005–2009. We are also grateful to K. Wolf-Schwenninger for preparing the photo, C. Stefen for reviewing the manuscript and R. Schoch and R. Böttcher for editorial work.

2. Systematic palaeontology

Family Castoridae Hemprich, 1820
Genus *Trogontherium* Fischer von Waldheim, 1809
Subgenus *Euroxenomys* Samson & Rădulesco, 1873

Trogontherium (Euroxenomys) minutum
(von Meyer, 1838)
Figs. 1–2

Material: Fragmentary horizontal ramus of right dentary with i, p4–m3, partly broken, labially embedded in matrix, SMNK-Pal. 6601 (Figs. 1–2).

Measurements: p4 4.45 × 3.93; m1 2.91 × 3.81; m2 2.80 × 3.90; m3 3.11 × 3.38.

Description. – The right dentary fragment preserves most of the horizontal ramus and is partly embedded in matrix with its labial side. Only the cheek teeth can be seen in occlusal view. The inferior margin and a part of the lingual side below m1-m2 were broken during the excavation. The tooth row is not in line, with the m2 being

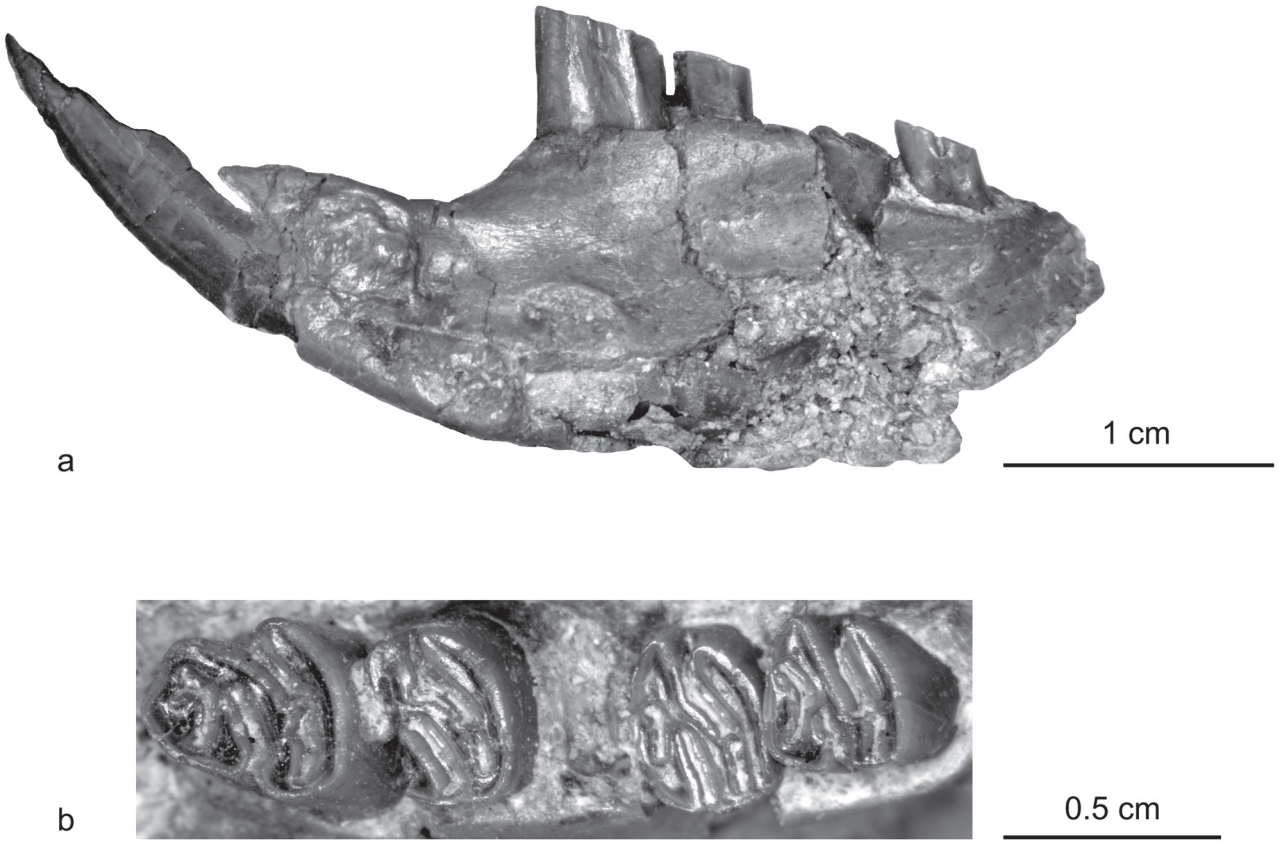

Fig. 1. *Trogontherium (Euroxenomys) minutum* (von Meyer, 1838); right dentary fragment with I, p4–m3, matrix virtually removed; Late Miocene, MN 9, Höwenegg. – **a**. Lingual view. **b**. Occlusal view of the tooth row.

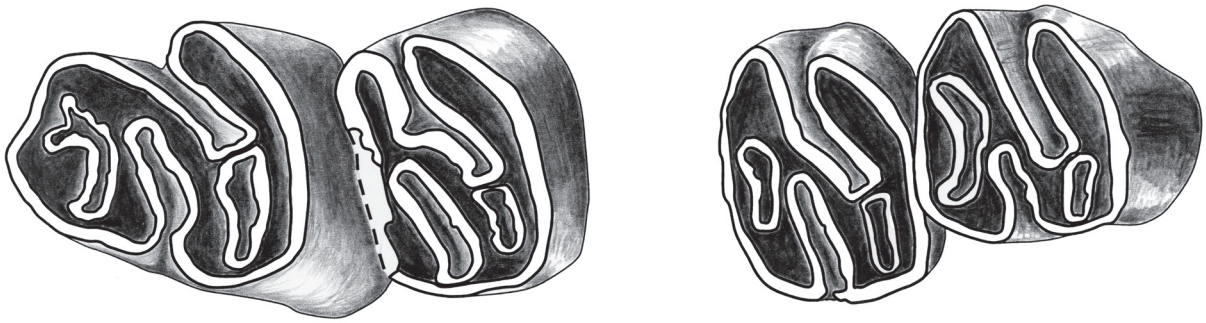

Fig. 2. *Trogontherium (Euroxenomys) minutum* (von Meyer, 1838), occlusal view of the tooth row; Late Miocene, MN 9, Höwenegg.

dislocated inferiorly and posteriorly. Hence, the length of the tooth row cannot be accurately measured. There are two vertical fractural lines between p4/m1 and between m1/m2, respectively.

The incisor is chisel-shaped, slightly curved upwards, and with a smooth enamel band on its frontal side. As it is labially embedded in matrix, no measurements can be taken.

The p4 is by far the largest tooth. The mesoflexid is still open lingually and not closed to a mesofossettid. The mesostriid is still 0.46 mm high, terminating well above the alveolar margin of the dentary. The parafossettid is wide

in labio-lingual direction. Hypoflexid and metafossettid are directly adjacent to each other. The hypostriid extends down to the crown base. The condition of the striids and flexids shows that the p4 is only moderately worn.

In the m1 the mesio-lingual part and the whole parafossettid are broken off. But enough of the anterior margin of the tooth is preserved to allow for a reliable measurement of length. The tooth is worn down to a closed mesoflexid. The hypostriid terminates above the tooth base and is only 0.27 mm high. The hypoflexid extends over more than half of the occlusal surface and is directly adjacent to the metafossettid.

In the slightly less worn m2 the mesostriid is just visible, and the mesoflexid is short before closure to a mesofossettid. The hypostriid extends halfway down the crown base with a height of 0.48 mm. Metafossettid and hypoflexid are directly adjacent to each other.

According to the height of the striids p4 and m3 are in the same stage of wear. m3 is less worn than m1 and m2 as the mesoflexid is more open. The hypoflexid extends nearly down to the alveolar margin, and the mesoflexid is 0.39 mm high. As in the other teeth metafossettid and hypoflexid are directly adjacent to each other.

D i s c u s s i o n . – The taxonomic assignment of this small Miocene beaver is a matter of continuous debate. The discussion is reviewed here in order to substantiate the determination of the Höwenegg specimen.

The species *minutus* was described by von Meyer (1838) as *Chalicomys minutus* on the basis of a dentary with p4–m2 from the brown coal of Elgg in Switzerland, which is figured in Schlosser (1884, pl. 10, fig. 15). The figure is only a very sketchy drawing, but it shows the p4 strongly enlarged with respect to the subequal m1 and m2. The species was referred to different genera: *Chalicomys* Kaup, 1832, *Steneofiber* Geoffroy-Saint-Hilaire, 1833, *Monosaulax* Stirton, 1935, and *Trogontherium* Fischer, 1809.

The genus *Trogontherium* is best known from its Pleistocene species *T. cuvieri* Fischer, 1809, which was painstakingly described by Schreuder (1929). It is dentally characterized by the co-occurrence of large p4/P4 and M3 and the granulated enamel of the incisors. The small Miocene species share with *Trogontherium* the enlarged premolars and M3, but they differ from it in the total absence of any striation or rugosity on the incisors. Franzen & Storch (1975) and Mayhew (1978) accepted *Trogontherium minutum* in spite of this difference. However, in the Dorn-Dürkheim sample Franzen & Storch (1975) mention a fine granulation of the incisor enamel in their *Trogontherium minutum rhenanum*, a subspecies with markedly elongated M3.

Samson & Rădulesco (1973) took *minutus* as type species for their genus *Euroxenomys*. This genus was synonymised subjectively with *Trogontherium* by Mayhew (1978), Savage & Russell (1983) and McKenna & Bell (1997). Hugueney (1999) downgraded it to a subgenus of *Trogontherium*. She was followed by Stefen & Rummel (2003), Daxner-Höck (2004) and Daxner-Höck & Bernor (2009) in this allocation, whereas Korth (2001) ranked *Euroxenomys* at genus level.

We believe that the differences between the early Middle to Late Miocene species *minutum* and the Pleistocene type species *cuvieri* are sufficiently taken into account by ranking *minutum* as the subgenus *Euroxenomys* of the genus *Trogontherium*. The absence of striation and rugosity in the incisors of the small *T. (E.) minutum* may be due to its small size, as this character occurs in large sized, but systematically unrelated beavers as *T. cuvieri*, *Castoroides*, and *Anchitheriomys*, as Stefen & Rummel (2003) pointed out. In her phylogenetic analysis Rybczynski (2007) showed, that these large beavers belong to different lineages. A hint of granulation in the incisors of the large-sized subspecies *T. (E.) minutum rhenanum* from Dorn-Dürkheim (Franzen & Storch 1975) may underscore the relationship between large size and striation of incisors.

Other authors, e. g. Engesser (1972), Stefen (1997) and Giersch (2004) used the nomen *Steneofiber minutus* for this small Miocene beaver referring to the fact that material lacking M3 is difficult to distinguish from *Steneofiber* (Stefen 1997, Hugueney 1999). Stefen & Rummel (2003) assumed the presence of another Miocene lineage of a small beaver besides *T. (E.) minutum*. This form differs from *T. (E.) minutum* by showing upper molars of equal size and therefore indicating a relation to *Steneofiber*. But a definite characterisation is still pending. However, the length of striids might support the identification of lower jaw elements: *Steneofiber* does not show any striae/striids which reach the crown base (Stefen 1997). In *Trogontherium* at least the hypostriid of p4 shows the tendency to extend down to the base of the crown. This elongated striid is present in *T. (E.) minutum rhenanum* from Dorn-Dürkheim, MN11 (Franzen & Storch 1975), and in the sample from Azelsdorf, MN 9 (Daxner-Höck & Bernor 2009, fig. 9/1b, 2b). A hypostriid, reaching the crownbase is also present on the p4 from Höwenegg (MN 9). An accordant striid is absent e. g. in the samples from Petersbuch 50, MN8 (Stefen & Rummel 2003) and Bohlinger Schlucht, MN6 (Giersch 2004). Probably the elongated striid is a derived character which occurs in stratigraphically younger findings of the subgenus *Euroxenomys*.

The teeth of the Höwenegg specimen are distinctly smaller than in *T. (E.) minutum rhenanum* from Dorn-Dürkheim and a bit larger than the record from the Austrian site Atzelsdorf. They compare well will the sample from the Bohlinger Schlucht (western Lake Constance), Petersbuch 50, Anwil, and Sansan (see fig. 3). The tooth size of *T. (E.) minutum* varies without clear trend in the stratigraphic succession of the samples. The characters

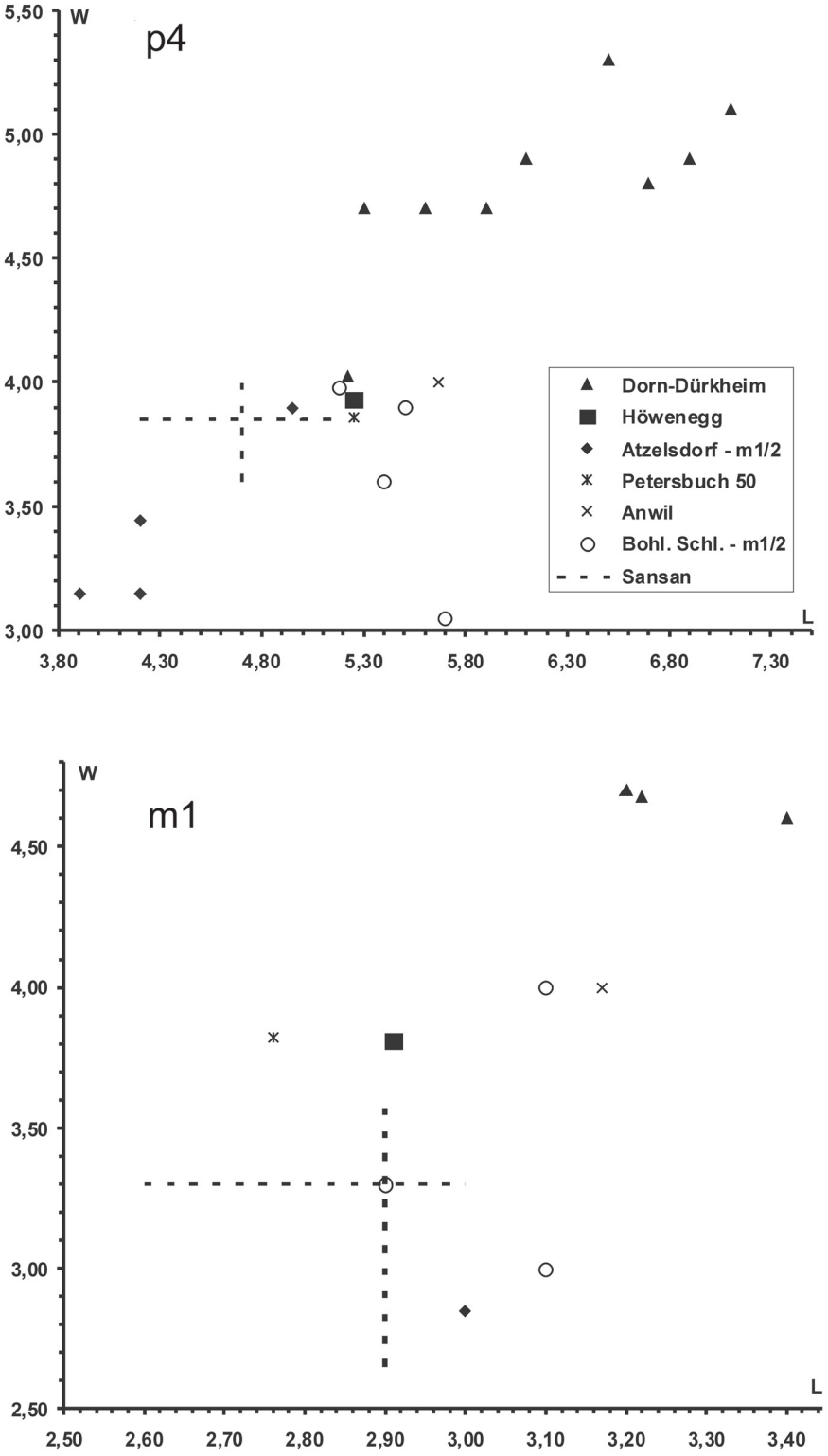

Fig. 3. Bivariate plot of the p4 and m1 of *Trogontherium (Euroxenomys) minutum* (von Meyer, 1838). – From Dorn-Dürkheim (subspecies *rhenanum*, Franzen & Storch 1975, tab. 7), Late Miocene, MN 11; Atzelsdorf (Daxner-Höck & Bernor 2009, tab. 5), Late Miocene, MN 9; Bohlinger Schlucht (Giersch 2004: 21), Middle Miocene, MN 6; Petersbuch 50 (Stefen & Rummel 2003, tab. 2), Middle Miocene, MN 8; Anwil (Engesser 1972, calculated from fig. 64), Middle Miocene, MN 7/8; Sansan (Baudelot 1972: 342), Middle Miocene, MN 6; Höwenegg, Late Miocene, MN 9.

shown on the Höwenegg castorid supports the affiliation to *Trogontherium (E.) minutum*.

Although generally rare in fossil assemblages, *T. (E.) minutum* is wide-spread in Europe, from Spain in the Southwest to Moldovia in the East, and ranges in age from the Early to Late Miocene (see Hugueney 1999, tab. 28.1).

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Manuscript received: 11 January 2010, accepted: 10 March 2010.