Castoridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland

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Several isolated teeth and jaw fragments of beavers (Rodentia: Castoridae), discovered at the Villafranchian (MN 16b?) site of Węże 2 in southern Poland, are attributable to two species: Dipoides ex gr. problematicus-sigmodus and Trogontherium (Euroxenomys) minus. The genus Dipoides and the species Trogontherium (Euroxenomys) minus have not previously been reported from Poland. Their presence at the Węże 2 site suggests that these lesser-known and extinct representatives of the Castoridae were adapted to similar conditions as the modern species (Castor fiber and C. canadensis).

Key words: Villafranchian, rodents, beavers, Węże, karst.

INTRODUCTION

This study describes the fossil dental beaver (Castoridae) remains from the Villafranchian (MN 16b?) site of Węże 2 in southern Poland. Although few, they are significant as they belong to taxa that apparently have not yet been reported from Polish sites, namely the genus Dipoides and the species Trogontherium minus. The Castoridae (true beavers) are a family of herbivorous rodents that, throughout their evolutionary history, developed large body sizes and, by adapting to a semi-aquatic lifestyle, became strongly associated with freshwater environments. Today the family is represented only by the genus Castor, consisting of two extant species – the North American C. canadensis and the Eurasian C. fiber. However, the fossil record of the Castoridae comprises around 30 valid genera (Hugueney and Escuillié, 1996; Rose, 2006; Rybczynski, 2007; Rybczynski et al., 2010; Stefens, 2011; Li et al., 2017). Present-day beavers are known from their iconic dam-building behavior, which allows them to create ponds that they subsequently inhabit, such an adaptation supposedly being driven by habitual acquiring and consumption of wood (Rosell et al., 2005; Rybczynski, 2007; Plint et al., 2020). Both Dipoides and Trogontherium (as well as the subgenus Euroxenomys) are thought to also represent the branch of the beaver evolutionary tree that encompasses woodcutting and a semi-aquatic lifestyle (Rybczynski, 2007; Rybczynski et al., 2010; Xu et al., 2017; Plint et al., 2020).

The earliest recognized member of the Castoridae, Agnotocastor, has been described from the latest Eocene of Wyoming. In the Early Oligocene the family was already present in Eurasia, Propalaeocastor (perhaps synonymous with Agnotocastor) being the earliest beaver found outside of North America (Rose, 2006; Li et al., 2017). Early occurrences of fossil Castoridae in Poland include the presence of Steneofiber jaegeri in the Early/Middle Miocene sites of Przeworno 1, Opole 1 and Opole 2, dated respectively to MN 5–6?, MN 6? and MN 7?. Moreover, Steneofiber eseri and Trogontherium (Euroxenomys) minutum have been recorded from Opole 2 (Kowalski, 1967; Kubiak and Wolsan, 1986; Nadachowski, 1989; Hugueney, 1999).

Out of the several beaver genera inhabiting Europe through the Miocene, Steneofiber is dominant form and is sometimes considered to be ancestral to Trogontherium. Although the purported transition from Steneofiber to Trogontherium is not well understood, the evolutionary lineage S. eseri–T. minutum–T. minus–T. cuvieri has been inferred from the fossil record (Mayhew, 1978; Stefens, 2011). The phylogenetical analysis performed by Rybczynski (2007) puts S. eseri and Trogontherium in separate clades, with Steneofiber closely related to Castor (within the clade Castorinae) and Trogontherium as a probable descendant of Dipoides (within the Castoridae). Rybczynski et al. (2010) considered Castor to be a close relative of Sinocastor with Steneofiber as an outgroup. Another study (Li et al., 2017) again argues for a very close relationship between Steneofiber and Castor, as well as between Trogontherium cuvieri and Dipoides. Trogontherium (Euroxenomys) minutum, however, has been placed at the stem of the clade encompassing Steneofiber eseri, Castor canadensis, Trogontherium cuvieri and Dipoides majori.
SYSTEMATIC PALAEONTOLOGY

Family Castoridae Hemprich, 1820
Subfamily Castoroidinae Allen, 1877
Genus Dipoides Jäger, 1835
Dipoides ex gr. problematicus-sigmodus
Genus Trogontherium Fischer de Waldheim, 1809
Trogontherium minus Newton, 1890

Material. — Dipoides ex gr. problematicus-sigmodus: isolated right M1/2 (ZPAL VMl–127/1; Fig. 1A and Table 1).
Trogontherium (Euroxenomys) minus: fragment of left maxilla with P4 in situ (ZPAL VMl–124/1; Fig. 1D); isolated left M1 (ZPAL VMl–125/1; Fig. 1C); isolated right M3 (ZPAL VMl–123/1; Fig. 1B); fragment of left mandible with M1 in situ (ZPAL VMl–122/1; Fig. 1E).

Description. — Dipoides ex gr. problematicus-sigmodus M1/2 (Fig. 1A). The occlusal surface displays the typical sigmoid pattern of the genus Dipoides formed by the paraflexus, the hypoflexus, the mesoflexus and the metaflexus (van de Weerd, 1976; García-Alix et al., 2007; Li et al., 2017; Xu et al., 2017; see: Fig. 2), although the paraflexus and the mesoflexus are barely discernible. Morphologically it strongly resembles the Dipoides problematicus material from the Pliocene localities of the Teruel-Alfambra region of Spain (van de Weerd, 1976; García-Alix et al., 2007). However, the dimensions of the occlusal surface (the length is 2.7 and the width equals 2.9 mm) are significantly smaller than the typical ranges of both D. problematicus and D. sigmodus (van de Weerd, 1976; Dema, 2000; García-Alix et al., 2007; Xu et al., 2017).

Trogontherium minus P4 (Fig. 1D). The occlusal surface resembles a circular triangle. The hypoflexus, the paraflexus, the mesoflexus and the metaflexus are discernible, showing the pattern typical of the genus Trogontherium (Stefen and Rummel, 2003; Fostowicz-Frelk, 2008; Kordos, 2020). The length of the occlusal surface is 7.4 while the width equals 6.6 mm. That puts the specimen within the typical range for T. minus with regard to the length and very close to that range in terms of the width, the Węże 2 specimen being slightly wider than the expected range for T. minus but nonetheless much narrower than the expected range for T. cuvieri (Fostowicz-Frelk, 2008).

M1 (Fig. 1C). The occlusal surface is roughly kidney-shaped. Only the hypoflexus and the metaflexus are discernible, which is probably indicative of tooth wear. Both the length and the width of the occlusal surface equal 6 mm, such dimensions being substantially larger than the typical range of Trogontherium minutum (Stefen and Rummel, 2003; Stefén, 2011; Apoltsev and Rekovets, 2015; Kordos, 2020) but smaller than expected for T. cuvieri (Stefen, 2011; Langeveld, 2013).

M3 (Fig. 1B). The shape of the occlusal surface resembles a circular triangle. The hypoflexus, the paraflexus, the mesoflexus and the metaflexus are present, showing the pattern typical for Trogontherium (Stefen and Rummel, 2003; Kordos, 2020). The length of the tooth is 6.5 mm and the width equals 7 mm which is larger than the expected range for Trogontherium minutum (Stefen and Rummel, 2003; Apoltsev and Rekovets, 2015; Kordos, 2020) but smaller than would be expected for T. cuvieri (Stefen, 2011; Langeveld, 2013).
Fig. 1. Dental beaver (Castoridae) remains from Węże 2

A – Dipoides ex gr. problematicus-sigmodus (M1/2); B – Trogontherium minus (M3); C – Trogontherium minus (M1); D – Trogontherium minus (fragment of maxilla with P4); E – Trogontherium minus (fragment of mandible with m1)
m1 (Fig. 1E). The occlusal surface is roughly rectangular. The paraflexid, the hypoflexid, the metaflexid and the mesoflexid are visible (see Fig. 2), displaying the pattern typical of *Trogontherium*. The length is 5.5 and the width 5.7 mm, such dimensions being larger than expected for *Trogontherium minutum* (Stefen and Rummel, 2003; Apoltsev and Rekovets, 2015; Kordos, 2020) but smaller than the typical range of *T. cuvieri* (Stefen, 2011; Langeveld, 2013; Yang et al., 2019).

**DISCUSSION**

The Mio-Plio-Pleistocene genus *Dipoides* includes several species, most of which are described from North America (Shotwell, 1955; Flynn and Jacobs, 2008). In Eurasia it is represented by *D. problematicus*, *D. sigmodus*, *D. anatolicus*, *D. majori* and *D. mengensis*, the former two comprising the Western/Central European branch, and the last three forming

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**Table 1**

Measurements of the Castoridae cheek teeth from Węże 2

<table>
<thead>
<tr>
<th>Species/tooth locus</th>
<th>Length [mm]</th>
<th>Width [mm]</th>
<th>Provenience</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dipoides</em> ex gr. problematicus-sigmodus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M1/2</td>
<td>2.7</td>
<td>2.9</td>
<td>W2/G</td>
</tr>
<tr>
<td><em>Trogontherium</em> minum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P4</td>
<td>7.4</td>
<td>8.6</td>
<td>W2/7</td>
</tr>
<tr>
<td>M1</td>
<td>6.0</td>
<td>6.0</td>
<td>W2/7</td>
</tr>
<tr>
<td>M3</td>
<td>6.5</td>
<td>7.0</td>
<td>W2/G</td>
</tr>
<tr>
<td>m1</td>
<td>5.5</td>
<td>5.7</td>
<td>W2/E</td>
</tr>
</tbody>
</table>
the Eastern Mediterranean/Asian branch. The Eurasian representatives of the genus are poorly known as compared to the American ones; their record is relatively sparse, and morphological differences between them are elusive (van de Weerd, 1967; García-Alix et al., 2007; Rekovets et al., 2009; Oiu and Li, 2016; Xu et al., 2017). It has been suggested that the genus Dipoides is actually polyphyletic, with the Eurasian species having evolved independently in Europe from a Eucastor-like ancestor and not constituting a clade with the New World Dipoides (Hugueney, 1999). The Wê¿e 2 tooth, which seems to be the first Dipoides specimen described from Poland, displays the usual sigmoid occlusal pattern of the D. problematicus-sigmodus species complex, which is also present in Eucastor (van de Weerd, 1976; Hugueney, 1999; García-Alix et al., 2007; Xu et al., 2017). Morphologically, the tooth seems most similar to D. problematicus from the Teruel-Alfambra region of Spain (van de Weerd, 1976). Nonetheless, the stratigraphic position of the Wê¿e 2 specimen suggests assigning it to D. sigmodus, which is considered a direct descendant of the former species (Montoya, 1993; García-Alix et al., 2007; Rekovets et al., 2009; Xu et al., 2017). The find would apparently be the second eastemmost occurrence of a representative of the D. problematicus-sigmodus species complex besides the D. ex gr. sigmodus discovery at the Ukrainian MN 17 site of Kotlovina 2 (Dema, 2000; Rekovets et al., 2009). However, the measurements of the Wê¿e 2 specimen are significantly smaller than the typical ranges of both D. problematicus and D. sigmodus (van de Weerd, 1976; García-Alix et al., 2007; Xu et al., 2017). The specimen probably belongs to an hitherto unknown minute subspecies or species of Dipoides.

Within the genus Trogotherium, T. cuvieri, ranging from the Late Pliocene to the Late Pleistocene, is by far the best known, owing to its widespread distribution across Eurasia and the relative abundance of the fossil material (Fostowicz-Frelik, 2008; Stefén, 2011; Yang et al., 2019). T. (Euroxenomys) minutum (MN 37–MN 157) and T. (Euroxenomys) minus (MN 137–MN 17?) are distinguished from T. cuvieri mainly by the size of their cheek teeth, T. minutum being the smaller and T. minus the larger of the two forms, and they are known mainly from Western and Central Europe (Newton, 1890; Mayhew, 1978; Stefén and Rummel, 2003; Stefén, 2011; Apoltsev and Rekovets, 2015; Kordos, 2020). However, the earliest representative of the subgenus Euroxenomys may be either T. (E.) nanus from the Early Miocene of Japan (Môrs and Tomida, 2018) or T. (E.) wilsoni from the Early Miocene of North America (Korth, 2001). Another Early Miocene form, T. (E.) inconnexus, is younger and may be considered a possible descendant of T. (E.) wilsoni from the Early Miocene of North America (Sutton and Korth, 1995; Korth, 2001). Trogotherium (Euroxenomys) minus itself was first described from eastern England (Newton, 1890) but is also known from mainland Europe. Seemingly it has not yet been reported from Poland, although it appears in fossil faunal assemblages of Germany (Môrs et al., 1998; Môrs, 2002), Slovakia (Sabol, 2001) and Ukraine (Apoltses and Rekovets, 2015). Two Wê¿e 2 specimens are attributed to T. (E.) minus on the basis of the occlusal morphology characteristic of Trogotherium and the occlusal measurements larger than the typical ranges of T. minutum but smaller than expected for T. cuvieri (Stefén and Rummel, 2003; Stefén, 2011; Langeveld, 2013; Apoltsev and Rekovets, 2015; Yang et al., 2019; Kordos, 2020).

The genus Castor is the only extant genus belonging to the once species-rich family Castoridae, a clade that underwent a substantial decline in diversity during the Pleistocene (Hugueney and Escuillié, 1996; Rose, 2006; Rybczynski, 2007; Rybczynski et al., 2010; Stefén, 2011; Li et al., 2017). Thus, C. fiber, present in Europe since at least the Late Miocene (Belyaeva, 1962; Zelenkov and Panteleyev, 2015), and C. canadensis, may be both considered relict species in modern faunas and are the only castorids the ecology of which can be directly observed. As they are both strongly specialized for utilizing freshwater and woodland habitats, their presence in a fossil fauna is also a reliable indication for such environmental conditions. The constant presence of forest within the Wê¿e 2 area during the formation of the fossil assemblage is also indicated by the appearance of the dormouse Glis ex gr. sackdillingensis-minor in each of the stratigraphic units (Czernielewski, 2021), while other modern mammalian genera linked to a semiaquatic lifestyle and recorded at Wê¿e 2 include the talpids Condylura and Desmana (Sulinski, 1962; Rzebik-Kowalska, 1989; Nadachowski et al., 2015). The presence of Trogontherium minus and Dipoides ex gr. problematicus-sigmodus at Wê¿e 2 agrees with the hypotheses that they were also woodcutting and semi-aquatic animals (Rybczynski, 2007; Rybczynski et al., 2010; Xu et al., 2017; Pint et al., 2020).

CONCLUSIONS

The Villafranchian (MN16b?) site of Wê¿e 2 in southern Poland has yielded a relatively diverse fossil assemblage of rodents including some beaver remains. These are attributable to two species: Dipoides ex gr. problematicus-sigmodus and Trogontherium (Euroxenomys) minus. The species T. (E.) minus and the genus Dipoides, although previously recorded in Central Europe, had apparently not previously been found in Poland. As the fossil assemblage of Wê¿e 2 is considered to represent a forested environment close to a constant freshwater source, the presence of T. (E.) minus and Dipoides ex gr. problematicus-sigmodus at the site suggests that these lesser known and extinct representatives of the Castoridae, although ultimately unsuccessful, were adapted to similar environments as are the modern species. The Eurasian Dipoides, despite having a wide range, apparently was never common, and its fossil record has a patchy geographical distribution, suggesting dependence on very specific environmental conditions.

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