

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 *Trogotherium* (*Euroxenomys*) *minus*. The genus *Dipoides* and the species *Trogotherium* (*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 *Trogotherium 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; Stefen, 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 *Trogotherium* (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, *Agnotocaster*, has been described from the latest Eocene of Wyoming. In the Early Oligocene the family was already present in Eurasia, *Propalaeocaster* (perhaps synonymous with *Agnotocaster*) 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 *Trogotherium* (*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 it is sometimes considered to be ancestral to *Trogotherium*. Although the purported transition from *Steneofiber* to *Trogotherium* is not well understood, the evolutionary lineage *S. eseri*–*T. minutum*–*T. minus*–*T. cuvieri* has been inferred from the fossil record (Mayhew, 1978; Stefen, 2011). The phylogenetical analysis performed by Rybczynski (2007) puts *S. eseri* and *Trogotherium* in separate clades, with *Steneofiber* closely related to *Castor* (within the clade Castorinae) and *Trogotherium* as a probable descendant of *Dipoides* (within the Castoroidinae). Rybczynski et al. (2010) considered *Castor* to be a close relative of *Sinocaster* 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 *Trogotherium cuvieri* and *Dipoides*. *Trogotherium* (*Euroxenomys*) *minutum*, however, has been placed at the stem of the clade encompassing *Steneofiber eseri*, *Castor canadensis*, *Trogotherium cuvieri* and *Dipoides majori*.

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GEOLOGICAL SETTING

The Węże 2 site is situated on the NW slope of Zelce Hill, near the village of Węże, on the Wieluń Upland, southern Poland (Pajęczno County). Upon its discovery, it comprised a vertical karst crevice (~10 m long and ~4 m wide) carved in Upper Jurassic (Oxfordian) limestone and infilled with clayey deposits containing fossil material. The resulting bone breccia is considered to have originated at least partly as water transported bones into the crevice, although some small animals were possibly buried *in situ* at the place of their death. The fossiliferous deposits (~3.5 t in total) were collected during fieldwork organized in the early 1960s by the Department of Paleozoology of the Polish Academy of Sciences in Warsaw (currently the Institute of Paleobiology PAS) and the Department of Paleozoology of Wrocław University (Samsonowicz, 1936; Sulimski, 1962; Szyrkiewicz, 2015a, b). Four to five clayey fossiliferous strata of slightly differing lithology were distinguished. These were initially named D1, D2, D3 and D4 by Sulimski (1962) and then renamed D (= upper D1), E (= lower D1), F, G and H (unpublished notes referred to in Szyrkiewicz, 2015a). However, not all fossil material collected has been attributed to a particular stratum and the faunal lists are generally given for the site as a whole (Szyrkiewicz, 2015a), which is also the case for the nearby and better known site of Węże 1 (Szyrkiewicz, 2015b).

The mammalian taxa described so far from Węże 2 include the flying squirrel *Pliopetaurista dehnelli* (Sulimski, 1964; Hordijk and de Bruijn, 2009), the lagomorph *Hypolagus beremendensis* (Fostowicz-Frelik, 2007), the cervids *Croizetoceros ramosus* and *Metacervoceros pardinensis*, an unidentified rhinocerotid, an elephantid probably assignable to the genus *Anancus* (Stefaniak et al., 2020), and the dormice *Glis minor* and *G. sackdillingensis* (Czernielewski, 2021). Preliminary records of many other taxa have been reported. These include the carnivores *Canis etruscus*, *Vulpes praeglacialis*, *Ursus minimus*, *Mustela pliocaenica*, *Homotherium latidens* and *Felis lunensis* (Sulimski, 1962; Nadachowski et al., 2015), the eulipotyphlans *Rzebikia polonica*, *R. skoczni*, *Condylura kowalskii*, *Desmana cf. kormosi*, *Petenya hungarica* and *Sorex cf. minutus* (Sulimski, 1962; Rzebik-Kowalska, 1989; Nadachowski et al., 2015; Sansalone et al., 2016), and the rodents *Hystrix cf. primigenia*, *Baranomys longidens*, *Mimomys gracilis*, *Prospalax priscus*, *Pliospalax* sp. and *Sciurus warthae* (Sulimski, 1962; Nadachowski, 1989; Nadachowski et al., 2015). In general, the fossil assemblage of Węże 2 is suggestive of a warm, Mediterranean-like climate and a forest environment around a constant freshwater source. Based on its faunal composition, the Węże 2 fossil assemblage is currently dated as Late Pliocene (Lower Villafranchian) and is considered to belong to the MN 16b zone of the European Land Mammal Age chronology, i.e. 2.9–2.6 Ma (Nadachowski et al., 2015; Stefaniak et al., 2020).

MATERIAL AND METHODS

The material here examined consists of five specimens clearly attributable to the Castoridae and belonging to two species of beaver: *Dipoides ex gr. problematicus-sigmoidus* and *Trogontherium (Euroxenomys) minus*. *Trogontherium minus* is represented by four specimens – a fragment of the left maxilla with P4 *in situ*, an isolated left M1, an isolated right M3, and a fragment of the left mandible with m1 *in situ*. An isolated right M1/2 is assignable to *Dipoides ex gr. problematicus-sigmoidus*.

The material was collected by handpicking during the fieldwork conducted in the early 1960s and is now housed in the collection of the Institute of Paleobiology of the Polish Academy of

Sciences (abbreviated ZPAL). In this study it was examined with a *Keyence VHX 900-F Digital Microscope System* and photographed with a *Nikon D1X* camera with MC 50 mm f/2.8.

SYSTEMATIC PALAEOONTOLOGY

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

Material. – *Dipoides ex gr. problematicus-sigmoidus*: isolated right M1/2 (ZPAL VM/I–127/1; Fig. 1A and Table 1).

Trogontherium (Euroxenomys) minus: fragment of left maxilla with P4 *in situ* (ZPAL VM/I–124/1; Fig. 1D); isolated left M1 (ZPAL VM/I–125/1; Fig. 1C); isolated right M3 (ZPAL VM/I–123/1; Fig. 1B); fragment of left mandible with m1 *in situ* (ZPAL VM/I–122/1; Fig. 1E).

Description. – *Dipoides ex gr. problematicus-sigmoidus* M1/M2 (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. sigmoidus* (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-Frelik, 2008; Kordos, 2020). The length of the occlusal surface is 7.4 while the width equals 8.6 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-Frelik, 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; Stefen, 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).

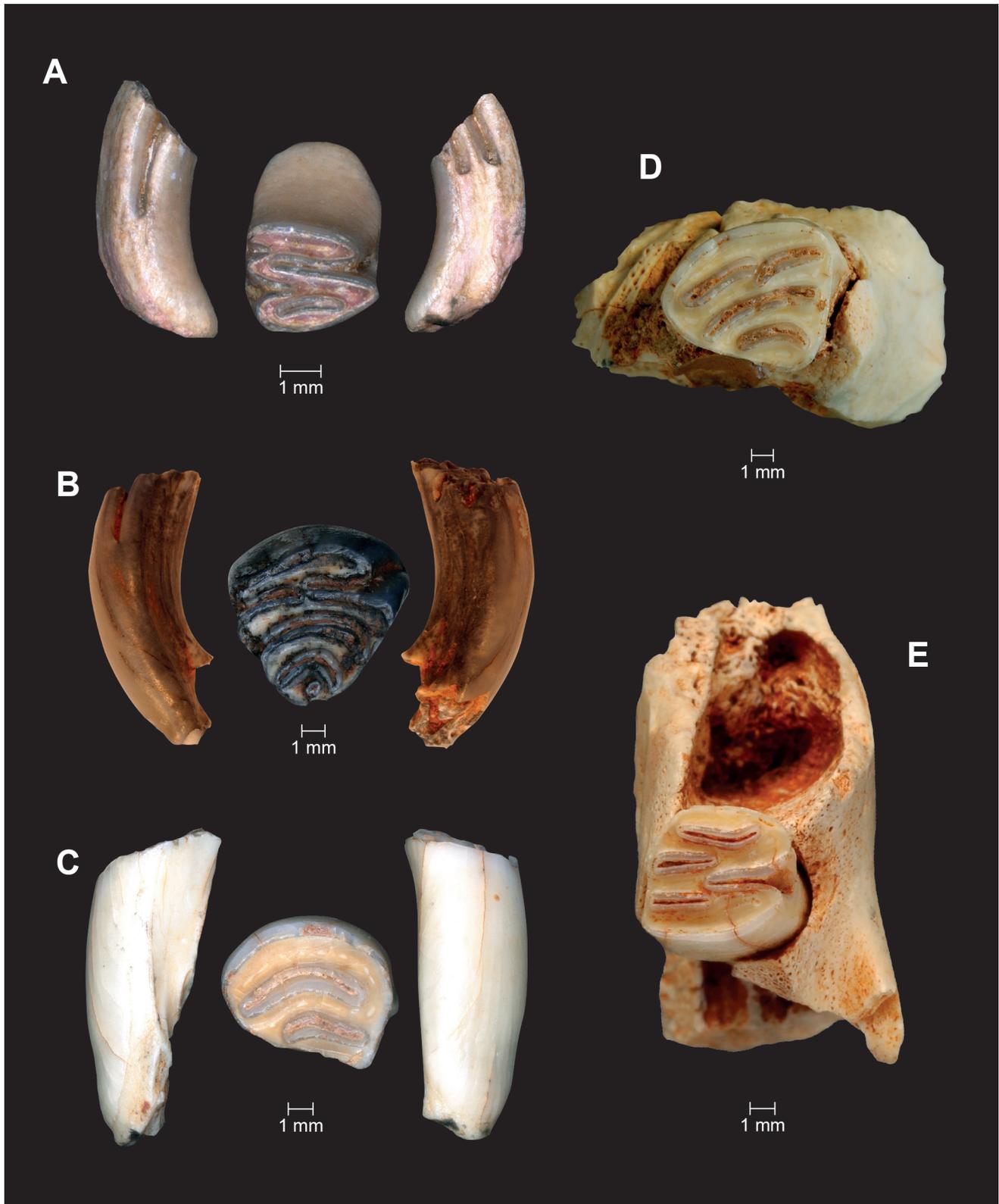


Fig. 1. Dental beaver (Castoridae) remains from Węże 2

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)

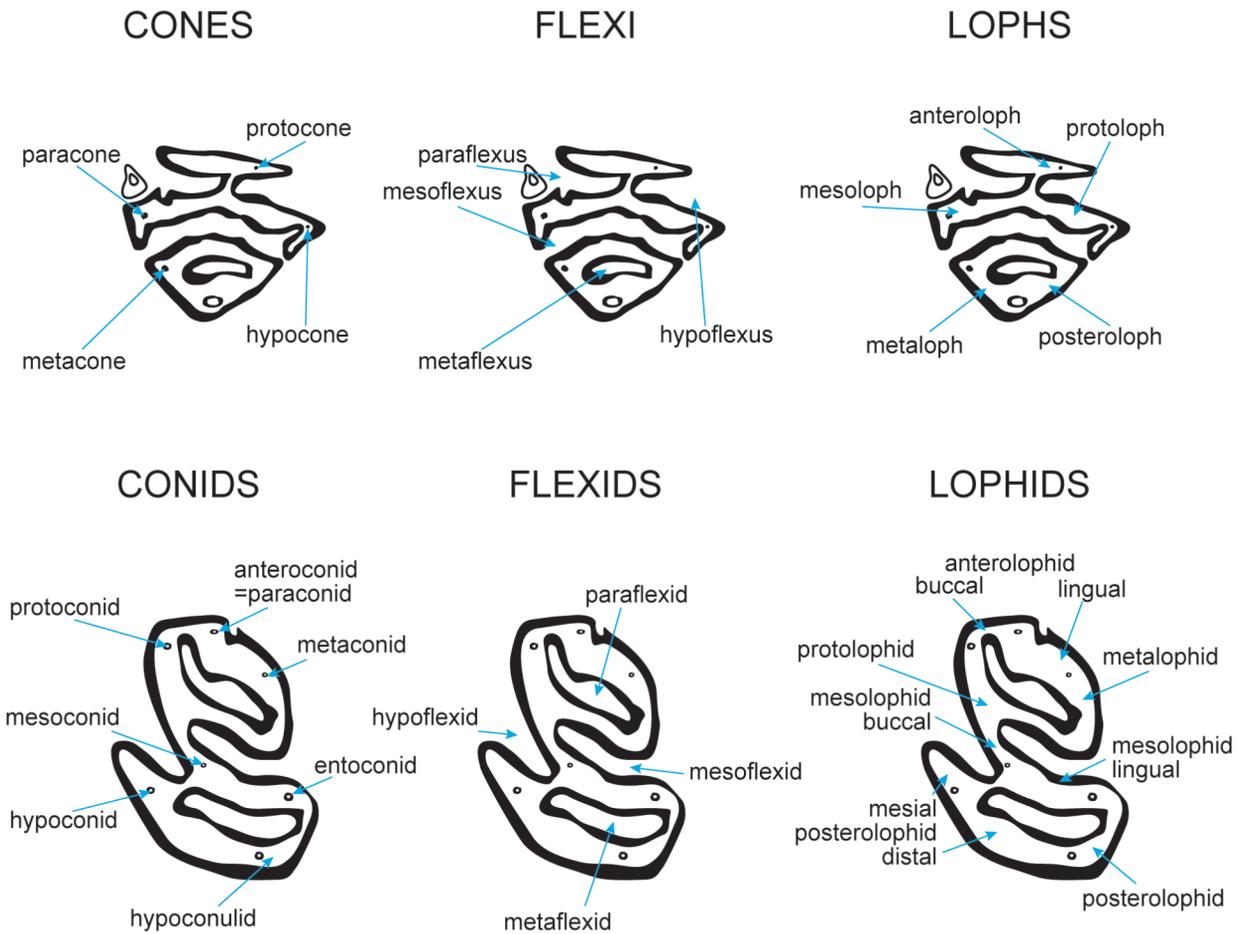


Fig. 2. Morphology of castorid cheek teeth exemplified by *Trogontherium* sp. P4 (upper row) and p4 (lower row)

The vertical axis is the height and the horizontal axis is the width of the specimens (after [Kordos, 2020](#))

Table 1

Measurements of the Castoridae cheek teeth from Węże 2

Species/tooth locus	Length [mm]	Width [mm]	Provenience
<i>Dipoides</i> ex gr. <i>problematicus-sigmodus</i>			
M1/2	2.7	2.9	W2/G
<i>Trogontherium minus</i>			
P4	7.4	8.6	W2/?
M1	6.0	6.0	W2/?
M3	6.5	7.0	W2/G
m1	5.5	5.7	W2/E

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

the Eastern Mediterranean/Asiatic 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, 1976; García-Alix et al., 2007; Rekovets et al., 2009; Qiu 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 Węże 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 Węże 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 easternmost 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 Węże 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 *Trogontherium*, *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; Stefen, 2011; Yang et al., 2019). *T. (Euroxenomys) minutum* (MN 3?–MN 15?) and *T. (Euroxenomys) minus* (MN 13?–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; Stefen and Rummel, 2003; Stefen, 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 (Mörs 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* (Sutton and Korth, 1995; Korth, 2001). *Trogontherium (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 (Mörs et al., 1998; Mörs, 2002), Slovakia (Sabol, 2001) and Ukraine (Apoltssev and Rekovets, 2015). Two Węże 2 specimens are attributed to *T. (E.) minus* on the basis of the occlusal morphology characteristic of *Trogontherium* and the occlusal measurements larger than the typical ranges of *T. minutum* but

smaller than expected for *T. cuvieri* (Stefen and Rummel, 2003; Stefen, 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; Stefen, 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 Węże 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 Węże 2 include the talpids *Condylura* and *Desmana* (Sulimski, 1962; Rzebiak-Kowalska, 1989; Nadachowski et al., 2015). The presence of *Trogontherium minus* and *Dipoides ex gr. problematicus-sigmodus* at Węże 2 agrees with the hypotheses that they were also woodcutting and semi-aquatic animals (Rybczynski, 2007; Rybczynski et al., 2010; Xu et al., 2017; Plint et al., 2020).

CONCLUSIONS

The Villafranchian (MN16b?) site of Węże 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 Węże 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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