

**Beavers and flying squirrels
(Rodentia: Castoridae, Pteromyini) from
the Late Pliocene of Hambach 11 C, Germany**

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Beavers and flying squirrels (Rodentia: Castoridae, Pteromyini) from the Late Pliocene of Hambach 11C, Germany

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ABSTRACT

This paper is a study of part of the rodent fauna collected at Hambach 11C, located in the Hambach lignite mine in north-western Germany. The deposits exposed here are fluvial channel fills of Late Pliocene age (MN16a) and the rodent material is compared to previously published material from the contemporaneous deposits of Hambach 11. Four species are discussed: two Castoridae, *Castor fiber* Linnaeus, 1758 and *Trogontherium minus* Newton, 1890 and two Sciuridae, *Blackia miocaenica* Mein, 1970 and *Pliopetaurista pliocaenica* Depéret, 1897. This new material is of great importance as the fossil records of *T. minus* and *B. miocaenica* are very scarce so far. *Blackia* is especially rare in the Late Pliocene and this occurrence is one of the three youngest of the genus. We also described the most complete juvenile material of *Trogontherium minus*. The fauna is indicative of fluvial environment surrounded by a forest of deciduous trees and of a temperate and humid climate.

RÉSUMÉ

Castors et écureuils volants (Rodentia: Castoridae, Pteromyini) du Pliocène supérieur d'Hambach 11C, Allemagne. Cette étude concerne une partie de la faune de rongeurs trouvés dans la couche Hambach 11C, de la mine de lignite d'Hambach située dans le nord-ouest de l'Allemagne. Ces affleurements de dépôts fluviaux sont datés du Pliocène supérieur. Le matériel étudié est comparé à d'autres spécimens d'âges contemporains précédemment publiés et provenant d'Hambach 11. Quatre espèces sont traitées ici : deux Castoridae, *Castor fiber* Linnaeus, 1758 et *Trogontherium minus* Newton, 1890 et deux Sciuridae, *Blackia miocaenica* Mein, 1970 et *Pliopetaurista pliocaenica* Depéret, 1897. Ce nouveau matériel est d'une grande importance du fait de la rareté des fossiles de *T. minus* et de *B. miocaenica*. *Blackia* est particulièrement rare dans le Pliocène supérieur et le présent spécimen est l'un des plus récents du genre. Nous présentons également le matériel juvénile le plus complet à ce jour de *Trogontherium minus*. La faune indique un environnement fluvial entouré d'une forêt de feuillus et d'un climat humide et tempéré.

KEY WORDS

Cenozoic,
Neogene,
Europe,
Mammalia,
Rodentia,
dental morphology,
MN16.

MOTS CLÉS

Cénozoïque,
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morphologie dentaire,
MN16.

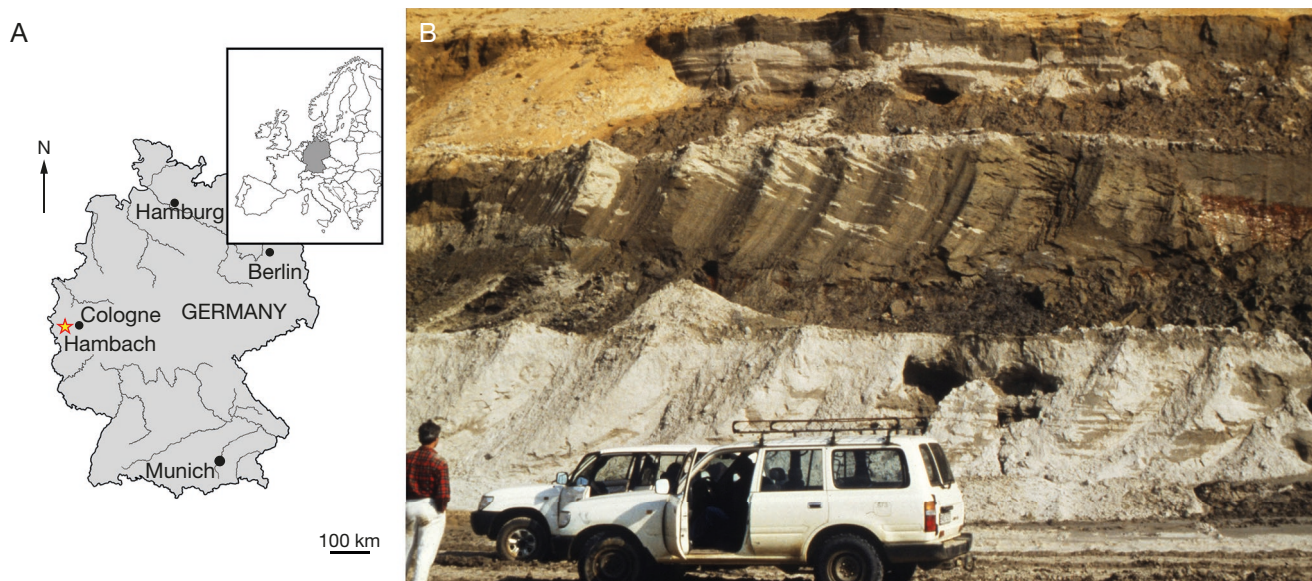


FIG. 1. — A, Map of the location of the Hambach lignite mine (from Mörs & Stefen 2010); B, picture of the outcrop.

INTRODUCTION

Hambach is an open cast lignite mine located in north-western Germany, in the southern part of the Lower Rhine Embayment (Mörs 2002) (Fig. 1A). This mine is one of the largest of its kind and is still exploited to this day by the RWE Power mining company. The mining activities regularly expose outcrops of geological and palaeontological interest that are the subject of several research papers. The material described here comes from the Late Pliocene deposits of Hambach 11C (Figs 1B; 2), dated at the Reuverian B (MN16a) based on palynological data and mammal biostratigraphy (Mörs 2002; Heumann & Litt 2002). Hambach 11C was previously considered to belong to stratum 13 according to the lithostratigraphic framework of the RWE Power mining company and therefore the fossil site has been published before as Hambach 13 in some papers (Heumann & Litt 2002; Dalsätt *et al.* 2006; Lacombat & Mörs 2008; Čerňanský *et al.* 2017). The Hambach 11C deposits are constituted of channel fills (Fig. 1B) and belong to the Öbel beds based on their litho- and magnetostratigraphy (Kemna 2005). The Late Pliocene fauna of Hambach has already been described by Mörs *et al.* (1998) from contemporaneous deposits of the site Hambach 11. The deposits of Hambach 11 and Hambach 11C are considered to be of the same age, based on their faunal composition, especially due to the occurrence of the arvicoline rodents *Mimomys hassiacus* Heller, 1936, and *Ungaromys altenburgensis* Rabeder, 1981 (Mörs 2002). This paper focuses on the rodent fauna and more specifically on the beavers (Castoridae) and the flying squirrels (Sciuridae). However, additional vertebrate fossils have been found in Hambach 11C but are not treated in this study. Among Eulipotyphla, the Desmaninae *Galemys kormosi* Schreuder, 1940, *Desmana nehringi* Kormos, 1913 and *Desmana thermalis* Kormos, 1930 and the Soricinae

Blarinoides mariae, Sulimski, 1959 have been found. Among rodents Rodentia, the forest mouse *Apodemus* sp. (Muridae), two genera of voles (Cricetidae), *Mimomys* (Cricetidae) and *Ungaromys* (Arvicolidae) and two teeth of the tree squirrel *Sciurus* sp. (Sciuridae) have been found. Among large mammals, there is evidence of a cervid based on teeth and postcranials and a carnivore based on canines, probably a Mustelidae considering the size, geographic occurrence, and stratigraphic age. Among birds Anatidae gen. et sp. indet. have been described by Dalsätt *et al.* (2006). Lastly, remains of several freshwater fishes, namely, Siluridae (*Silurus*), Esocidae (*Esox*) and specimens of Cyprinidae have also been collected but will not be treated in this article.

The material presented here is richer than what has previously been published from the MN16a of Hambach. The fossil record of flying squirrels is generally poor and mainly composed of isolated teeth, making any new specimens important as they improve our knowledge on these animals (Mansino *et al.* 2018). In particular, their fossils are not common in the Plio-Pleistocene of Western Europe (Reumer & Van den Hoek Ostende 2003). *Blackia* is especially rare and not often found in the Late Pliocene and was more common in the Miocene (Hellmund and Ziegler, 2012). *Trogontherium minus* is also not common and less known than the larger *Trogontherium cuvieri* Fischer de Waldheim, 1809 (Stefen 2011). Juvenile material of *T. minus* is especially rare in the literature and, to our knowledge, only a dP4 from Hambach (Mörs *et al.* 1998) has previously been reported.

MATERIAL AND METHODS

The specimens were collected by one of the authors (TM) in 2001. Pictures of the material were taken using a stacking software (Zerene Stacker) and a Canon EOS 5D Mark III camera

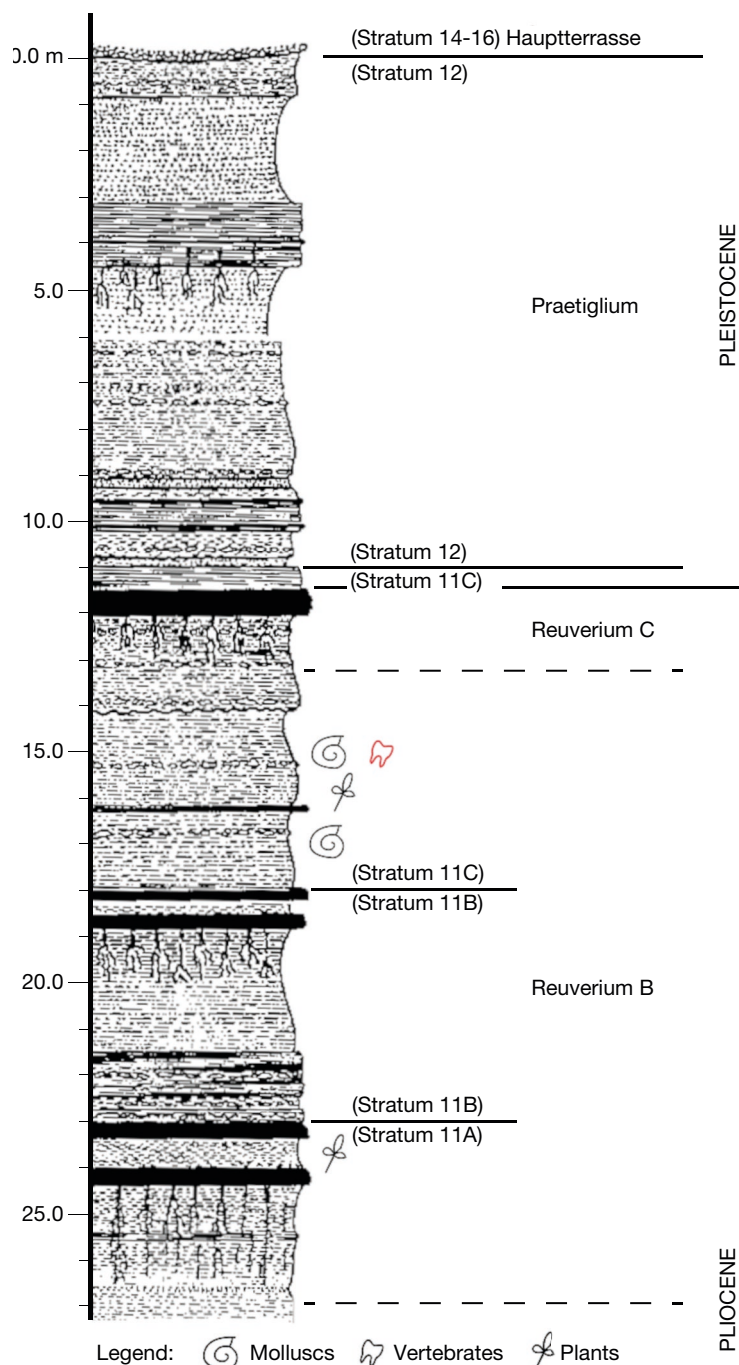


FIG. 2. — Stratigraphic column of the section.

after whitening with ammonium chloride for the Sciuridae and without whitening for the Castoridae. Tooth measurements of the flying squirrels were taken using a Leica MZ6 discussion microscope equipped with an ocular micrometre and the beaver teeth were measured with an Olympus SZX2-ILLT microscope and Image View. All measurements are given in mm.

The descriptions of the Sciuridae teeth follow the nomenclature of Qiu (1996) and those of Castoridae follow Barisone *et al.* (2006) the terms hypostria and parafochette are taken from Stefen & Mörs (2008). For extant taxa, the classification is based on Wilson & Reeder (2005).

The material studied consists for the Sciuridae of eleven isolated teeth of flying squirrels representing two genera.

All specimens are housed in the collections of the Steinmann Institute, Rheinische Friedrich Wilhelms-Universität Bonn, Germany.

ABBREVIATIONS

Anatomical abbreviations

P4/p4	upper and lower fourth premolar;
M1/m1	upper and lower first molar;
M2/m2	upper and lower second molar;
M3/m3	upper and lower third molar;

TABLE 1. — Measurements (in mm) of *Castor fiber* teeth from Hambach 11C.

Museum number	Species	Dex/Sin	Tooth position	Length	Width
HaR-5637	Castor fiber	Sin	P4	8,24	7,18
HaR-5638	Castor fiber	Sin	M1/2	6,27	6,55
HaR-5639	Castor fiber	Sin	M1/2	6,97	6,83
HaR-5641	Castor fiber	Sin	m1/2	5,62	4,31

dP4/dp4
I/i

upper and lower milk tooth;
upper and lower incisors.

Institutional abbreviations

IPB-HaR Institut für Paläontologie Bonn, Hambach Reuerton-Sammlung – Palaeontological Institute Bonn University, Hambach Reuver clay collection;
NRM Naturhistoriska riksmuseet, Stockholm – Swedish Museum of Natural History.

SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder CASTORIMORPHA Wood, 1945
Family CASTORIDAE Hemprich, 1820
Genus *Castor* Linnaeus, 1758

Castor fiber Linnaeus, 1758
(Fig. 3)

MATERIAL EXAMINED. — Left m1/2 (IPB-HaR-5641), left P4 (IPB-HaR-5637 and IPB-HaR-5640), left M1/2 (IPB-HaR-5638 and IPB-HaR-5639), incisor fragment (IPB-HaR-5653).

MEASUREMENTS. — See Table 1.

DESCRIPTIONS

I – HaR-5653 (Fig. 3A).

A fragment of an incisor exhibits the smooth enamel and a rather flattened surface with both lateral edges curved. N

m1/2 – HaR-5641 (Fig. 3B)

Unworn tooth germ showing the original cusp configuration. Rectangular shape, the labial side is slightly shorter than the lingual side. There is a small cusplet on the labial side of the protoconid, below the occlusal surface (Fig. 3B₂). All the striids reach the base of the tooth. There is some cement in the striids. The metaconid is the highest cusp, followed by the paraconid. The hypoflexid and metaflexid are “face to face”. The hypoflexid is oriented posteriorly. The paraflexid and mesoflexid are oriented anteriorly. No roots are developed.

P4 – HaR-5637 and HaR-5640 (Fig. 3C, D)

HaR-5637 (Fig. 3C) is slightly worn and preserved in a maxillary fragment with no other tooth in situ whereas HaR-5640 (Fig. 3D) has an occlusal surface too damaged to determine

a wear stage. There is clearly cement in the striae. On HaR-5637, they all seem to run through the entire height of the tooth. This is not the case on HaR-5640 where the end of the parastria is visible and the mesostria seems to be closing. The anterior and posterior sides are slightly rounded. The lingual side is shorter than the labial. Although on HaR-5640, the outer wall is damaged, it seems that its posterior side was flatter than that of HaR-5637. The hypoflexus and the paraflexus are “face to face”. On HaR-5637, the hypoflexus is curving anteriorly. The mesoflexus and paraflexus are curving anteriorly, then posteriorly and are parallel to each other. The mesoflexus and metaflexus almost reach the posterior wall. On HaR-5640, the mesoflexus is broken but seems to be curving posteriorly and the metaflexus is not preserved. HaR-5637 does not have formed roots, the base is still open. On HaR-5640, this part is not preserved.

M1/2 – HaR-5638 and HaR-5639 (Fig. 3E, F)

Both teeth are slightly worn. The shape is square with the anterior side slightly rounded and the lingual side slightly smaller than the labial side. Both characteristics are less marked than on the P4. The hypostria runs through the entire height of the tooth. On the labial side, the parastria is the shortest on HaR-5638 and the mesostria the longest almost reaching the end of the tooth crown. On HaR-5639 the metastria is the shortest and the parastria and mesostria are about the same length. There is clearly cement in the striae. The paraflexus and hypoflexus are “face to face”. On HaR-5638, they are both oriented towards the anterior side and on HaR-5639, the hypoflexus is going anteriorly and the paraflexus is rather straight and horizontal. The mesoflexus changes orientation mid-way to go toward the posterior side and almost reaches the posterior wall, the angle of the curve is close to 90° on HaR-5639. On this tooth, the metaflexus is dipping anteriorly at its mid-point whereas on HaR-5638, the metaflexus is going slightly posteriorly but is relatively straight and reaches the end of the mesoflexus. The enamel of the hypoflexus is thickened on its anterior side and so is the enamel of the mesoflexus. Both do not have roots.

REMARKS

The attribution to *Castor fiber* was made based on the observation of several characters. Firstly, the smooth enamel of the incisor and its almost flat face (Newton 1902; Fostowicz-Frelik 2008; Cuenca-Bescós *et al.* 2015) but also the presence of cement (Mayhew 1978) and the lack of roots (Rekovets *et al.* 2009) as well as the fact that the hypostria runs down the entire height of the tooth, unlike in *Trogontherium* (Fostowicz-Frelik 2008). Moreover, the size and morphology of the specimens are coherent with other finds, for example from Early Pleistocene sites in Romania and Spain (Olteț River Valley, Gran Dolina and Sima del Elefante) and from the Middle Pleistocene of Portugal (Gruta da Aroeira) (Cuenca-Bescós *et al.* 2015; 2021; Terhune *et al.* 2020) and with recent specimens (personal observations in the collections of the NRM). *Castor fiber* has previously been reported from the Late Pliocene of Hambach 11 (MN16a) by Mörs



FIG. 3. — *Castor fiber* Linnaeus, 1758 from Hambach 11C: **A**, IPB-HaR-5653, incisor fragment labial view and section; **B**, IPB-HaR-5641, left m1/2 labial, occlusal and lingual views; **C**, IPB-HaR-5637, left P4 in maxillary fragment, labial, occlusal, and lingual views; **D**, IPB-HaR-5640, left, P4 labial, occlusal, and lingual views; **E**, IPB-HaR-5639, left M1/2, labial, occlusal, and lingual views; **F**, IPB-HaR-5638, left M1/2 labial, occlusal, and lingual views. Scale bar: 2 mm.

et al. (1998). It was also found in the Late Pliocene (MN16a) Slovakian locality of Hajnačka I (Sabol *et al.* 2006). *Castor fiber* is one of two species of *Castor* still present today (Ste-

fen 2011). The genus *Castor* appears in the European fossil record during the Late Miocene (Huguency 1999), and is already present in Germany at this time (Cuenca-Bescós

TABLE 2. — Measurements (in mm) of *Trogontherium minus* teeth from Hambach 11C.

Museum number	Species	Dex/Sin	Tooth position	Length	Width
HaR-5642-1	<i>Trogontherium minus</i>	Sin	i	—	4.77
HaR-5642-2	<i>Trogontherium minus</i>	Sin	p4	4.05	3.01
HaR-5642-3	<i>Trogontherium minus</i>	Sin	m1	5.68	6.27
HaR-5642-4	<i>Trogontherium minus</i>	Sin	m2	5.94	6.07
HaR-5643-1	<i>Trogontherium minus</i>	Dex	P4	8.24	8.87
HaR-5643-2	<i>Trogontherium minus</i>	Dex	M1	5.99	6.21
HaR-5643-3	<i>Trogontherium minus</i>	Dex	M2	5.73	6.21
HaR-5644	<i>Trogontherium minus</i>	Dex	M3	7.71	6.05
HaR-5645	<i>Trogontherium minus</i>	Sin	P4	8.31	9.03
HaR-5646	<i>Trogontherium minus</i>	Sin	M1/2	5.84	6.19
HaR-5647	<i>Trogontherium minus</i>	Sin	M1/2	6.06	6.43
HaR-5648	<i>Trogontherium minus</i>	Sin	M3	7.75	5.97
HaR-5649	<i>Trogontherium minus</i>	Dex	P4	7.2	8.53
HaR-5650	<i>Trogontherium minus</i>	Sin	dP4	5.18	5.06
HaR-5651	<i>Trogontherium minus</i>	Dex	M3	5.92	5.96
HaR-5652	<i>Trogontherium minus</i>	Dex	M1/2	6.08	5.53

et al. 2015). The species *Castor fiber* appears in the middle Villafranchian (Barisone *et al.* 2006). The quasi absence of wear on HaR-5641 indicates that it belonged to a really young individual, less than five months old according to the tooth pattern (Stefen 2009).

Genus *Trogontherium* Fischer de Waldheim, 1809

Trogontherium minus Newton, 1890
(Figs 4–6)

MATERIAL EXAMINED. — Left mandibular fragment with incisor to m2 (IPB-HaR-5642), right maxillary fragment with P4 to M2 (IPB-HaR-5643). Isolated teeth: left dP4 (IPB-HaR-5650), left P4 (IPB-HaR-5645), right P4 (IPB-HaR-5649), right M1/2 (IPB-HaR-5652), left M1/2 (IPB-HaR-5646 and IPB-HaR-5647), right M3 (IPB-HaR-5644 and IPB-HaR-5651), left M3 (IPB-HaR-5648) and incisor fragment (IPB-HaR-5654).

MEASUREMENTS. — See Table 2.

DESCRIPTIONS

i – HaR-5642 (Fig. 4)

The specimen exhibits the only complete incisor presented here despite several fragments also being found. The rounded enamel band is finely wrinkled but does not show longitudinal grooves. The wear facet is slightly curved and runs from the tip of the incisor to the lower jaw symphysis.

m1/2 – HaR-5642 *m1* and HaR-5642 *m2* (Fig. 4)

The hypostridium reaches the base of the exposed tooth. No cement is in the striids. The anterior half of the tooth is higher than the posterior half. The paraflexid is curving anteriorly. The hypoflexid and mesoflexid seem to be “face to face” and meet at the middle of the tooth. The mesoflexid is horizontal and the hypoflexid seems to be oriented posteriorly. The metaflexid is oriented anteriorly. The rectangular shaped m1 is slightly worn. The tooth is dipping anteriorly (Fig. 4A, C). The labial side is shorter than the lingual. The entire height of the striids is exposed. The

hypostridium closes at the end of the exposed tooth. There is no cement in the striids. The hypoflexid is curving posteriorly. The metaflexid is horizontal and reaches the middle of the tooth. The mesoflexid is short, slightly curving anteriorly. The paraflexid is curving anteriorly, almost reaching the anterior wall. The m2 is slightly worn. There is no cement in the striids. The tooth morphology identical with the m1.

p4 – HaR-5642 (Fig. 4)

The p4 is erupting. It has not reached the occlusal surface yet and is therefore completely unworn. There is no cement in the striids. The hypostridium reaches the base of the exposed tooth. The anterior half is higher than the posterior half. The paraflexid is curving anteriorly. The hypoflexid and mesoflexid seem to be “face to face” and meet at mid-length of the tooth. The mesoflexid is horizontal to the width and the hypoflexid seems to be oriented posteriorly. The metaflexid is oriented anteriorly.

I – HaR-5654 (Fig. 5A)

The figured incisor fragment shows the characteristic crenulations and the longitudinal lines. The other incisor fragments from this site which are not figured, also show these features although not as clearly as in this one. All fragments show a convex surface.

dP4 – HaR-5650 (Fig. 5B)

This medium worn tooth is very low crowned. The shape is close to triangular, although quite rounded. The anterior and posterior sides are rounded and the anterior one is wider. The parastria and the mesostria span the whole preserved height of the tooth, the metastridium is almost worn off. The hypostridium is longer than the others but does not reach the base of the tooth crown. The paraflexus is facing the hypoflexus although the hypoflexus ends slightly more anteriorly. The mesoflexus is open on both sides of the tooth and creates an indentation on the labial side. The metaflexus is curving anteriorly before dipping posteriorly (with a smaller angle).

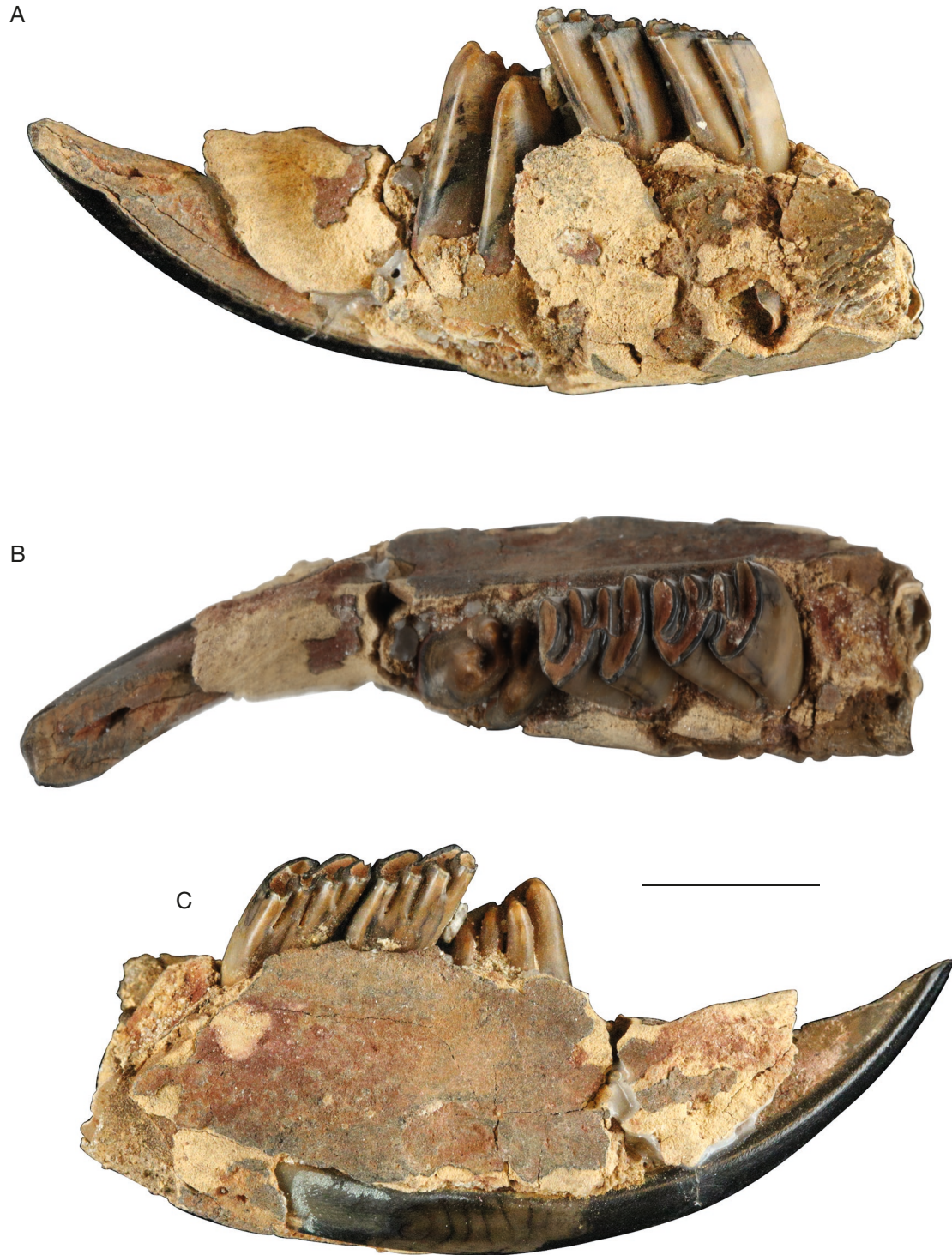


FIG. 4. — *Trogontherium minus* Newton, 1890 from Hambach 11C, IPB-HaR-5642, left jaw with i to m2: **A**, labial view; **B**, occlusal view; **C**, lingual view. Scale bar: 1 cm.

P4 – HaR-5643, HaR-5645 and HaR-5649 (Fig. 5C-G) The three teeth are heavily worn with the hypoflexus closing. HaR-5643 is preserved in a bone fragment with two other teeth (Fig. 5C-E). Shape is triangular, the anterior side is rounded and the labial side shorter than the lingual side. The hypostria is the only remaining stria. There is no cement in the fossettes nor the hypoflexus. The enamel of

HaR-5649 (Fig. 5G) is wrinkled, which is more strongly visible on its antero-lingual side. The hypoflexus meets the parafofsette. It is oriented anteriorly on HaR-5645 (Fig. 5F) and rather straight on HaR-5643 and HaR-5649. On this tooth the fossettes are also rather straight whereas they are more curved on HaR-5645. Both metafofsette and mesofossette are parallel to the anterior wall except on HaR-5643



FIG. 5. — *Trogontherium minus* Newton, 1890 from Hambach 11C: **A**, IPB-HaR-5654, labial view of an incisor fragment; **B**, IPB-HaR-5650, left dp4 labial, occlusal, and lingual views; **C**, IPB-HaR-5643, upper right jaw fragment with teeth P4 to M2 labial view; **D**, IPB-HaR-5643, occlusal view; **E**, IPB-HaR-5643, lingual view; **F**, IPB-HaR-5645, left P4 labial, occlusal, and lingual views; **G**, IPB-HaR-5649, right P4 labial, occlusal, and lingual views. All teeth are figured as left teeth, an underlined letter indicates a right tooth. Scale bar: 2 mm.



FIG. 6. — *Trogontherium minus* Newton, 1890 from Hambach 11C: **A**, IPB-HaR-5646, left M1/2 labial, occlusal, and lingual views; **B**, IPB-HaR-5647, left M1/2 labial, occlusal, and lingual views; **C**, IPB-HaR-5652, right M1/2 labial, occlusal, and lingual views; **D**, IPB-HaR-5644, upper right M3 occlusal, labial and lingual views; **E**, IPB-HaR-5648, left M3 labial, occlusal, and lingual views; **F**, IPB-HaR-5651, right M3 labial, occlusal, and lingual views. All teeth are figured as left teeth, an underlined letter indicates a right tooth. Scale bar: 2 mm.

where they are tilting postero-labially. They are touching the outer walls of the tooth. The fossettes and the hypoflexus are more or less parallel to each other's. The enamel of the

anterior wall, on the posterior side of the fossettes and of the hypoflexus are thicker. On HaR-5645 and HaR-5649, the posterior root is broken off (Fig. 5F₁; G₁).

*M1/2 – HaR-5643, HaR-5646, HaR-5647
and HaR-5652 (Figs 5C-E; 6A-C)*

HaR-5643 (M1 and M2, Fig. 5C-E), HaR-5646 (Fig. 6A) and 5647 (Fig. 6B) are heavily worn. On HaR-5643 and HaR-5647, the hypoflexus is not fully closed yet and the hypostria is still visible on HaR-5643 although shorter on the M2 than on the M. HaR-5652 (Fig. 6C) is only slightly worn and is the only specimen still retaining striae. The parastria is really short and the mesostria a little longer. The metastria is not observable. On this specimen the hypostria is quite long, although not reaching the base of the tooth. Due to the early wear stage, this tooth still has a relatively triangular shape with a rounded anterior side, wider than the posterior side. The postero-buccal face, below the occlusal surface is damaged. The shape of the other four teeth is close to square with the anterior side rounded and the labial side shorter than the lingual. On HaR-5646 and 5647, the parafofsette and the metafofsette are small, although smaller on HaR-5647. They are also really small on the M1 and M2 on HaR-5643. The hypofossette touches the parafofsette. The fossettes are more or less parallel to the anterior side. On HaR-5643, the fossettes are titling postero-lingually and more or less parallel to the hypoflexus. On these teeth, the hypoflexus is going anteriorly and meeting the parafofsette. The parafofsette and metafofsette of the M2 on HaR-5643 are bigger than in the M1 and hence, the hypoflexus is shorter. The metafofsette of HaR-5647 is a round island (Fig. 6B₂). On HaR-5652, only the metafofsette is closed and it has a curving shape, pointing toward the anterior side. The hypoflexus is facing the parafofsette and the fold anterior to the hypoflexus is not as wide as the posterior fold. The mesoflexus is curving posteriorly, reaching the labial wall. There is no cement in the fossettes of all the specimens. On HaR-5646, two roots are preserved. An anterior one, wide, and a small, postero-lingual one (Fig. 6A₁). On HaR-5647, only one root is preserved, the postero-lingual one is broken off. On HaR-5652, no roots are formed but the base of the crown is visible on the anterior side. The roots of the M2 on HaR-5643 are more exposed than for the M1 and a postero-labial small root seem to have been broken off.

*M3 – HaR-5644, HaR-5648 and HaR-5651
(Fig. 6D-F)*

The shape of the specimens is elongated and triangular. The anterior side is rounded, and the posterior side is narrower than the anterior. HaR-5644 (Fig. 6D) and 5648 (Fig. 6E) are heavily worn with only the hypoflexus not closed. In these two teeth, the height of the hypostria, which is the only stria remaining, indicates that it is closing. HaR-5651 (Fig. 6F) is slightly to medium worn. Its parastria and mesostria are visible, although quite short. The metastria is worn off. The hypostria does not span the whole height of the tooth but is clearly visible and about twice the length of the parastria. The parafofsette

and metafofsette of HaR-5644 and 5648 are rather small and about the same size. There is an additional posterior fossette of approximately the same size (Fig. 6D₁, E₁). The metafofsette and the additional posterior fossette are oriented towards the postero-lingual side. On HaR-5644, the hypoflexus is oriented towards the anterior side. On HaR-5648, the hypofossette meets the anterior side of the parafofsette. The occlusal surface of HaR-5651 is different from the other two teeth due to a difference in wear. On this tooth, the parafofsette is facing the hypoflexus and the fold anterior to the hypoflexus is not as wide as the posterior fold. The mesoflexus is open on the whole width of the tooth and forms a small indentation on the labial side. The metafofsette is closed but the metafofsette is slightly open on the labial side indicating that the metafofsette was probably spanning the whole width of the occlusal surface. There is a small hole posteriorly, potentially indicating the presence of a posterior fossette. On HaR-5644, three roots are preserved. The anterior-most one is the widest and is curving like the anterior wall of the tooth. The antero-lingual one is small, erupting from the wider, most anterior root. The third one is located posteriorly. On HaR-5648, two roots are present. The anterior one is wide and following the anterior curve of the tooth. The posterior one is oval. On HaR-5651, no roots are preserved but the base of the crown is visible on the anterior side.

REMARKS

The right maxillary fragment HaR-5643 and the potentially corresponding M3, HaR-5644, have been matched based on size, position, and degree of wear. The similarity in size and wear stages of the two upper tooth rows of *Trogontherium* (specimens HaR-5643 to HaR-5648) indicate that they might have belonged to the same individual. The lack of longitudinal lines on the incisor of HaR-5642 is probably due to the fact that it is a juvenile specimen and therefore smaller and less developed (Hugueney *et al.* 1989). The attribution of our material to *Trogontherium* is based on several characteristics. These are the presence of elongated, cone shaped upper M3s, P4 substantially bigger than the molars and a wrinkled enamel on the incisors (Mayhew 1978) as shown in Fig. 6G. The taxonomy of smaller species of *Trogontherium* is very debated but we can safely attribute our material to *Trogontherium minus* based on stratigraphic age and on size. A comparison with data from different species found in the literature confirms this (Fig. 7). The P4 in our material are larger than most *T. minus* which could be a result of wear or of the tendency of the *Trogontherium* lineage to increase in size (Stefen 2011). We also notice that while the length of our specimens matches the range for *T. minus*, they are wider and reach the lower width range of *Trogontherium cuvieri* that is visible in the figure 3 of Fostowicz-Frelik 2008. This is coherent with the age and the assumption that *T. minus* and *T. cuvieri* are two representatives in the

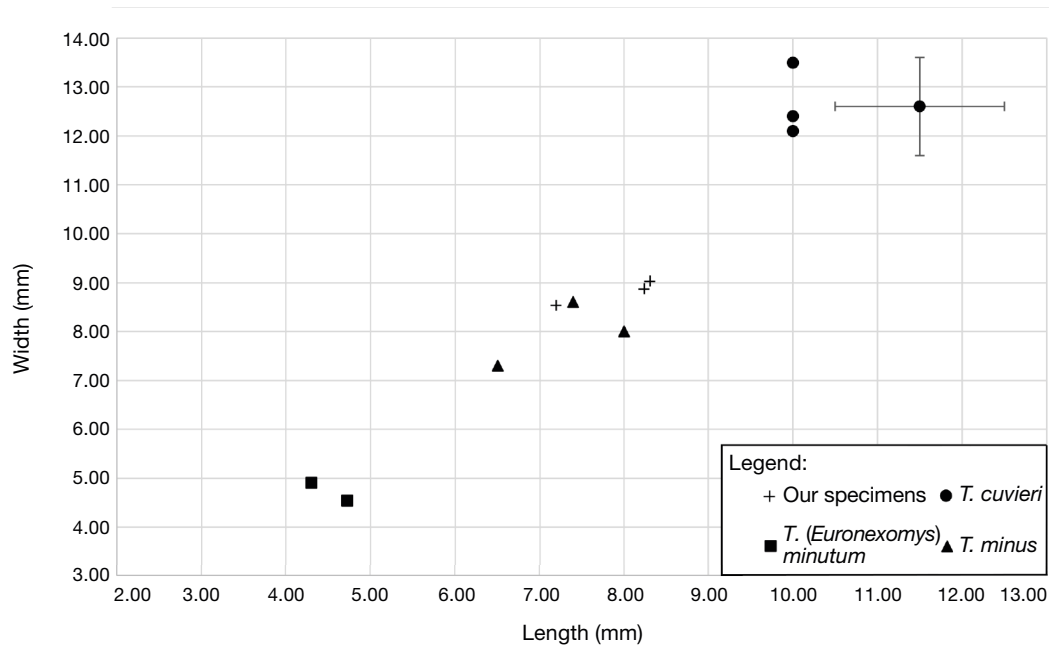


FIG. 7. — Size comparison of our specimens with different species. *Trogontherium minus* Newton, 1890 from Czernielewski 2022, Hugueney *et al.* 1989 and Newton 1890. *Trogontherium cuvieri* Owen, 1846 from Fostowicz-Frelik 2008 and Langeveld 2013. *Trogontherium (Euroxenomys) minutum* (von Meyer, 1838) from Stefen & Rummel 2003.

same evolutionary lineage proposed by Mayhew (1978) who also stated that only one species of *Trogontherium* was present at a time. However, Hugueney *et al.* (1989) have shown that *T. cuvieri* and *T. minus* coexisted during the Late Pliocene/Early Pleistocene. Some argue against the lineage hypothesis based on a too great size disparity (Fostowicz-Frelik 2008). However, our specimens show that the size disparity might not be as big as previously thought when compared to the data in the literature (Fostowicz-Frelik 2008, Heinrich 1998). This is mainly observed in the P4s as the width of the M1/2 is closer to others found in the literature (Hugueney *et al.* 1989, Newton 1890). The measurements used for comparison are the maximum occlusal surface and can vary with wear, therefore one of our specimens is much less wide than the rest (Fig. 7). The shape and appearance of the incisor are comparable to that of *T. cuvieri* described by Newton (1902), although much smaller, further confirming the attribution to *T. minus*. This species is rare (Hugueney *et al.* 1989) and less well known than *T. cuvieri* (Stefen 2011), which makes it hard to compare our material. As stated by Mörs *et al.* (1998), there are only a few previously reported occurrences of *Trogontherium* in Germany from the Miocene and Pliocene. *T. minus* was previously found in deposits from Hambach of the same age (Mörs *et al.* 1998). It was also reported from the Slovakian MN16a locality of Hajnačka I (Sabol *et al.* 2006) and from the MN16 of Podpusk-Lebyazh'e (Western Siberia) where the most complete material was found (Vislobokova 1996). *Trogontherium* aff. *minus* was reported by Pascari (2021) from the Pliocene of Musaitu

in the Taraclia district (Moldova), but the published measurements are inconsistent and were therefore not used here for comparison. Apoltsev & Rekovets (2015) place *T. minus* in the sub-genus *Euroxenomys*. However, we follow Hugueney & Duranthon (2012) and Mörs & Tomida (2018) who only place the Miocene *Euroxenomys minutus* and *Euroxenomys nanus* in the genus *Euroxenomys*. *Trogontherium* is an extinct genus of beavers, found from the Late Miocene (Mayhew 1978) to the Late Pleistocene (Yang *et al.* 2021). *T. minus* seems to have been restricted to Europe (Yang *et al.* 2021). Unlike *Castor*, *Trogontherium* is subhypsodont (Hugueney 1999; Stefen 2011), and seems to have a more terrestrial lifestyle (Fostowicz-Frelik 2008).

The lower jaw HaR-5642 belongs to a juvenile individual, according to its erupting P4 and the early wear stage of the two preserved molars. Tentative age determination was done based on the timing of eruption of the p4. Different possible ages have been found in the literature based on studies of recent *Castor*. According to Mayhew (1978) the premolars erupt between six to ten months after birth and according (Heinrich & Maul (2020) p4s come into wear around the end of the first year. Hugueney & Escuillié (1996) consider individuals of *Steneofiber* with erupting p4s to be yearlings which correspond to individuals one year old or in their second year. According to these authors, it seems that our individual was around one year old, although probably a little less. However, these estimates are to be taken with caution as we do not know the lifespan nor the postnatal development of fossil species (Stefen & Rummel 2003).

TABLE 3. — Measurements (in mm) of *Pliopetaurista pliocaenica* (Depéret, 1897) and *Blackia miocaenica* Mein, 1970 teeth from Hambach 11C.

Museum number	Locality	Species	Position	Maximum length (mm)	Maximum width (mm)	Minimum length (mm)	Minimum width (mm)	Mean length (mm)	Mean width (mm)	Number of specimens
HaR-5614, 5625, 5627	Hambach 11/2	<i>Pliopetaurista pliocaenica</i>	m1/2	3.08	3.23	2.95	2.86	3	3	3
HaR-5628	Hambach 11/2	<i>Pliopetaurista pliocaenica</i>	m3	2.62	2.28	–	–	–	–	1
HaR-5629, 5631	Hambach 11/2	<i>Pliopetaurista pliocaenica</i>	P4	3.38	3.08	3.02	2.89	3.2	2.99	2
HaR-5632, 5633, 5634, 5635	Hambach 11/2	<i>Pliopetaurista pliocaenica</i>	M1/2	2.83	3.14	2.55	2.8	2.7	2.97	4
HaR-5636	Hambach 11/2	<i>Blackia miocaenica</i>	M3	1.6	1.51	–	–	–	–	1

Suborder SCIUROMORPHA Brandt, 1855
Family SCIURIDAE Fischer de Waldheim, 1817
Subfamily SCIURINAE Fischer de Waldheim, 1817
Tribe PTEROMYINI Brandt, 1855
Genus *Blackia* Mein, 1970

Blackia miocaenica Mein, 1970
(Fig. 8)

MATERIAL EXAMINED. — A left M3 (IPB-HaR-5636).

MEASUREMENTS. — See Table 3.

DESCRIPTION

M3 – HaR-5636 (Fig. 8A)

This tooth is triangular and has a deep trigon basin with rugose enamel. The protocone is very marked with no accessory inner loph. The anterior valley delimited by the parallel anteroloph and protoloph, exhibits some rugosity although less marked than in the trigon basin. The paracone and metacone, while also marked, are dominated by the protocone. The protocone is linked to the paracone by a low protoloph and to the metacone by a low posteroloph. The anteroloph is low as well and the parastyle is very small. There is no mesostyle. Two roots are preserved, one is broken, one is under the protocone and the other is on the posterior side of the tooth. Both are tilting posteriorly but the root under the protocone has more length preserved. The posterior root seems to be oval.

REMARKS

The small size, simple morphology coupled with the lack of metaloph on the M3, and the granulated enamel (Mein 1970) of this specimen easily permit its attribution to the genus *Blackia*, a genus of small sized flying squirrels. Because our specimen is an M3 whereas most specimens in the literature are M1/2 and m1/2 comparisons are difficult. We found that its dimensions are similar to those of the left M3 of *Blackia miocaenica* from the Late Miocene (MN9) of Richardhof-Golfplatz in Daxner-Höck

(2004) and the M3s from the Miocene of Oberdorf (de Bruijn 1998) as well as the Miocene tooth from La Grive mentioned in Mein (1970). It is smaller than the ones from the Early Miocene of Aliveri (de Bruijn *et al.* 1980). de Bruijn (1999) accepts only two species in this genus, *B. miocaenica* Mein, 1970 and *Blackia woelfersheimensis* Mein, 1970. Additionally, in the original diagnoses of the species, (Mein 1970) states that *B. woelfersheimensis* is slightly bigger than *B. miocaenica*. However, this is inconsistent in the more recent literature. For example, the molar in Fejfar & Storch (1990) from the Pliocene of Gundersheim is assigned to *B. woelfersheimensis* despite being in the range of *B. miocaenica* and smaller than the specimens of de Bruijn *et al.* (1980) from the Early Miocene of Aliveri, assigned to *B. miocaenica*. Considering the similarity in size ranges and the lack of strong morphological differences between the two species (Daxner-Höck 1975), we follow here Dahlmann (2001) and consider these two species synonymous, with *B. woelfersheimensis* being the junior synonym. This interpretation is the one followed by Daxner-Höck (2004), Hellmund & Ziegler (2012) and us. Therefore, and since its size fits well into the species (Daxner-Höck 2004), we attribute the M2 of *Blackia* aff. *woelfersheimensis* from the Pliocene of Hambach in Mörs *et al.* (1998) to *B. miocaenica* instead. *Blackia* has been found in the Late Miocene of Eichkogel (MN11) in Austria (Daxner-Höck 1975) as well as in the Pliocene Sondershausen Lower Muschelkalk fissure filling (MN15) in Thuringia, Germany (Hellmund & Ziegler 2012). Both findings have been attributed to *B. miocaenica* for the reasons discussed above. *Blackia* has also, as mentioned previously, already been found in the Pliocene of Gundersheim, Wölfersheim, Hambach, and Frechen (Fejfar & Storch 1990; Mörs *et al.* 1998; Kolfschoten *et al.* 1998; Dahlmann 2001). These are the only four other recorded occurrences of *Blackia* in the Pliocene. *Blackia* is a rare genus in the German Neogene (Mörs *et al.* 1998) with most findings of Miocene age. In the Pliocene, where it finally gets extinct, it seems to be especially rare (Hellmund & Ziegler 2012). *Blackia* is considered to be relatively stable in size and morphology

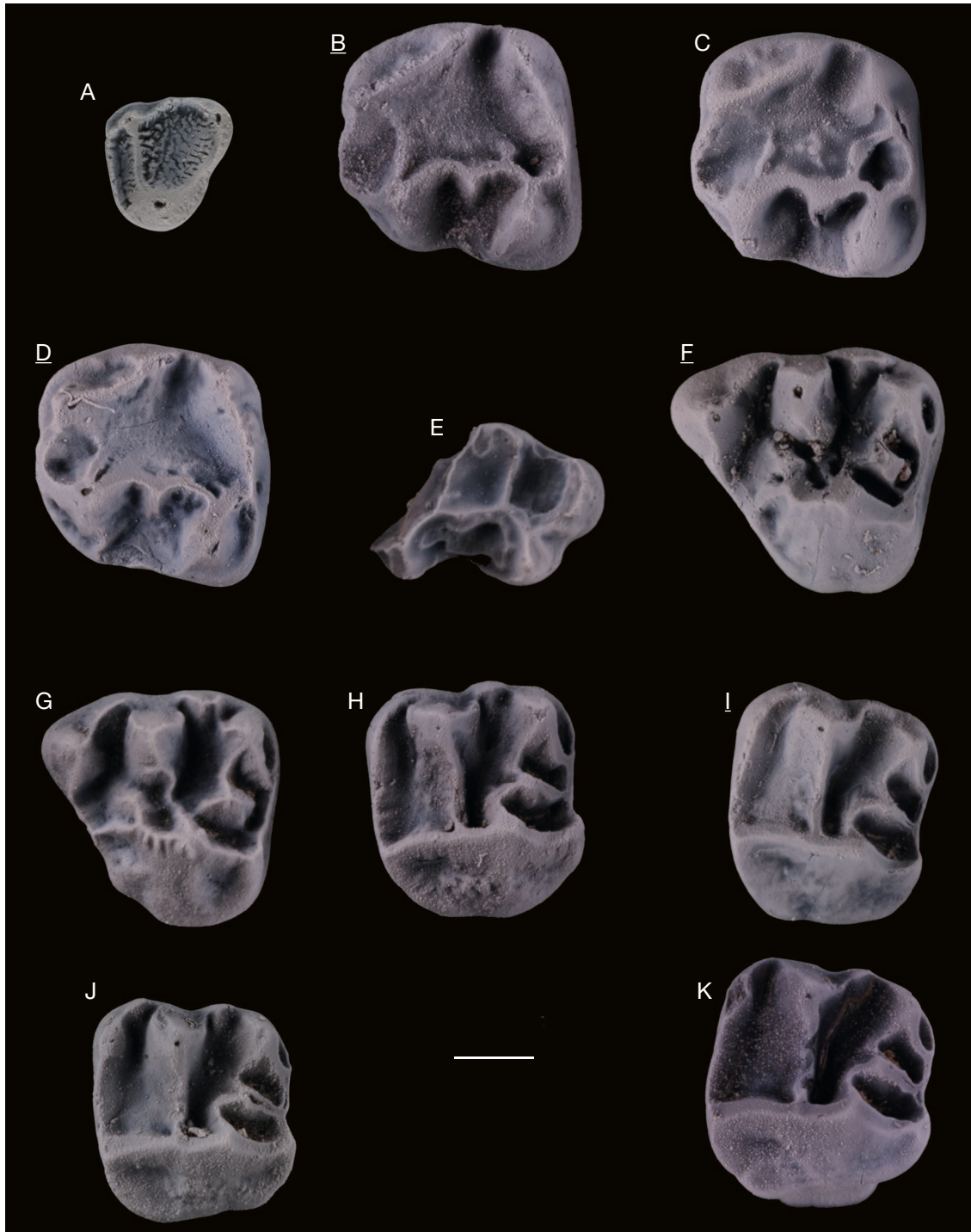


FIG. 8. — **A**, *Blackia miocaenica* Mein, 1970 from Hambach 11C, IPB-HaR-5636, left M3; **B-K**, *Pliopetaurista pliocenica* from Hambach 11C: **B**, IPB- HaR-5614, right m1/2; **C**, IPB- HaR-5625 left m1/2; **D**, IPB- HaR-5627, right m1/2; **E**, left m3; **F**, IPB-HaR-5629, right P4; **G**, IPB- HaR-5631, left P4; **H**, IPB- HaR-5632, left M1/2; **I**, IPB- HaR-5634, right M1/2; **J**, IPB- HaR-5633, left M1/2; **K**, IPB- HaR-5635, left M1/2. All the teeth are shown as left teeth, the teeth that have been mirrored are indicated by underlined letters. Scale bar: 1 mm.

from the lower Miocene and throughout the Pliocene (Daxner-Höck 2004). The occurrence in Hambach 11C is one of the youngest of the genus *Blackia*, alongside that

reported in Mörs *et al.* (1998) from Hambach 11 and that reported by Kolfschoten *et al.* (1998) from Frechen, which is the youngest record (MN16b).

Genus *Pliopetaurista* Kretzoi, 1962

Pliopetaurista pliocaenica Depéret, 1897 (Fig. 8)

MATERIAL EXAMINED. — Right m1/2 (IPB-HaR-5614 and IPB-HaR-5627), left m1/2 (IPB-HaR-5625), left m3 (IPB-HaR-5628), right P4 (IPB-HaR-5629), left P4 (IPB-HaR-5631), left M1/2 (IPB-HaR-5632, IPB-HaR-5634 and IPB-HaR-5635), right M1/2 (IPB-HaR-5633).

MEASUREMENTS. — see Table 3.

DESCRIPTIONS

m1/2 – HaR-5614, HaR-5625 and HaR-5627 (Fig. 8B–D)

Outline almost square but the anterior side is slightly less wide than the posterior side. The enamel is smooth. On HaR-5614 (Fig. 8B), the labial side is also longer than the lingual side and there is a contact facet on the anterior side. This specimen also shows a wear facet on top of the protoconid and the mesostylid also shows signs of wear. HaR-5627 (Fig. 8D) is more worn with the anterior and posterior side showing contact facets. The metaconid, protoconid, and hypoconid exhibit wear facets. The facet on the hypoconid is smaller than the other two. The mesoconid of HaR-5627 as well as the postero-lingual side of the hypoconid and the protoconid seem quite worn. The metalophid is very low on all specimens although less in HaR-5614. The anterolophid is low. The talonid basin is large and deep, and the trigonid basin is also quite large although on HaR-5625 (Fig. 8C), the metalophid is so faint that it does not close the trigonid basin. On this specimen, there is also a small basin delimited at the posterior part by the posterolophid and the entolophid. On HaR-5614, a small lophid is erupting towards the talonid basin from the lophid between the hypoconid and mesoconid. The protoconid and hypoconid are high and dominate the lower mesostylid, mesoconid and entoconid. There is no anteroconid. The syncline between the mesostylid and entoconid is quite wide, deep and its walls are steep. The mesostylid is linked to a high metaconid by a pronounced lophid. No roots are preserved on HaR-5614 and 5625. On HaR-5627 however, four roots are preserved. The one on the labial side is the most prominent. The anterior roots go straight down and are quite round whereas the posterior ones are dipping posteriorly. The lingual root is more oval. The posterior roots are fused at the crown base (at least 1/3rd of their length). The anterior roots are completely separated and more broken off.

m3 – HaR-5628 (Fig. 8E)

The surface of the enamel is smooth. This specimen is broken mid protoconid. The anterior arc, including the metaconid, is missing. The anterior wall of the protoconid is preserved as well as the hypoconid, entoconid, and mesostylid. The lophid between metaconid and hypoconid is quite worn as well as the syncline between the entoconid and the mesostylid. The anterior part of the entoconid is also worn and the labial side

of the mesostylid shows a small wear facet. The protoconid is high, dominating the three remaining cusps and has a wear facet on its top. The lophid going from the mesostylid to the labial side creates a basin. No roots are preserved.

P4 – HaR-5629 and HaR-5631 (Fig. 8F, G)

The outline is triangular and the enamel smooth. The hypocone is very weak. The protocone and the paracone are high although the highest is the protocone. On HaR-5629 (Fig. 8F), the paracone exhibits a wear facet on its anterior side and so does the parastyle, which also bears scratches, although on its posterior side. There is also a big wear facet on the lingual side of the protocone of this specimen. On this specimen, the metaconule and protoconule also appear worn. The mesostyle is well defined and on HaR-5631 (Fig. 8G), linked to the metacone by a very small loph. The mesostyle appears worn on HaR-5629. The metaconule is well delimited and is separated by a syncline from the protocone on HaR-5631. The trigon basin is deep but narrow. There is a deep valley between the paracone and the parastyle. The small protoconule is separated from the paracone by a small syncline. A posterior lophule erupts from the metacone and almost reaches the low posteroloph forming depressions and there is a depression on the posterior side of the metacone. No roots are preserved.

M1/2 – HaR-5632, HaR-5633, HaR-5634 and HaR-5635 (Fig. 8H–K)

The specimens have a square/rhomb shape, the enamel is smooth, and the posterior side is slightly less wide than the anterior one. This difference is more marked on HaR-5635 (Fig. 8K). On HaR-5632 (Fig. 8H), small wear facets are visible on the anterior side of the paracone and the metacone. Moreover, the protoloph shows signs of wear. The presence of a wear facet is observed on the anterior side of the paracone on HaR-5633 (Fig. 8I). On HaR-5634 (Fig. 8J), there are wear facets on the paracone (posterior side), the metacone (anterior side) and two small ones on the parastyle as well as on the metaconule. On HaR-5635, there is a big wear facet visible on the parastyle and one postero-lingually on the paracone and the metacone seems worn. The anterior sides of HaR-5634 and 5635 appear more worn than on the other two specimens. The anteroloph is very faintly crenulated on HaR-5633. The protocone is the highest cusp. The protoconule is, when present, very faint and the protoloph is slightly curving posteriorly on HaR-5632. A deep and wide valley separates the paracone and parastyle. The latter is higher and more developed on HaR-5634 and 5635 than on HaR-5632 and 5633. The mesostyle is less expressed than on the P4s and most visible on HaR-5634. It is separated from the metacone on HaR-5632 and 5634, by a medium syncline. The hypocone is present. The posteroloph is very low. A posterior lophule erupts from the metaconule and reaches the posteroloph forming depressions on both sides. A small depression is visible on the posterior side of the metacone. No roots are preserved, except in HaR-5633 where a small part of three roots is present.

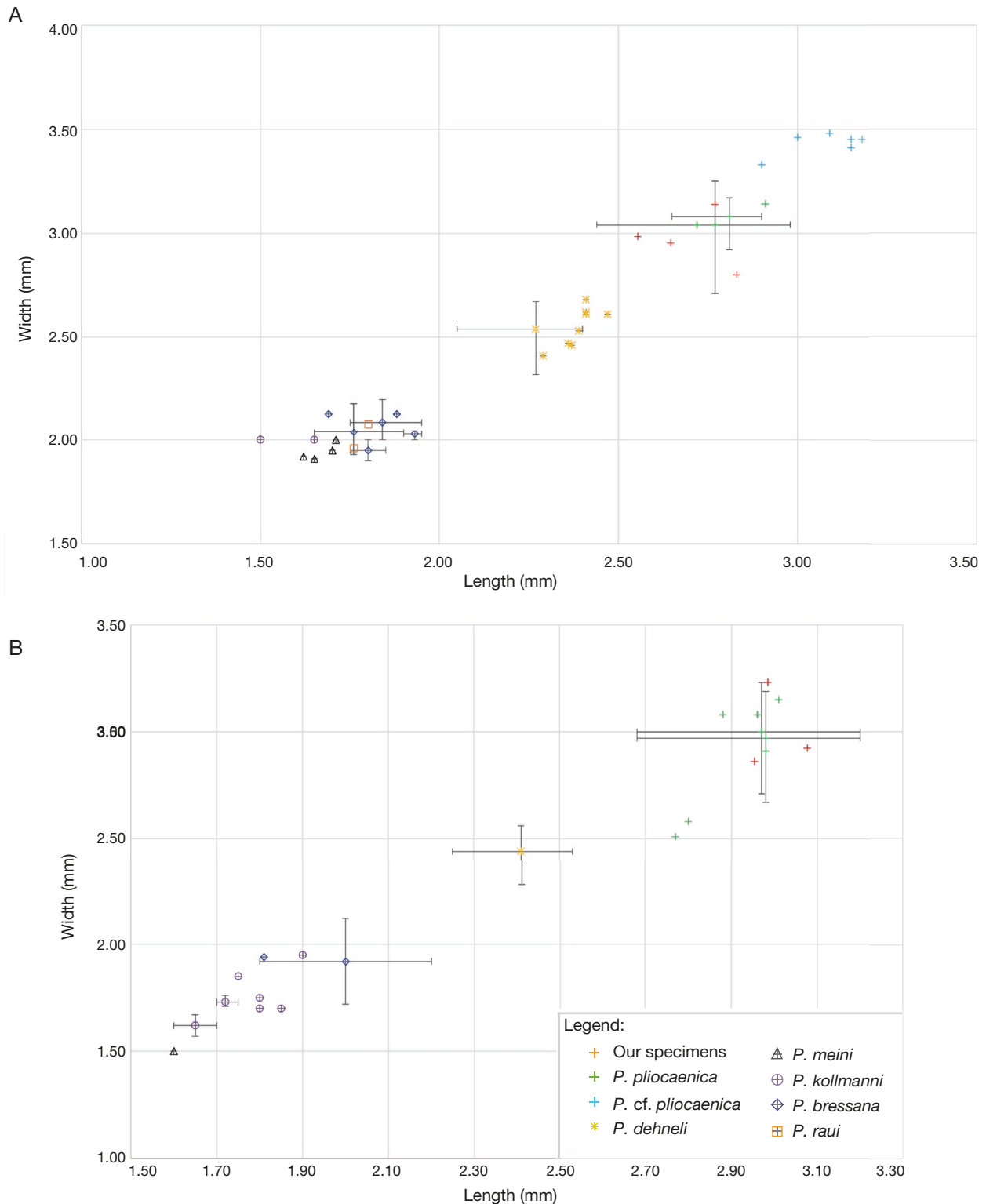


FIG. 9. — **A**, Size comparison of *Pliopetaurista pliocaenica* (Depéret, 1897) M1/2 from Hambach 11C with other published specimens. Black & Kowalski (1974): *Pliopetaurista dehnelli* Sulimski, 1964, *Pliopetaurista meini* Black & Kowalski 1974, *Pliopetaurista cf. pliocaenica* (Depéret, 1897); Daxner-Höck (1975): *Pliopetaurista bressana* Mein, 1970; Dahlmann (2001): *P. pliocaenica*, *Pliopetaurista raii* Dahlmann, 2001; Daxner-Höck (2004): *P. bressana*, *Pliopetaurista kollmanni* Daxner-Höck, 2004; de Bruijn (1995): *P. dehnelli* Sulimski, 1964; Fejfar & Storch (1990): *P. pliocaenica*; García-Alix et al. (2007): *P. pliocaenica*, *P. cf. pliocaenica*; Vasileiadou et al. (2012): *P. dehnelli*. In red are our specimens from Hambach 11C, in green the *P. pliocaenica* specimens and in blue the *P. cf. pliocaenica*. **B**, Size comparison of *Pliopetaurista pliocaenica* m1/2 from Hambach 11C with other published specimens. Black & Kowalski (1974): *Pliopetaurista meini*; Dahlmann (2001): *P. pliocaenica*; Daxner-Höck (1975): *Pliopetaurista bressana*; Daxner-Höck (2004): *P. bressana*, *Pliopetaurista kollmanni*; de Bruijn (1995): *P. dehnelli*; Colombero & Carnevale (2016): *P. pliocaenica*; Mansino et al. (2018): *P. pliocaenica*; Mörs et al. (1998): *P. pliocaenica*. In red are our specimens from Hambach 11C, in green the *P. pliocaenica* specimens and in blue the *Pliopetaurista cf. pliocaenica*.

REMARKS

The relatively large size coupled with the complex morphology of our specimens are fitting into the *Pliopetaurista* genus (Mörs *et al.* 1998). Moreover, the smooth enamel differs from *Miopetaurista* where it is wrinkled or “chagriné” (Mein 1970) and the convergent protoloph and metaloph on the upper molars further confirm this identification (Mein 1970; Qiu & Li 2016). The dimensions of our specimens fit into the range of *Pliopetaurista pliocaenica* (Fig. 9) and are bigger than other species such as *Pliopetaurista dehnelli* Sulimski, 1964 (Mein 1970) as confirmed by Fig. 9. This species is the closest in size and morphology to *P. pliocaenica* (Mörs *et al.* 1998; García-Alix *et al.* 2007; Mansino *et al.* 2018). Moreover, we observe the presence of a faint but present mesostyle or bulged mesostylar crests that is absent in *P. dehnelli* (García-Alix *et al.* 2007). The low metalophids and the presence of hypocones on the molars also point in the direction of *P. pliocaenica*. It is not attributed to *Pliopetaurista* cf. *pliocaenica sensu* de Bruijn (1995) and García-Alix *et al.* (2007) because our specimens are not large enough (Fig. 9A). All these observations allow us to attribute the specimens to *P. pliocaenica*. This species ranges from the latest Miocene to the Plio-Pleistocene (Colombero & Carnevale 2016) which is coherent with the age of our locality. There are only four previous records of *Pliopetaurista* in the Pliocene of Germany, from three different localities. Mein (1970) and Dahlmann (2001) both described specimens from Wölfersheim, Fejfar & Storch (1990) reported an isolated molar from Gundersheim and Mörs *et al.* (1998) reported several specimens from Hambach. Most of these reports are of *P. pliocaenica*, with the exception of the specimens of *P. rauti* Dahlmann, 2001 in Dahlmann (2001).

DISCUSSION

All the species described here were already reported from Hambach 11 by Mörs *et al.* (1998), which seems to indicate a shared environment, and further confirms their assignment to a similar age. This new material is, however, richer than what was reported by Mörs *et al.* (1998) and contains different tooth positions. The material does not show signs of transportation and is very well-preserved. The fossils were found in channel fill deposits indicative of a river. This is coherent with the presence of two genera of beavers. Although *Trogontherium* had a more terrestrial lifestyle than *Castor* (Fostowicz-Frelik 2008), both are considered semi-aquatic (Fostowicz-Frelik 2008). Moreover, the beavers and the squirrels are indicating of the presence of trees. Indeed, *Castor fiber* is wood cutting, a trait that is assumed to be shared with *Trogontherium* by Rybczynski (2007) based on its phylogenetic position. The flying squirrels are indicators of tall deciduous trees in mixed forests (de Bruijn 1998) and of a warm and humid climate (Casanovas-Vilar *et al.* 2018) although some modern forms are tolerant to dryer climates and inhabit evergreen forests (Daxner-Höck 2004).

The climate in Central Europe during the Reuverian was corresponding to the type CfA *sensu* Köppen (Thiel *et al.* (2012). This indicates a temperate climate with no dry season and a hot summer. The climate during the Pliocene was both warmer and wetter than today (Salzmann *et al.* 2011). As pointed out by Mörs *et al.* (1998) these conditions are indicative of the epoch and precede the changes happening during the transition to the Pleistocene.

Our material is mainly composed of isolated teeth and no postcranial material. This poses problems for the taxonomy, which is amplified by the rarity of the material, especially of smaller specimens such as the Sciuridae (Colombero & Carnevale 2016) and the smaller species of *Trogontherium* (Stefen 2011). Most of the squirrels found in Hambach 11C belong to taxa considered as flying squirrels and only two teeth of tree squirrel (*Sciurus* sp.) were recovered. The flying squirrels belong to two different genera. Castoridae are nowadays only represented by two species, belonging to one genus, but appear in the fossil record during the Eocene (Stefen 2011). *Castor fiber* and *Trogontherium minus* were already previously found together in the MN16a of Hambach (Mörs *et al.* 1998) but also in the MN16a Slovakian locality of Hajnáčka I (Sabol *et al.* 2006). Interestingly, the Slovak occurrences are also found in association with *P. pliocaenica* indicating a similar type of climate and environment. The present *T. minus* material is the richest and most complete reported to date when it comes to juvenile specimens, the most complete specimen overall being the skull and mandible reported by Vislobokova (1996) from the MN16 of Western Siberia. The dP4 and the lower jaw fragment are similar in size and could potentially belong to the same individual although this is not verifiable.

CONCLUSION

The fauna of Hambach 11C is almost the same as that of Hambach 11 indicating a similar fluvial and forested environment. This environment would have been composed of a river surrounded by closed forested areas with deciduous trees and a humid and temperate climate. All the genera found are only represented by one species each. Two genera of flying squirrels were found: *Pliopetaurista pliocaenica* and *Blackia miocaenica*. The specimen of *B. miocaenica* represents one of its youngest occurrences to date and one of only three in MN16. However, here and in the two previously mentioned latest Pliocene occurrences, only a single tooth was reported indicating the rarity of the taxon in the Pliocene. It is also worth noting that they were all from German localities. Two genera of Castoridae have been found in Hambach 11C, one extant and one extinct. The extant genus *Castor* is represented by the species *Castor fiber* and the extinct genus *Trogontherium* is represented by the species *Trogontherium minus*. *Trogontherium minus* is a rare species, making our new material important, especially since different ages are represented with the best documented juvenile specimens to date.

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