



Insectivores and marsupials from the upper Oligocene of Banovići (Bosnia and Herzegovina)

Froukje N. van der Sar, Roos van Glabbeek, Wilma Wessels, Zoran Marković & Hans de Bruijn

To cite this article: Froukje N. van der Sar, Roos van Glabbeek, Wilma Wessels, Zoran Marković & Hans de Bruijn (2017) Insectivores and marsupials from the upper Oligocene of Banovići (Bosnia and Herzegovina), *Journal of Vertebrate Paleontology*, 37:6, e1368529, DOI: 10.1080/02724634.2017.1368529

To link to this article: <https://doi.org/10.1080/02724634.2017.1368529>



© 2017 The Author(s). Published with license by the Society of Vertebrate Paleontology © Froukje N. Van Der Sar, Roos Van Glabbeek, Wilma Wessels, Zoran Marković, and Hans De Bruijn



Published online: 27 Nov 2017.



Submit your article to this journal [↗](#)



Article views: 380



View related articles [↗](#)



View Crossmark data [↗](#)

INSECTIVORES AND MARSUPIALS FROM THE UPPER OLIGOCENE OF BANOVIĆI (BOSNIA AND HERZEGOVINA)

FROUKJE N. VAN DER SAR,^{1,†} ROOS VAN GLABBEK,^{1,††} WILMA WESSELS,^{*,1} ZORAN MARKOVIĆ,² and HANS DE BRUIJN¹

¹Department of Earth Sciences, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands, froukjevandersar@gmail.com; roos_glabbeek@hotmail.com; w.wessels@uu.nl; HdBruijn@uu.nl;

²Natural History Museum in Belgrade, Njegoševa 51, 11000 Belgrade, Serbia, zoran.markovic@nhmbeo.rs

ABSTRACT—The insectivore and marsupial assemblage from the Banovići Basin (MP30/MN1, Bosnia and Herzegovina) provides, in addition to the Rodentia, a better understanding of the faunal exchange between Europe and Anatolia and the biostratigraphic, paleoecological, and paleobiogeographic interpretations of the area. The small and rather poorly preserved collection of fossil remains of insectivores and marsupials from Banovići includes three genera of Talpidae, three genera of Soricidae, one genus of Erinaceidae, one genus of Heterosoricidae, and one marsupial. At the genus level, this assemblage is a mix of genera known from the late Oligocene–early Miocene of Europe (MP29–MN3) and Anatolia (~MP30–MN3). The presence of the talpids *Suleimania* aff. *ruemkae* and *Desmanodon* aff. *ziegleri* indicates an age within the Oligocene/Miocene boundary interval (MP30/MN1), which is consonant with the age estimate based on the rodents and magnetostratigraphy. The diversity of Soricidae and the presence of *Geotrypus* indicate that the Banovići biotope was rather warm and humid during the late Oligocene.

Citation for this article: Van der Sar, F. N., R. van Glabbeek, W. Wessels, Z. Marković, and Hans de Bruijn. 2017. Insectivores and marsupials from the upper Oligocene of Banovići (Bosnia and Herzegovina). *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2017.1368529.

INTRODUCTION

The small-mammal fauna of Banovići from the late Oligocene of Bosnia and Herzegovina provides new information on the dynamics of mammal migrations between western Europe and Anatolia (De Leeuw et al., 2011; De Bruijn et al., 2013). The similarity between the rodent assemblage from Bosnia and Herzegovina and assemblages from Anatolia and western Europe indicates a selective and restricted faunal exchange between Anatolia and western Europe during the late Oligocene. The rodent assemblage is best compared with localities attributed to the European MP30/MN1 small-mammal zones (De Bruijn et al., 2013). The magnetostratigraphic pattern of the section correlates to the C6Cr–C6Cn.2n interval of the GTS (Geological Time Scale), which indicates an age of around 24 Ma for the Banovići Basin infill (De Leeuw et al., 2011).

Insectivores from the late Oligocene and early Miocene are well documented from many localities in Europe, and about 10 insectivore assemblages from late Oligocene–early Miocene localities are known from Anatolia (Van den Hoek Ostende, 1992, 1995a,

1995b, 1997, 2001a, 2001b, 2001c). However, in the area between Europe and Anatolia, only one late Oligocene insectivore assemblage and a few early Miocene insectivore assemblages from Greece have been described thus far (Doukas, 1986; Doukas and Theocharopoulos, 1999; Vasileiadou and Koufos, 2005; Doukas and Van den Hoek Ostende, 2006; Vasileiadou and Zouros, 2012). In the Banovići small-mammal assemblage, a few marsupial specimens are also present. Marsupials, common in Europe until the late Oligocene, disappear during the middle Miocene (Ziegler, 1999). They are not known from the Oligocene and early Miocene of southeastern Europe and Anatolia. Therefore, the insectivores and marsupials from this locality in the Balkan region can help us to gain a better understanding of the faunal exchange between Anatolia and Europe during the late Oligocene–early Miocene.

The insectivore and the marsupial materials from Banovići are described here in detail, and the biostratigraphic and paleobiogeographic implications and paleoecological interpretation are discussed. The diversity of insectivores, especially shrews, seems to be related to humidity (Reumer, 1984; Furió et al., 2011).

Abbreviations—**BAN**, specimens from the Banovići locality in Bosnia and Herzegovina, housed in the Natural History Museum in Belgrade; specimens from the Banovići locality in Bosnia and Herzegovina, housed in the Natural History Museum in Belgrade, Serbia; **dex**, dextral; **Isup**, upper incisor; **L**, length; **LL**, length lingual side; **LT**, length talon; **N**, number of specimens; **R**, range of measurements; **sin**, sinistral; **W**, width; **WA**, width anterior; **WP**, width posterior; **WTa**, width talonid; **WTr**, width tigonid.

GEOLOGY

The Dinarides emerged from the Tethys Sea in the late Eocene to early Oligocene, and within the Dinarides

*Corresponding author.

[†]Current address: Schoolsteeg 2B, 2311 TD Leiden, The Netherlands.

^{††}Current address: Livingstonelaan 602, 3526 JE Utrecht, The Netherlands.

© Froukje N. Van Der Sar, Roos Van Glabbeek, Wilma Wessels, Zoran Marković, and Hans De Bruijn.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way.

intramontane basins were formed (De Leeuw et al., 2011). One of these basins is the Banovići Basin, which is situated in the northwestern part of Bosnia and Herzegovina (Fig. 1). The Banovići Basin is filled with 320 m of Oligocene to Miocene lacustrine sediments. The fossiliferous layer, a greenish clay that contains very thin layers of lignite, is situated just below the main coal seam in the Turija opencast mine near Banovići (De Bruijn et al., 2013). The geological setting of the Banovići Basin, with emphasis on the regional stratigraphic and regional paleogeographic development of the basin infill, has been described in detail in De Leeuw et al. (2011).

MATERIALS AND METHODS

In total, 133 insectivore and marsupial jaw fragments, isolated teeth, and a humerus present in the Banovići fossil assemblage were identifiable to the family level, and 84 of these could be assigned more specifically. Not included in the descriptions are 49 dental elements, comprising fragments of molars, as well as some incisors and antemolars: 35 Talpidae, gen. et sp. indet., 11 Soricidae, gen. et sp. indet., and three Heterosoricidae, gen. et sp. indet.

The dimensions of the humerus of *Desmanodon zieglerei* from Harami (Turkey) are taken from Van den Hoek Ostende (1997: pl. 3). The measurements of the cheek teeth were taken with an Orthoplan (Leitz) microscope with a precision of 0.01 mm. All teeth are figured as left ones to facilitate comparison. Lower and upper dentitions are indicated with lower- and uppercase letters, respectively. The collection is housed in the Natural History Museum in Belgrade, Serbia.

The measurement method follows Crochet (1980) for the marsupials, Rümke (1985) and Van den Hoek Ostende (1989) for the Talpidae, and Reumer (1984) for the Soricidae and Heterosoricidae. For the terminology of the molars, we follow Crochet (1980), Reumer (1984), and Van den Hoek Ostende (1989) except for the oblique crest and entoconid crest, which here are called oblique cristid and entocristid, following Van den Hoek Ostende (2001b). Terminology of the humerus follows Hutchison (1974).

All measurements are in millimeters (mm). Molars from the right side of a jaw are indicated with ‘dex’ (dextral) and those from the left with ‘sin’ (sinistral). Measurements of the specimens are given as L × W, unless otherwise indicated.

Only species occurring in the late Oligocene and early Miocene of Europe and western Asia are mentioned in the systematic part, in the included species and occurrences, of this paper.

The percentages of all the dental elements of Talpidae, Soricidae, Heterosoricidae, and Erinaceidae that are identified to family level only are also included in the faunal comparison.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Subclass THERIA Parker and Haswell, 1897
 Infraclass METATHERIA Huxley, 1880
 Family HERPETOTHERIIDAE Trouessart, 1879
 Genus *AMPHIPERATHERIUM* Filhol, 1879

Type Species—*Amphiperatherium frequens* (Von Meyer, 1946).

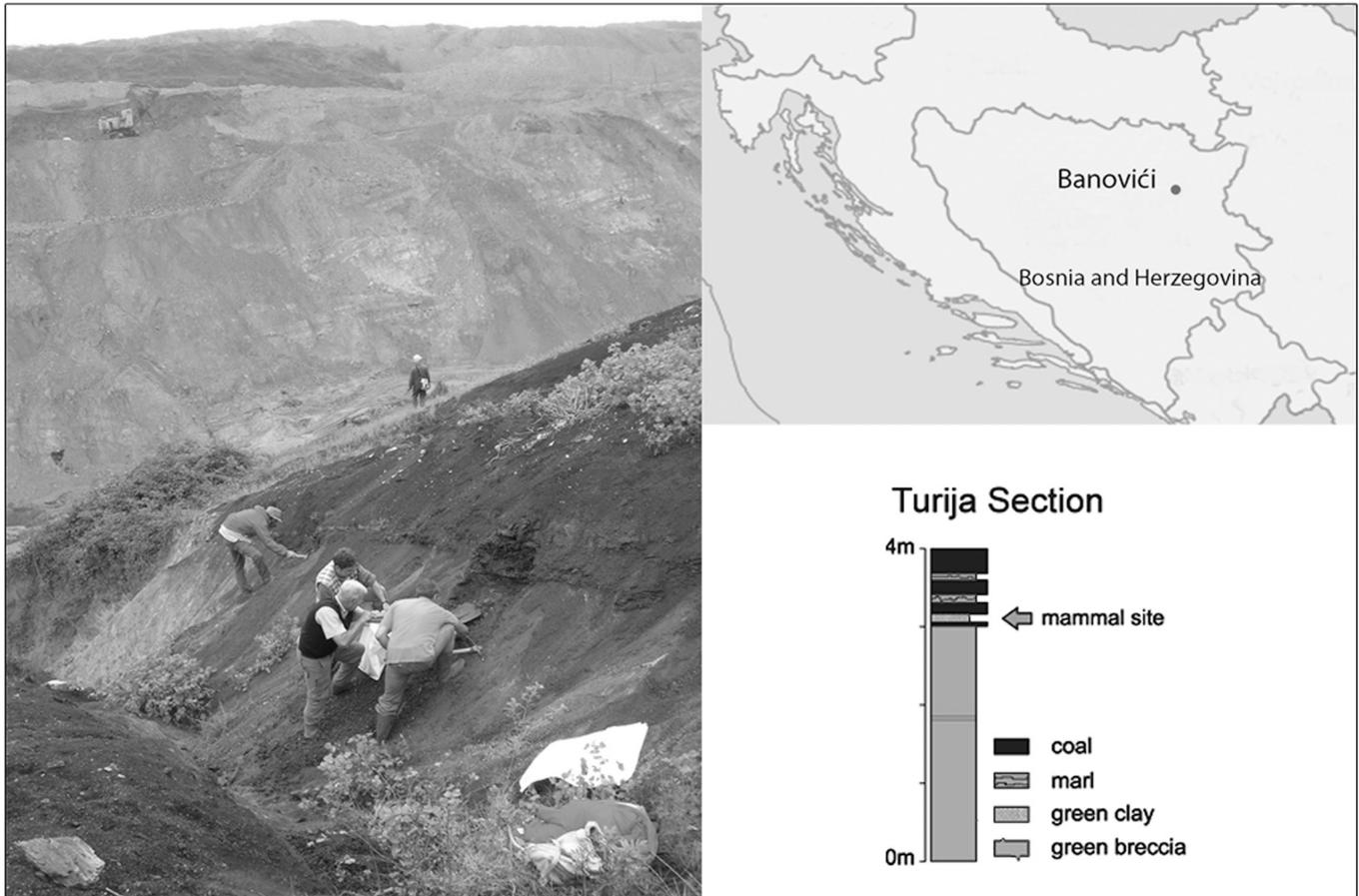


FIGURE 1. Picture of the mammal locality Banovići, Turija section, in the open-pit coal mine Banovići (Bosnia and Herzegovina) and a stratigraphic column of the section. The fossiliferous layer is just below the main coal seam (from De Bruijn et al., 2013).

Other Included Species—*Amphiperatherium exile* (Gervais, 1848–52).

Occurrences—*Amphiperatherium frequens* in early Miocene localities in Germany and France (Von Koenigswald, 1970; Crochet, 1980; Ziegler, 1990b; Klietmann et al., 2014).

Amphiperatherium exile (Gervais, 1848–52) in the early Oligocene (Crochet, 1980) and in many assemblages from the late Oligocene of France, e.g., Cournon, Pech du Fraysse, Coderet (Crochet, 1980), and Germany, e.g., Gaimersheim, Ehrenstein 4, Eggingen-Mittelhart 1, Herrlingen 8 and 9, Oberleitersbach (Von Koenigswald, 1970; Ziegler, 1990b, 1998; Engesser and Storch, 2008).

AMPHIPERATHERIUM CF. *EXILE*

(Fig. 2)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN752, mandible fragment dex, m1 (2.06 × 1.06), m2 (2.17 × 1.25), and m3 (2.20 × 2.17); BAN753, m2 or 3 dex (~2.08 × 1.35); BAN754, m2 or 3 sin (2.23 × 1.35); BAN755, m2 or 3 sin (2.14 × 1.30); BAN756, m2 or 3 sin (~2.20 × 1.21).

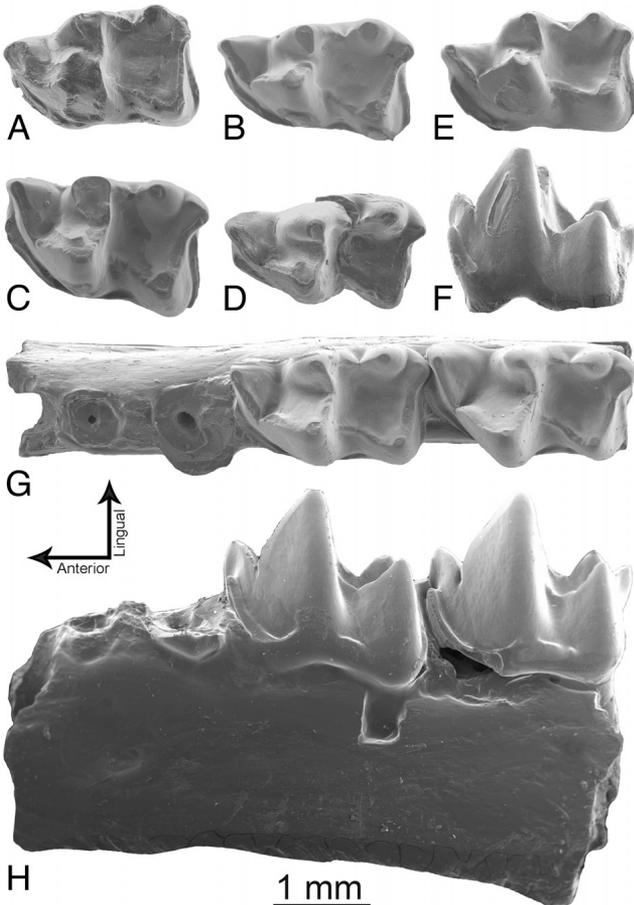


FIGURE 2. *Amphiperatherium* cf. *exile*. **A**, BAN753, m2 or 3 dex (reversed image); **B**, BAN755, m2 or 3 sin; **C**, BAN754, m2 or 3 sin; **D**, BAN756, m2 or 3 sin; **E**, BAN752, m1 dex part of the jaw in occlusal view (reversed image); **F**, BAN752, m1 dex part of the jaw (F1) in labial view (reversed image); **G**, BAN752, dextral jaw fragment with roots of m1, m2, and m3 in occlusal view (reversed image); **H**, BAN752, dextral jaw fragment with area of m1, m2, and m3 in labial view (reversed image).

Description—The molars are very much alike in morphology and size. The m1 in the jaw fragment is slightly shorter and less wide than all other molars. The trigonid is taller and slightly larger than the talonid. On the trigonid, the protoconid is the tallest cusp, the metaconid is slightly lower, and the paraconid is the lowest cusp. The paraconid and the metaconid are rounded cones; the protoconid is triangular. The paraconid and metaconid are not connected. A distal metacristid is present on the posterolabial side of the metaconid and connects to the anterior base of the entoconid. The hypoconid and entoconid are of about the same height; the hypoconulid is lower. The hypoconulid and the triangular hypoconid are connected by the postcristid. The entoconid, isolated from metaconid and hypoconulid, is oval. The cristid obliqua is distinct and not buccally oriented. The position of the hypoconulid is posterolabial to the entoconid. The anterior cingulum, as well as the posterior cingulum, is well developed.

Discussion—The molars have a prominent talonid with an oval entoconid, a strong postcristid with the hypoconulid on the posterolabial side of the entoconid, and a strong posterior cingulum. These are all characteristics of *Amphiperatherium exile* (Gervais, 1848–52). Our tentative specific allocation is due to the absence of upper molars, which are also important in differentiating between species of *Amphiperatherium*.

Infraclass EUTHERIA Gill, 1872

Order EULIPOTYPHILA Waddell, Okada, and Hasegawa, 1999

Family ERINACEIDAE Fischer, 1814

Subfamily ERINACEINAE Gill, 1872

ERINACEINAE, gen. et sp. indet.

(Fig. 3)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN721, m3 sin (2.31 × 1.85).

Description—The complete m3 consists of the trigonid only. The cingulum is pronounced on the labial and posterior sides. The protoconid and metaconid are of the same height. The well-developed paralophid connects the protoconid and paraconid. The paraconid is small compared with the protoconid and metaconid. The roots are fused.

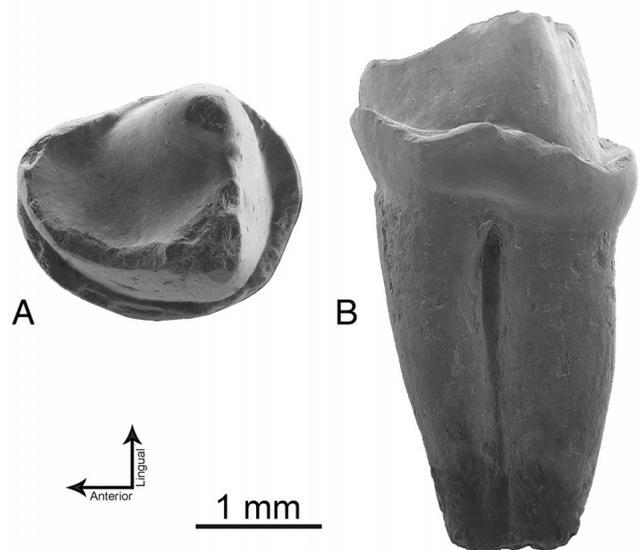


FIGURE 3. Erinaceinae, gen. et sp. indet., BAN721, m3 sin in **A**, occlusal and **B**, labial views.

Discussion—The morphology, and the presence of one root, of this m3 from Banovići is very similar to that of m3 of *Amphechinus arvernensis* and *A. robustus*. The size of the Banovići m3 is within the range of the m3 of *Amphechinus robustus* (MP29, Herrlingen 9; Ziegler, 1998). However, the presence of one m3 alone precludes us from a more exact determination.

Family TALPIDAE Fischer, 1814
 Subfamily TALPINA Fischer, 1814
 Genus *DESMANODON* Engesser, 1980

Type Species—*Desmanodon major* Engesser, 1980.

Other Included Species—Late Oligocene and early Miocene: *Desmanodon minor* Engesser, 1980; *Desmanodon antiquus* Ziegler, 1985 (= *D. meuleni* Doukas, 1986); *Desmanodon ziegleri* Van den Hoek Ostende, 1997; *Desmanodon burkartii* Van den Hoek Ostende, 1997; *Desmanodon daamsi* Van den Hoek Ostende, 1997; *Desmanodon crocheti* Prieto 2010; *Desmanodon fluegeli* Prieto, 2010; *Desmanodon larsi* Furió, Van Dam, and Kaya, 2014.

Occurrences—Late Oligocene and early Miocene: *Desmanodon antiquus* from the early Miocene of Germany (MN5; Püttenhausen; Ziegler, 1985) and Greece (MN4; Karidyá; Doukas and Van den Hoek Ostende, 2006); *D. ziegleri* from the early Miocene of Anatolia (MN1–2; Harami and Kilçak; Van den Hoek Ostende, 1997) and cf. *D. ziegleri* from the late Oligocene of Anatolia (~MP30; Kargı; Van den Hoek Ostende, 2001c); *D. burkartii* from the early Miocene of Anatolia (MN3; Keseköy; Van den Hoek Ostende, 1997); *D. daamsi* and *D. aff. daamsi* in the early Miocene of Spain (MN3–MN4; Van den Hoek Ostende, 1997, 2003); *Desmanodon* sp. in the early Miocene of Spain (MN2b–MN5, Van den Hoek Ostende, 1997; MN4, Hordijk et al., 2015).

DESMANODON AFF. *ZIEGLERI* Van den Hoek Ostende, 1997
 (Fig. 4B, C)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN635, maxilla fragment sin with P4 (1.49 × 0.94), M1 (2.38 × 1.46). Both M2 have a slightly damaged parastyle and metastyle: BAN636, M2 dex (~1.56 × ~1.81); BAN650, M2 dex (~1.38 × 1.44).

Description—The outline of the occlusal surface of the P4 is subtriangular. The paracone is very large and tall; the tip of the paracone is at the anterior side. The parastyle, small and low, is situated anterior to the paracone. The posterocrista is slightly curved; it bends off to the lingual side in the posterolingual corner and continues into the posterior lingual cingulum that connects to the ridge-like protocone. An anterior cingulum connects the parastyle to the protocone; however, it is narrow lingual to the paracone. Van den Hoek Ostende (1989) distinguished morphotypes of the P4 in *Desmanodon* and *Paratalpa*; the morphology of the Banovići P4 resembles morphotype B, except for the anterior ridge, which resembles morphotype C.

The outline of the occlusal surface of the M1 is subtriangular. The metacone is the largest and tallest cusp. The posterior arm of the metacone is about twice the length of its anterior arm. The mesostyle cusps are not completely separated. The paracone is remarkably smaller than the metacone, and taller than the protocone. The anterior arm of the protocone is shorter than the posterior arm. The anterior arm ends at the protoconule, which is situated at the base of the paracone. The posterior arm connects to the small, distinct hypocone at the base of the metacone. The posterior arm of the hypocone connects to the posterior cingulum. The posterior cingulum becomes broader towards the labial side, and the metastyle is at the labialmost side of the posterior cingulum. There is a weak labial cingulum. The parastyle is next to the paracone at the anterolabial corner of the molar.

Both M2 have damaged parastyles and metastyles. The outline of the occlusal surface is subtriangular. The posterior arm of the metacone is partly broken off; its anterior arm bends slightly and continues in the mesostyle. The mesostyle cusps are not completely separated. The paracone is somewhat lower than the metacone; the tip of its anterior arm (the parastyle) is broken off, and its posterior arm bends slightly and connects to the mesostyle. The height of the protocone is about the same as that of the paracone, and the protocone lies more to the anterior side. The small protoconule lies at the anterior side of the protocone. The posterior arm of the protocone connects to the small, but distinct, hypocone, which lies at the base of the metacone. The posterior arm of the hypocone continues into a posterior cingulum. The M2 has three roots.

Discussion—The specimens described above are somewhat smaller than the *Desmanodon antiquus* specimens from

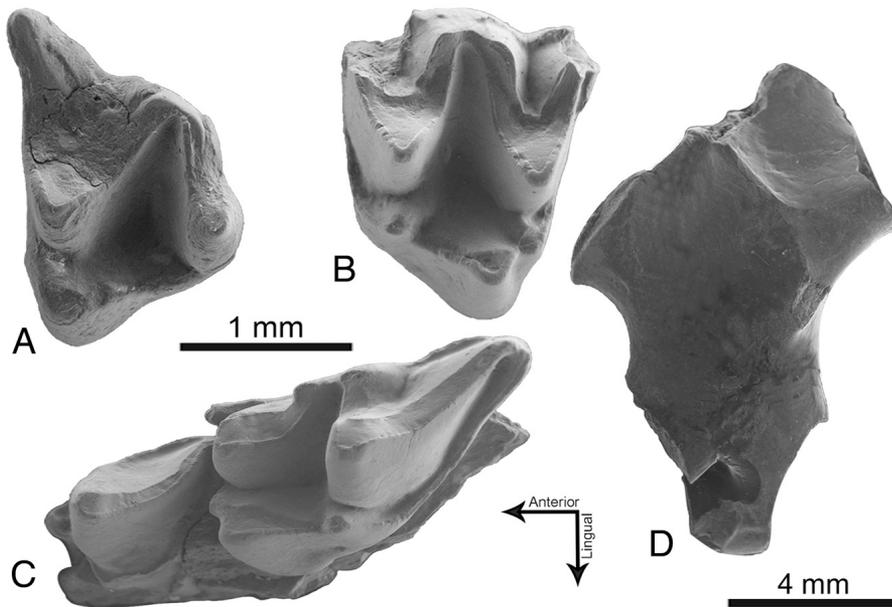


FIGURE 4. *Geotrypus* sp. **A**, BAN637, M3 sin. *Desmanodon* aff. *ziegleri*; **B**, BAN650, M2 dex (reversed image); **C**, BAN635, jaw fragment sin with P4 and M1. *Desmanodon* sp. **D**, BAN720, partial humerus.

Germany and from the Greek locality Karydiá (Ziegler, 1985; Doukas and Van den Hoek Ostende, 2006) and somewhat larger than specimens from Aliveri (Ziegler, 1985; Doukas, 1986). The specimens of *Desmanodon* from Banovići are of roughly the same size as, or are smaller than, specimens of *Desmanodon zieglerti* (Van den Hoek Ostende, 1997). The P4 is less wide than in all known species. The *Desmanodon* specimens from Banovići have a protoconule in the M1 as well as in the M2, which is typical for *D. zieglerti*. The mesostyle, especially in M2, is less divided than in *D. zieglerti* (with about half of the specimens with incompletely separated mesostyle). The L/W ratio between the dental elements differs from *D. zieglerti*. The specimens are placed in *D. aff. zieglerti* because of the narrower P4 and the difference in L/W ratio between the dental elements.

DESMANODON sp.
(Fig. 4D)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN720, dextral humerus with shaft breadth of 4.48 mm and length >11.3 mm.

Description—Some parts of the proximal and distal ends of the humerus are broken off; the top of the pectoral process is damaged, and the caput, the entepicondyle, and the capitulum are missing. However, the long prominent teres tubercle, which is typical for the genus *Desmanodon*, is present. The pectoral process stands out in anterior view, and it is, as far as it is undamaged, surrounded by a weak ridge. The humerus is quite large; even incomplete it has a shaft breadth of about 4.5 mm and is more than 11 mm in length.

Discussion—*Paratalpa* Lavocat, 1951, and *Desmanodon* Engesser, 1980, differ in their humeri; their dental elements are very similar (Van den Hoek Ostende, 1997). The presence of a humerus in our collection that is more typical for *Desmanodon* than for *Paratalpa*, made us decide to allocate the teeth from Banovići to *Desmanodon*.

The humerus of *Desmanodon* sp. is more robust and much longer and wider than other species of *Desmanodon* (all with a shaft breadth between 2 and 2.9 mm and a length between 9 and 11 mm; Engesser, 1980; Van den Hoek Ostende, 1997; Prieto, 2010; Prieto et al., 2010).

The humerus of *Desmanodon* sp. is too large for all known *Desmanodon* species, and *Desmanodon* sp. most probably represents a new species.

Subfamily TALPINAЕ Fischer, 1814
Tribe TALPINI Fischer, 1814
Genus *GEOTRYPUS* Pomel, 1848

Type Species—*Geotrypus antiquus* (Blainville, 1839). The holotype of *Geotrypus acutidens* is lost, and *Geotrypus antiquus* becomes the type species of this genus (Schwermann and Martin, 2012).

Other Included Species—Late Oligocene and early Miocene: *Geotrypus tomerdingensis* Tobien, 1939; *Geotrypus acutidentatus* (Blainville, 1839); *Geotrypus ehrensteinensis* Ziegler, 1990a; *Geotrypus montisasini* Ziegler, 1990a; *Geotrypus haramiensis* Van den Hoek Ostende, 2001a; *Geotrypus kesekoeyensis* Van den Hoek Ostende, 2001a.

Occurrences—Late Oligocene and early Miocene: *Geotrypus antiquus* from middle and late Oligocene of France (MP25: Quercy; Crochet, 1995; MP28: Cournon; Lavocat, 1951) and late Oligocene of Germany (MP28: Empel; Schwermann and Martin, 2012); *G. acutidentatus* from the late Oligocene of France (MP30: Coderet; Hugueney, 1972); *G. tomerdingensis* from the early Miocene of Germany (MN1: Tomerdingen; Ziegler, 1990a); *G. ehrensteinensis* from the late Oligocene of Germany (MP30: Ehrenstein 4; Ziegler, 1990a); *G. montisasini* from the

early Miocene of Germany (MN2 a: Ulm-Westtangente; Ziegler, 1990a); *G. haramiensis* from the early Miocene of Anatolia (MN1–2: Kilçak 3 A and Harami 1 and 3; Van den Hoek Ostende, 2001a); *G. kesekoeyensis* from the early Miocene of Anatolia (MN3: Keseköy; Van den Hoek Ostende, 2001a). Many *Geotrypus* sp. in the range of MP23–MN4 (Schwermann and Martin, 2012).

GEOTRYPUS sp.
(Fig. 4A)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN637, M3 sin (1.41 × 2.09); BAN638, M3 sin (L = 1.38); BAN639, M3 dex (L = 1.40).

Description—The occlusal surface of the M3 is subtriangular. The paracone is the tallest cusp. The anterior arm of the paracone is longer than its posterior arm. The anterior arm curves near the parastyle; the posterior arm connects to the mesostyle. The mesostyle, damaged in two specimens, is only very slightly interrupted. The metacone is somewhat taller than the protocone in one specimen; in the other two, the metacone and protocone are of about the same height. The protocone lies to the anterior side of the molar. The anterior arm of the protocone ends at the base of the paracone; the posterior arm ends at the base of the metacone. Cingula are absent.

Discussion—The presence of only M3 specimens of *Geotrypus* hampers identification, because characteristics such as the morphology of the M2 (e.g., development of the anterior cingulum) and the presence of P2 are essential for determining *Geotrypus* at the species level. The M3 are smaller than the M3 of *G. antiquus* and *G. ehrensteinensis* from Ehrenstein. They are of about the same size as the M3 of *Geotrypus* sp. from Eggingen-Mittelhart and *G. haramiensis* from Anatolia. The poorly divided mesostyle differentiates this tooth from the other species.

Subfamily SULEIMANINAE Van den Hoek Ostende, 2001a
Genus *SULEIMANIA* Van den Hoek Ostende, 2001a

Type Species—*Suleimania ruemkae* Van den Hoek Ostende, 2001a.

Occurrences—*Suleimania ruemkae* in the early Miocene of Anatolia (Kilçak 0^o, 0, 3 A, 3B, Harami 1, 2, 3, Keseköy; Van den Hoek Ostende, 2001a).

SULEIMANIA AFF. *RUEMKAЕ* Van den Hoek Ostende,
2001a
(Fig. 5)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN601–603, six P4; BAN604–606, three P4; BAN607–609, three M1; BAN610–614, five M1; BAN615 and BAN616, two M2; BAN617, an M2; BAN620 and BAN621, two m1; BAN618 and BAN619, two m1; BAN625 and BAN626, two m2; BAN627–633, seven m3; BAN634, an m3. Thirty-one isolated specimens in total (Fig. 5; Table 1).

Description—The outline of the occlusal surface of the P4 is an irregular ellipse. The P4 consists mainly of a very large paracone. The highest point of the paracone is in the middle or more to the anterior side of the tooth. The parastyle is well developed. The posterocrista extends in a straight line from the tip of the paracone to the posterior part of the tooth. A strong cingulum connects the top of the paracone with the posterior part of the molar. In some specimens, the anterior lingual cingulum is absent; in others, it is complete along the whole lingual side. The P4 has four roots.

The outline of the occlusal surface of the M1 is irregular. The metacone is the tallest cusp. The metastyle is, in varying degrees, damaged in all specimens; in most M1, its posterior arm is

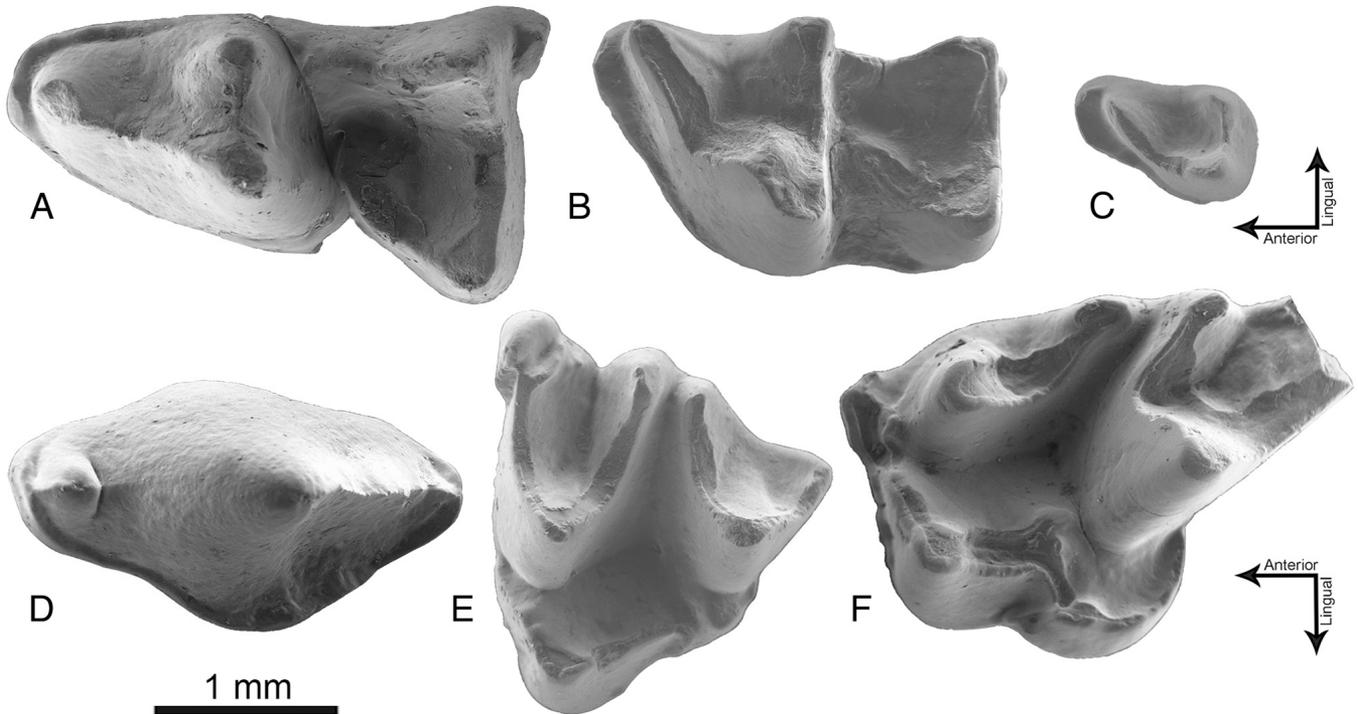


FIGURE 5. *Suleimania* aff. *ruemkae*. **A**, BAN619, m1 sin; **B**, BAN625, m2 sin; **C**, BAN632, m3 sin; **D**, BAN602, P4 sin; **E**, BAN609, M1 sin; **F**, BAN615, M2 sin.

somewhat longer than the anterior arm. The two mesostyle cusps are distinctly separated. The paracone is clearly smaller than the metacone and is of about the same height as the protocone. The parastyle is small. The anterior arm of the protocone connects to the protoconule and the posterior arm to the hypocone, which is more developed than the protoconule. The posterior arm of the hypocone ends against the posterior side of the metacone; the anterior arm ends at the base of the metacone. There are no cingula. The M1 has three roots.

The outline of the occlusal surface of the M2 is irregular. A cingulum is absent. The large paracone and metacone are of the same height. The anterior arm of the metacone is clearly longer than its posterior arm. The posterior and anterior arms of the paracone are of roughly the same length. The two mesostyle cusps are distinctly separated. The protocone is the main cusp on the lingual part. The anterior arm of the protocone connects to a

very small protoconule at the base of the paracone. The posterior arm ends against the small hypocone. The M2 has three roots.

The outline of the occlusal surface of the m1 is an elongated triangle. The talonid is wider and longer than the trigonid. The protoconid is connected to the paraconid and metaconid by ridges. The protoconid is the tallest cusp of the m1. The paraconid is smaller than the metaconid; the latter is of about the same height as the entoconid. Posterior to the entoconid, a small, but distinct, entostylid is present. The entoconid is connected to the hypoconid by a ridge. The hypoconid is the largest cusp of the talonid. The oblique cristid ends close to the protoconid. In four of the seven specimens, an anterior cingulum is present. The m1 has two large roots.

The outline of the occlusal surface of the m2 is subrectangular. The talonid is narrower than the trigonid. The protoconid is the tallest cusp of the m2. The sharp anterior arm of the protoconid connects to the paraconid. The posterior arm of the protoconid connects to the metaconid, which is somewhat taller than the paraconid. The anterior cingulum is broader on the lingual side than on the labial side. On the lingual side of the anterior cingulum the parastylid lies in front of the paraconid. The hypoconid and entoconid are of about the same height and both are lower than the metaconid. The oblique cristid ends at the middle of the ridge between the metaconid and protoconid. The entostylid is small. The m2 has two large roots.

The outline of the occlusal surface of the m3 is subrectangular. The m3 consists of the trigonid only and has a strong anterior cingulum. The protoconid is the tallest cusp. The anterior arm of the protoconid is connected to the paraconid, and its posterior arm to the metaconid. The metaconid is lower than the paraconid. The anterior arm of the protoconid is longer than its posterior arm. The m3 has one root.

Discussion—*Suleimania* is a dimylid-like, large-sized talpid with only one species, *Suleimania ruemkae*, which is known from early Miocene Anatolian assemblages (Van den Hoek Ostende,

TABLE 1. Measurements (in mm) of *Suleimania* aff. *ruemkae* from Banovići, Bosnia and Herzegovina.

Element	Dimension	N	Range	Mean
P4	L	6	2.42–2.75	2.63
	W	6	1.27–1.59	1.48
M1	L	1	~2.90	~2.90
	W	2	1.74–2.11	~1.93
M2	L	3	1.94–2.27	2.11
	W	2	1.92–2.36	2.14
m1	L	1	—	2.91
	W	3	1.60–1.66	1.62
m2	L	1	—	2.46
	W	2	1.37–1.38	1.38
m3	L	8	0.97–1.13	1.06
	W	8	0.63–0.82	0.70

The M1 are only slightly damaged on their posterolingual part.

TABLE 2. Ranges of length and width (in mm) of *Suleimania ruemkae* from all Anatolian assemblages in Turkey (Van den Hoek Ostende, 2001a).

Element	Dimension	N	Range
P4	L	51	2.41–3.00
	W	51	1.29–1.52
M1	L	17	3.60–3.83
	W	17	2.02–2.83
M2	L	28	1.65–2.32
	W	28	2.24–2.89
P4	L	38	1.80–2.33
	W	38	0.80–1.08
m1	L	32	2.63–3.08
	W	32	1.39–1.98
m2	L	22	2.46–2.92
	W	22	1.22–1.62
m3	L	30	1.11–1.69
	W	30	0.63–0.93

2001a). The P4, M2, m1, and m2 from Banovići are in the same size range as the molars from *Suleimania ruemkae* from Anatolia (Table 2), whereas the M1 and the m3 are smaller.

The paracone and metacone of the M2 from Banovići are of the same height and size, whereas the paracone of the M2 is larger and higher than the metacone in *Suleimania ruemkae*. In some specimens of *Suleimania* aff. *ruemkae*, the anterior part of the lingual cingulum of P4 is absent; in others, it is present along the whole lingual side; this is in contrast to *Suleimania ruemkae* where only a short posterolingual cingulum is present in the P4. Considering these differences, we assign the material from Banovići to *Suleimania* aff. *ruemkae*.

Family SORICIDAE Fischer, 1814

The Soricidae are divided into the subfamilies Allosoriinae, Crocidosoricinae, Crocidurinae, Limnoecinae, and Soricinae by Reumer (1987), a classification used in this paper; however, there has been much debate on the validity of the subfamily Crocidosoricinae and on the synonymy of *Crocidosorex* and *Oligosorex* (Reumer, 1987, 1994). *Oligosorex* was generally considered to be a junior synonym of *Crocidosorex*. Based on a literature review by Van den Hoek Ostende (2001b), the genera *Crocidosorex* and *Oligosorex* are maintained as separate genera.

The Soricidae fossils from Banovići are mainly isolated molars and a few pieces of mandibles without alveoli or antemolars. The number of antemolars and the morphology of the p4 are crucial in identifying Soricidae at the species and even subfamily level. The classification of the Banovići soricids is tentative because the determination is based on the morphology of the molars only.

Subfamily CROCIDOSORICINAE Reumer, 1987

?*CROCIDOSOREX* sp. Lavocat, 1951
(Fig. 6A)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN698, a mandible fragment with two molars: m2 (L = 1.27, W trigonid = 0.73, W talonid = 0.66) and m3 (0.96 × 0.54).

Description—The occlusal surface of the m2 is subrectangular. The talonid is broader than the trigonid. The protoconid is the tallest cusp. The anterior arm of the protoconid is longer than its posterior arm; however, the difference in length is less than in ?*Srinitium* sp. and in the *Oligosorex* specimens from Banovići. The oblique cristid ends at the middle of the protoconid-metaconid crest. The entoconid is a distinct cusp and fused to the entocristid.

The hypolophid is not connected to the entoconid. There are strong anterior and posterior cingula; the labial cingulum is absent.

The occlusal surface of the m3 is subrectangular. The talonid is strongly reduced. The protoconid is the tallest cusp in this molar. The oblique cristid ends at the middle of the protoconid-metaconid crest. The oblique cristid, hypoconid, hypolophid, entoconid, and entocristid form one ridge encircling the talonid basin. The anterior cingulum is strong, and the labial cingulum is almost absent.

Discussion—The absence of the labial cingulum is a prominent character only seen in *Crocidosorex* (Hugueney and Maridet, 2011). The well-developed entoconid is a characteristic for *Crocidosorex* also. The length of the m2 is about the same as in *Crocidosorex piveteaui* Lavocat, 1951 (Crochet, 1975), but the width is much smaller. The m3 is smaller than the m3 of *Crocidosorex piveteaui*. Because of the absence of a complete labial cingulum in the m2, but lack of information on the other dental elements, we assign this mandible fragment to ?*Crocidosorex* sp. *Crocidosorex* occurs in late Oligocene and early Miocene assemblages from Germany, France, Switzerland, and Spain (Werner, 1994; Ziegler, 1998; Fortelius, 2003).

SRINITIUM Hugueney, 1976

Type Species—*Srinitium marteli* Hugueney, 1976.

Other Included Species—*Srinitium caeruleum* Ziegler, 1998.

Occurrences—*Srinitium marteli* in the Oligocene of France (MP23: Saint Martin de Castillon; Hugueney, 1976); *Srinitium caeruleum* in the Oligocene of Germany (MP28: Herrlingen 8; Ziegler, 1998); *Srinitium* sp. in the Oligocene of France (MP28: Pech-du-Fraysse; Crochet, 1974).

?*SRINITIUM* sp.
(Fig. 6C–I)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN681–684, four I_s; BAN687–690, four m1; BAN691–694, four m2; BAN685, a P4; BAN686 and BAN703, two M1. Fifteen isolated specimens, of which 10 are complete (Fig. 6B–F; Table 3).

Description—The upper incisor is large. The labial cingulum is slightly curved and strong, becoming less strong towards the anterior side. The angle between the apex and talon is sharp. The apex is slightly more pointed than the talon. The apex and talon reach downwards to about the same level.

The anterolingual side of the hypoconal flange of the P4 is damaged. The hypoconal flange of the P4 reaches far to the posterior side. The tip of the paracone lies in front of the middle of the P4. The posterocrista connects the top of the paracone to the posterior edge and is slightly bent. The distinct parastyle is connected to the small protocone by a short, curved anterior arm of the protocone. The protocone lies posterolingual to the top of the paracone. The posterior arm of the protocone is very short and curves posteriorly. The undamaged part of the hypoconal flange has a thick ridge at the posterolingual corner, which becomes very narrow to the posterior side and continues into a well-developed cingulum along the lingual side of the paracone.

The posterolingual sides of both M1 are damaged and missing (part of) the hypoconal flange. The metacone is the largest and highest cusp of the M1. The posterior arm of the metacone is longer than its posterior arm; the same applies to the arms of the paracone. The mesostyle is undivided. In one of the two M1, a thin cingulum is present on the labial edge. A strong cingulum connects the metastyle to the lingual edge in both M1. The anterior arm of the protocone ends at the anterior flank of the paracone. The metaloph ends just in front of the metacone. A cingulum is present on the lingual edge of the protocone.

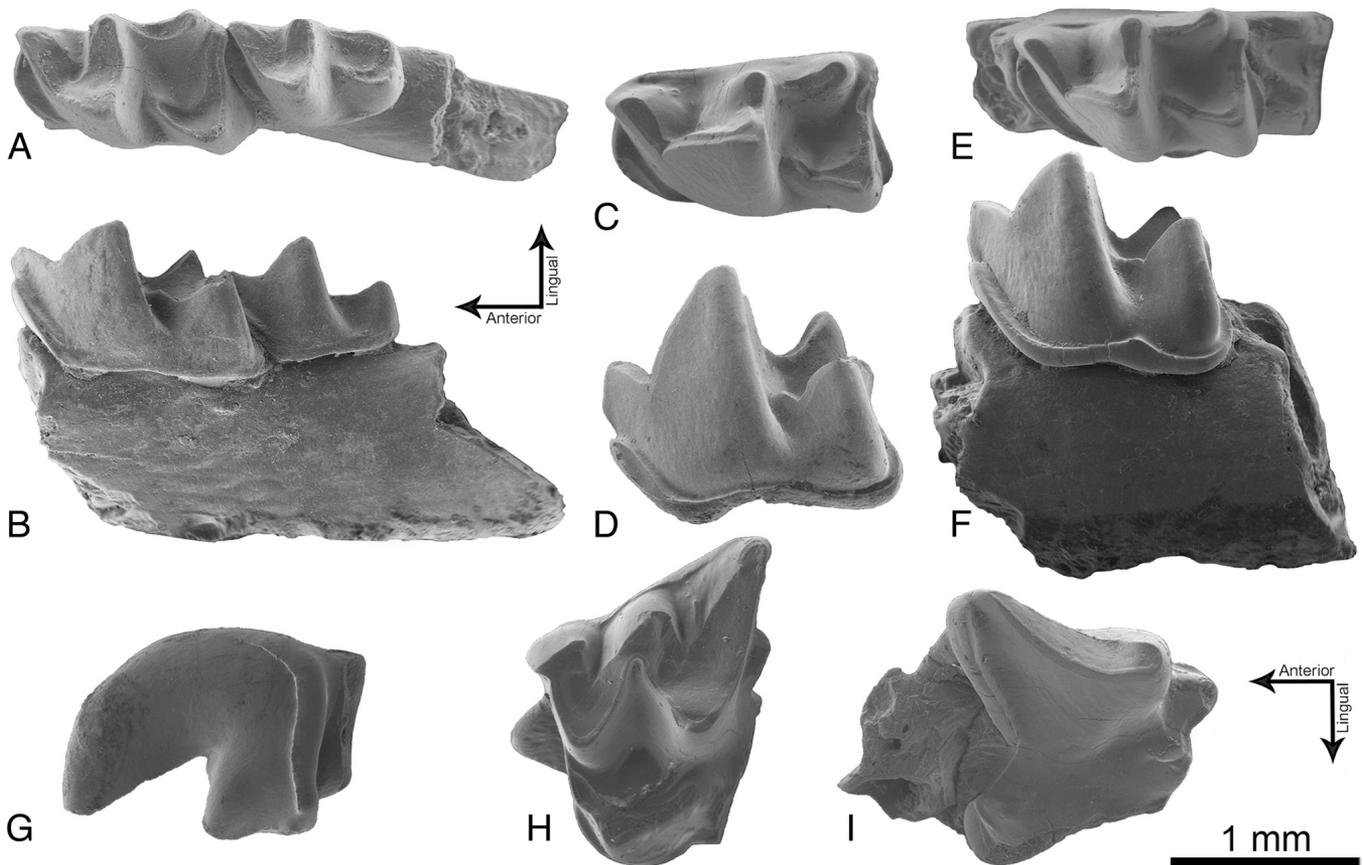


FIGURE 6. *?Crocidosorex* sp. **A**, BAN698, lower jaw fragment dex with m2 and m3 (reversed image). **B–I**, *?Srnitium* sp. **B**, BAN698 in labial view (reversed image); **C**, BAN689, m2 sin; **D**, BAN689, labial view; **E**, BAN691, lower jaw fragment sin with m2; **F**, labial view of BAN691; **G**, BAN681, Isup sin; **H**, BAN703, M1 sin; **I**, BAN685, P4 dex (reversed image).

The m1 occlusal surface is subrectangular. The talonid is slightly broader than the trigonid. The protoconid is the tallest cusp of the m1, with a longer anterior than posterior arm. The anterior arm connects to the paraconid, and the posterior arm connects to the slightly lower metaconid. The oblique cristid is short. The well-developed entoconid is fused to the entocristid. The hypolophid is behind the entoconid, forming a small valley between the entostylid and the entocoid and continues along the posterior side until the hypocoid. The well-developed anterior cingulum continues into the

labial cingulum, which continues into the posterior cingulum. A cingulum is also present at the lingual side, but is much thinner.

The m2 resembles the m1 closely, but there are some differences: The distance between the metaconid and protoconid in the m2 is somewhat larger than in the m1. This results in a somewhat broader trigonid than in the m1. The talonid and trigonid are of equal width or differ only slightly. The protoconid is the tallest cusp of the m2, but the difference in height from the other cusps is less than in the m1.

Discussion—The measurements of *?Srnitium* sp. from Banovići fall within or near the range of many species, such as *Srnitium caeruleum* Ziegler, 1998, *Ulmensia ehrensteinensis* Ziegler, 1989, *Ulmensia antecessens* Ziegler, 1998, *Soricella discrepans* Doben-Florin, 1964, and species of *Carposorex* Crochet, 1975. The specimens resemble *Srnitium caeruleum* closest in size (Tables 4 and 5). The *?Srnitium* sp. specimens from Banovići are larger than specimens of both *Claposorex* Crochet, 1975, and *Oligosorex* Kretzoi, 1959 (including the *Oligosorex* species from Anatolia; Van den Hoek Ostende, 2001c).

The typical characteristics, such as the fused entoconid and hypoconid of *Soricella discrepans* and the wrinkled enamel of *Carposorex*, are absent in the *?Srnitium* sp. specimens. Differences between *Srnitium* and *Ulmensia* are the presence in *Srnitium* of a higher number of antemolars, the less anteriorly positioned foramen mentale, the stronger labial cingulum, and the presence of a lingual cingulum in the lower molars. In the assemblage of Banovići, mandibles and antemolars are absent. Therefore, it is not possible to assign these specimens with

TABLE 3. Measurements (in mm) of *?Srnitium* sp. from Banovići, Bosnia and Herzegovina.

Element	Dimension	N	Range	Mean
Isup	L	3	1.37–1.45	1.42
	LT	4	0.54–0.62	0.58
	H	4	1.13–1.25	1.19
P4	L	1	—	1.43
	W	1	—	1.39
	LL	1	—	1.17
M1	L	2	1.39–1.42	1.41
	WA	1	—	1.52
m1	L	4	1.45–1.52	1.47
	WTa	4	0.88–0.97	0.92
	WTr	4	0.80–0.93	0.87
m2	L	4	1.39–1.47	1.44
	WTa	4	0.82–0.90	0.85
	WTr	4	0.81–0.89	0.85

TABLE 4. Ranges of length and width (in mm) of *Srinitium caeruleum* from Herrlingen 8, Germany (Ziegler, 1998b).

Element	Dimension	N	Range
Isup	L	2	1.30–1.45
Isup talon	LT	2	0.59–0.70
P4		0	—
M1	L	3	1.33–1.46
	W	3	1.46–1.66
m1	L	2	1.43–1.49
	W	2	0.86–0.89
m2	L	2	1.36–1.40
	W	2	0.84–0.85

certainly to *Ulmensia* or *Srinitium*. However, the presence of the lingual cingulum in the lower molars fits *Srinitium* best.

Genus *OLIGOSOREX* Kretzoi, 1959

Type Species—*Oligosorex antiquus* (Pomel, 1853).

Other Included Species—*Oligosorex antiquus* (Pomel, 1853) (type species); *O. thauensis* Crochet, 1975; *O. reumeri* Van den Hoek Ostende, 2001b.

Occurrences—*Oligosorex antiquus* in the early Miocene of Italy (Oschiri; De Bruijn and Rümke, 1974); *O. antiquus* in the early Miocene of France (MN2 a: Languedoc a.o. Montaigu-le-Blin; Crochet, 1975; Huguency and Maridet, 2011); *O. thauensis* in the early Miocene of France (MN2: Bouzigues; Crochet, 1975) and Spain (MN2–MN3: Ramblar 1, 3, 7 and Valhondo 1; Van den Hoek Ostende, 2003); *O. reumeri* in the early Miocene of Anatolia (MN3: Keseköy; Van den Hoek Ostende, 2001b); *O. aff. reumeri* in the late Oligocene and early Miocene of Anatolia (MP30–MN2: Inkonak, Kılçak and Harami; Van den Hoek Ostende, 2001b); *Oligosorex* sp. in Cournon (MP28; Brunet et al., 1981); *Oligosorex* sp. in the early Miocene of Serbia (MN4: Snegotin; Marković and Milivojević, 2010).

OLIGOSOREX sp. 1
(Fig. 7)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN672, maxilla dextral fragment with P3 and P4; BAN678, mandible fragment with p4 and m1; BAN679, mandible fragment with part of m1 and m2. Seven isolated teeth: BAN671 and BAN673, two P4; BAN674–677, four M1; BAN680, an m2 (Fig. 7; Table 6).

Description—The outline of the occlusal surface of the P4 is triangular. The tip of the paracone lies in the anterior part of the P4. The posterocrista is slightly curved; it extends from the tip of the paracone backwards. The parastyle lies in front of the paracone, and there is no parastylar crest. The protocone is small, but distinct. Its anterior arm is connected to the parastyle, whereas

TABLE 5. Ranges of length and width in mm of *Ulmensia antecedens* from Herrlingen 9, Germany (Ziegler, 1998b).

Element	Dimension	N	Range
Isup	L	20	1.23–1.43
	LT	20	0.57–0.68
P4	L	9	1.45–1.68
	W	9	1.37–1.59
M1	L	3	1.33–1.46
	W	3	1.46–1.66
m1	L	18	1.45–1.64
	W	20	0.85–0.99
m2	L	22	1.36–1.54
	W	23	0.81–0.96

its posterior arm continues in a ridge bordering the hypoconal flange on the lingual side. There is no hypocone. The ridge on the posterior side of the hypoconal flange continues into a well-developed lingual cingulum along the paracone, which becomes broader towards the end.

The posterolingual sides of all M1 are damaged. The metacone is the largest cusp of the M1. Its posterior arm is longer than its anterior arm, which connects to the undivided mesostyle. The paracone is much lower than the metacone; its anterior arm is somewhat shorter than its posterior arm. The protocone is larger than the paracone. The anterior arm of the protocone ends at the base of the paracone. The metaloph is of about the same length as the anterior arm of the protocone and ends freely in front of the base of the metacone. The hypocone is a small cone. There is a ridge from the hypocone in the posterior direction along the hypoconal flange.

The outline of the p4 is a tetrahedron, with a ‘Y’-shaped wear surface. The occlusal surface is triangular, with a pointed anterior side and a straight or slightly curved posterior side. On the posterior, labial and lingual sides, a cingulum extends around the premolar. The main cusp of the p4, the protoconid, lies at the anterior side of the tooth. The posterocristid is divided into two arms of about equal length, forming the ‘Y’-shaped wear surface.

The occlusal surface of the m1 is subrectangular. The talonid is broader than the trigonid. The lengths of the trigonid and talonid are about the same. The protoconid is the tallest cusp; its long anterior arm connects to the paraconid, and its short posterior arm connects to the metaconid. The oblique cristid ends at about one third of the protoconid-metaconid crest. The entoconid is small, but distinct, and is fused to the entocristid. The hypolophid extends from the entoconid along the posterior side of the molar. The m1 has a well-developed cingulum on its anterior and posterior sides. Along the labial side, a thin cingulum is present that is thinner and not as curved as the labial cingulum of *Oligosorex* sp. 2.

The m2 resembles the m1 closely, but there are some differences: the distance between the protoconid and metaconid is somewhat greater than in the m1. The trigonid is broader than in the m1, but it is still narrower than the talonid. The oblique cristid ends in some specimens more to the middle of the protoconid-metaconid crest; in other specimens, it ends at one third of the crest, resembling the m1. The protoconid is the tallest cusp in the m2; however, the difference in height with the other cusps is less than in the m1.

Discussion—The arms of the ‘Y’-shaped wear surface of p4 are of equal length, which is typical for Crocidoloricinae. The size of the m1 and m2 of *Oligosorex* sp. 1 from Banovići are in the range of of *O. antiquus* from Limagne and *O. aff. reumeri* from Anatolia (Huguency and Maridet, 2011; Van den Hoek Ostende, 2001b; Table 7). The morphological difference between these species is the presence of the labial cingulum, as in *O. reumeri*, or absence, as in *O. antiquus*, or variations in its continuity as in *O. aff. reumeri*. The labial cingulum in the lower molars of *Oligosorex* sp. 1 is present and uninterrupted. Because of the small number of specimens, we refrain from assigning it to one of the formal species.

OLIGOSOREX sp. 2
(Fig. 8)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN695, mandible sin fragment with p4 and m1; BAN696, mandible sin fragment with m1 and m2; BAN697, isolated m2 sin (Fig. 8; Table 8).

Description—The occlusal surface of the p4 is triangular; the anterior side is pointed, and the posterior side is slightly curved. The p4 has a ‘Y’-shaped wear surface. The strong cingulum on

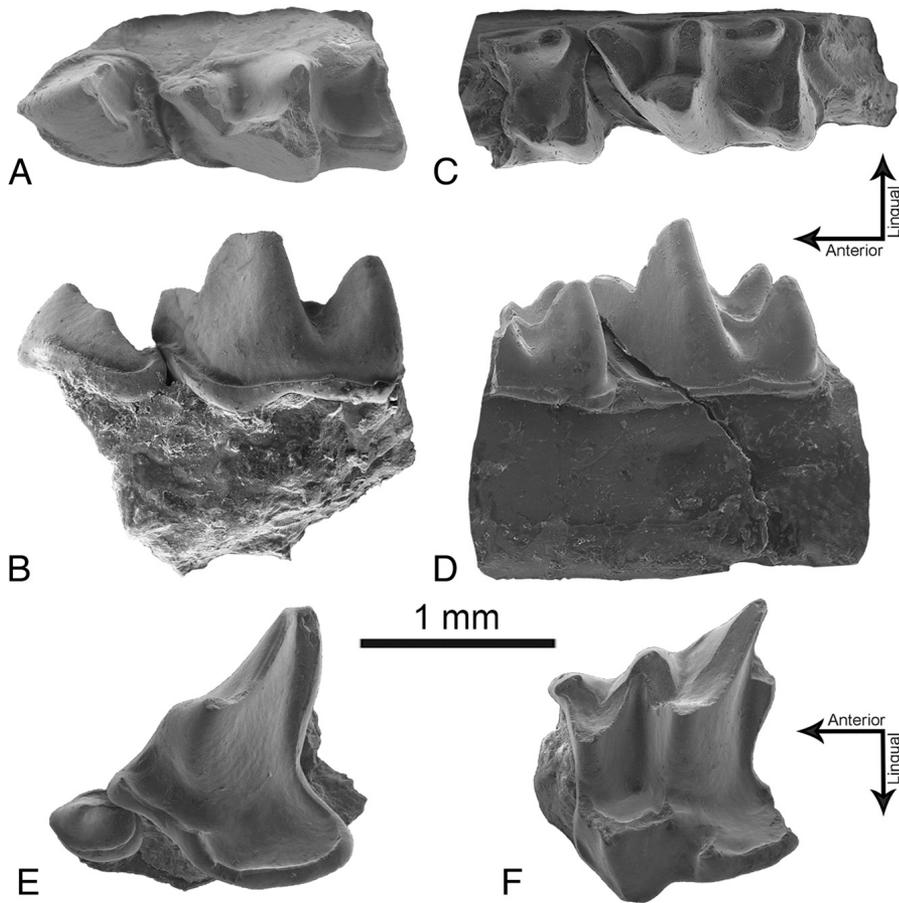


FIGURE 7. *Oligosorex* sp. 1. **A**, BAN678, lower jaw fragment sin with p4 and m1; **B**, BAN678, labial view; **C**, BAN679, lower jaw fragment sin; **D**, BAN679, labial view; **E**, BAN672, upper jaw fragment sin with p3 and p4; **F**, BAN675, M1 dex (reversed image).

the posterior side of the premolar has a small cusplet in its central part. On the labial and lingual sides, a cingulum is present as well. The posterocristid is divided into two arms forming the ‘Y’-shaped wear surface, of which the labial and lingual arms are of equal length.

The occlusal surface of the m1 is subrectangular. The talonid is broader than the trigonid. The protoconid is the largest and tallest cusp; its anterior arm is much longer than its posterior arm. The oblique cristid ends at about a third of the protoconid-metaconid crest. In one m1, the entoconid and cristid are damaged. In the other, the entoconid is small, but distinct, and fused to the entocristid. The hypolophid forms a

small valley between the entoconid and entostylid. The well-developed posterior cingulum continues into a broad labial cingulum, which is continuous and curved at the base of the protoconid. The anterior cingulum of the m1 is also well developed.

The m2 resembles the m1 closely. However, there are some differences: The distance between the metaconid and the protoconid is somewhat greater than in the m1. The trigonid is somewhat broader than in the m1. The widths of the trigonid and talonid are about the same. The oblique cristid ends somewhat more to the middle of the protoconid-metaconid crest than in the m1. The labial cingulum is slightly less curved than in the m1.

Discussion—*Oligosorex* sp. 2 has a typical Crocidosoricinae ‘Y’-shaped wear surface on the p4. It differs from *Oligosorex* sp. 1 from Banovići in having a narrower p4, a small cusplet in the middle of the posterior cingulum in the p4, and in having larger molars. The presence of the cusplet on the posterior cingulum in the p4 and its size are similar to the conditions in *Oligosorex* aff. *reumeri* from Anatolia. However, it differs from that species in the presence of a strong continuous labial cingulum. Therefore, we assign these specimens to *Oligosorex* sp. 2.

Family HETEROSORICIDAE Viret and Zapfe, 1951

The Heterosoricidae used to be considered a subfamily; however, Reumer (1987) raised the group to family level, based on the hypothesis that the Heterosoricidae and the Soricidae originated separately from the Nycteriidae. The Heterosoricidae are

TABLE 6. Measurements (in mm) of *Oligosorex* sp. 1 from Banovići, Bosnia and Herzegovina.

Element	Dimension	N	Range	Mean
P4	L	3	1.34–1.39	1.36
	W	3	1.19–1.28	1.24
	LL	3	0.86–1.06	0.96
M1	L	4	1.14–1.24	1.18
	WA	2	1.01–1.10	1.06
p4	L	1	—	0.76
	W	1	—	0.69
m1	L	2	1.16–1.17	1.17
	WTa	1	—	0.72
	WTr	2	0.67–0.77	0.72
m2	L	2	1.16–1.23	1.20
	WTa	2	0.69–0.74	0.72
	WTr	2	0.69–0.70	0.70

TABLE 7. Ranges of length and width (in mm) of *Oligosorex reumeri*, *Oligosorex* aff. *reumeri* from Anatolia, Turkey (Van den Hoek Ostende, 2001b), and *Oligosorex antiquus* from Limagne, France (Huguéney and Maridet, 2011).

Element	Dimension	N	Range
<i>Oligosorex reumeri</i> ; Anatolia (Turkey)			
P4	L	13	1.19–1.29
	W	11	1.06–1.20
M1	LL	11	0.77–1.08
	L	21	1.06–1.18
p4	WA	21	1.03–1.30
	L	7	0.75–0.81
m1	W	7	0.50–0.56
	L	41	1.07–1.28
m2	WTa	41	0.62–0.81
	WTr	41	0.59–0.73
	L	42	1.05–1.21
	WTa	42	0.65–0.77
P4	WTr	42	0.66–0.75
	<i>Oligosorex</i> aff. <i>reumeri</i> ; Anatolia (Turkey)		
	L	1	1.39
	W	1	1.11
M1	LL	1	0.75
	L	13	1.22–1.33
p4	WA	13	1.18–1.40
	L	1	0.82
m1	W	1	0.53
	L	25	1.11–1.31
m2	WTa	25	0.74–0.88
	WTr	25	0.66–0.79
	L	26	1.14–1.34
	WTa	26	0.65–0.84
P4	WTr	26	0.62–0.83
	<i>Oligosorex antiquus</i> ; Limagne (France)		
	L	2	1.37–1.47
	W	2	1.27–1.35
M1	LL	—	—
	L	2	1.26–1.35
p4	W	2	1.45–1.54
	L	4	0.80–1.00
m1	W	4	0.60–0.86
	L	5	1.24–1.28
m2	WTa	5	0.85–0.97
	WTr	5	0.79–0.92
	L	5	1.19–1.36
	WTa	5	0.85–0.92
P4	WTr	5	0.80–0.92

known from the early Oligocene until the late Miocene and are represented by three genera: *Quercysorex*, *Heterosorex*, and *Dinosorex* (Engesser, 1975).

HETEROSORICIDAE, gen. et sp. indet.
(Fig. 9)

Locality—Banovići, Bosnia and Herzegovina.

Material—BAN707–709, three A1; BAN710–712, three P4; BAN713–715, three M1; BAN716, an M3 (Table 9; Fig. 9).

Description—The outline of the occlusal surface of the A1 is sub-elliptical. It consists mainly of one large cusp, which lies in the antero-labial corner. A ridge extends from the tip of the main cusp to the posterolingual side, bending more to the end. Another ridge connects the tip of the main cusp to the lingual side. There is a well-developed cingulum on the labial and posterior side. The lingual side is partly damaged; there is no clear cingulum distinguishable on that side.

The outline of the occlusal surface of the P4 is subtriangular. The paracone is the tallest and main cusp of the P4. The parastyle is damaged in all specimens. The posterocrista connects the top of the paracone to the posterolabial corner of the P4. The protocone is elevated and lies lingual to the tip of the paracone. The hypocone is not clearly distinguishable. A broad posterior cingulum extends from the protocone to the posterolingual corner of the premolar, bordering a deep basin.

The outline of the occlusal surface of the M1 is subquadrate. The breadth is somewhat greater than the length. The metacone and paracone are both tall cusps, but the metacone is somewhat larger and taller than the paracone. The posterior arm of the paracone is longer than its anterior arm. The mesostyle is undivided. The posterior arm of the paracone is slightly longer than its anterior arm. The protocone is pronounced, but clearly lower than the paracone. Its anterior arm ends at the base of the paracone. The posterior arm of the protocone extends towards the metacone but bends in front of the base of the metacone in the direction of the hypocone. The hypocone is conical, and is lower than the protocone. The posterior arm of the hypocone continues into a posterior ridge that ends at the posterior arm of the metacone.

The outline of the occlusal surface of the M3 is subtriangular. The posterior lingual corner is rounded. The paracone is somewhat higher than the protocone. The anterior arm of the protocone ends at the base of the paracone; its posterior arm ends in the trigon basin. The anterior arm of the paracone is longer than its posterior arm. The mesostyle is undivided. The metacone is part of a posterior ridge that connects the mesostyle to the posterolingual side of the molar.

Discussion—The material consists of (fragmentary) isolated upper molars only. Allocation of this material to a particular genus is not possible because mandible characteristics are important in the classification of the Heterosoricidae (Engesser, 1975). Moreover, Ziegler (2009) emphasizes that younger species of *Quercysorex* and species of *Dinosorex* are not distinguishable when the lower incisor

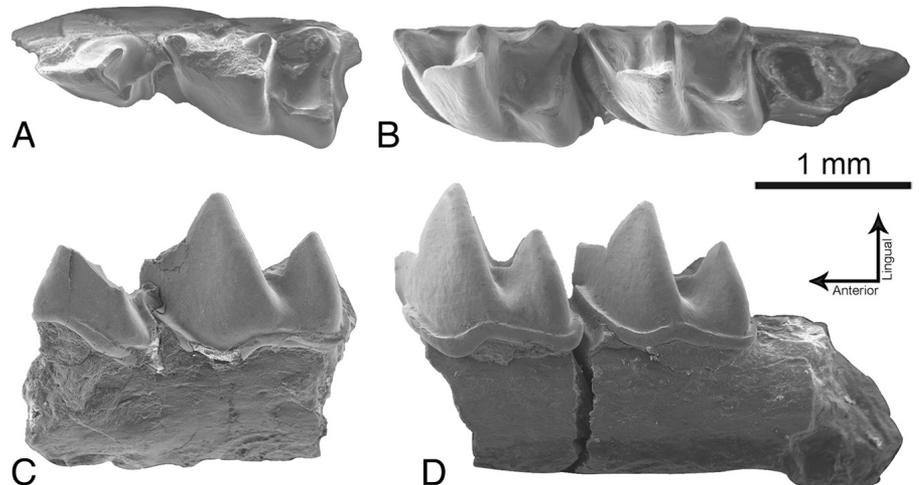


FIGURE 8. *Oligosorex* sp. 2. **A**, BAN695, lower jaw fragment sin with p4 and M1; **B**, BAN695, labial view; **C**, BAN696, lower jaw fragment sin with m1 and m2; **D**, BAN696, labial view.

TABLE 8. Measurements (in mm) of *Oligosorex* sp. 2 from Banovići, Bosnia and Herzegovina.

Element	Dimension	N	Range	Mean
p4	L	1	—	0.83
	W	1	—	0.52
m1	L	2	1.21–1.35	1.28
	WTa	2	0.80–0.80	0.80
	WTr	2	0.73–0.74	0.74
m2	L	2	1.24–1.26	1.25
	WTa	2	0.75–0.79	0.77
	WTr	2	0.73–0.77	0.75

TABLE 9. Measurements (in mm) of Heterosoricidae, gen. et sp. indet., from Banovići, Bosnia and Herzegovina.

Element	Dimension	N	Range	Mean
A1	L	2	2.03–2.41	2.22
	W	3	1.20–1.40	1.34
P4	L	3	1.71–1.94	1.85
	W	1	—	1.96
M1	L	2	2.16–2.16	2.16
	WA	1	—	2.31
	WP	2	2.23–2.36	2.30
M3	L	1	—	1.14
	W	1	—	1.48

is absent. Although our specimens, especially the triangular P4, are very similar to *Dinosorex anatolicus* from Anatolia (Van den Hoek Ostende, 1995a), we refrain from a generic assignment.

DISCUSSION

Biostratigraphy

Marsupials and insectivores from Banovići:

Infraclass METHATHERIA Huxley, 1880

Family HERPETOTHERIIDAE Trouessart, 1879

Amphiperatherium cf. *exile* (Gervais, 1848–52)

Infraclass EUTHERIA Gill, 1872

Order EULIPOTYPHILA Waddell, Okada, and Hasegawa, 1999

Family ERINACEIDAE Fischer, 1814

Subfamily ERINACEINEA Gill, 1872

Erinaceinae, gen. et sp. indet.

Family TALPIDAE Fischer, 1814

Talpidae, gen. et sp. indet.

Subfamily TALPINAЕ Fischer, 1814

Desmanodon aff. *ziegleri* Van den Hoek Ostende, 1997

Desmanodon sp.

Subfamily TALPINAЕ Fischer, 1814

Tribe TALPINI Fischer, 1814

Geotrypus sp.

Subfamily SULEIMANINAE Van den Hoek Ostende, 2001a

Suleimania aff. *ruemkae* Van den Hoek Ostende, 2001a

Family SORICIDAE Fischer, 1814

Soricidae, gen. et sp. indet.

Subfamily CROCIDOSORICINAE Reumer, 1987

?*Crocidosorex* sp.

?*Srinitium* sp.

Oligosorex sp. 1

Oligosorex sp. 2

Family HETEROSORICIDAE Viret and Zapfe, 1951

Heterosoricidae, gen. et sp. indet.

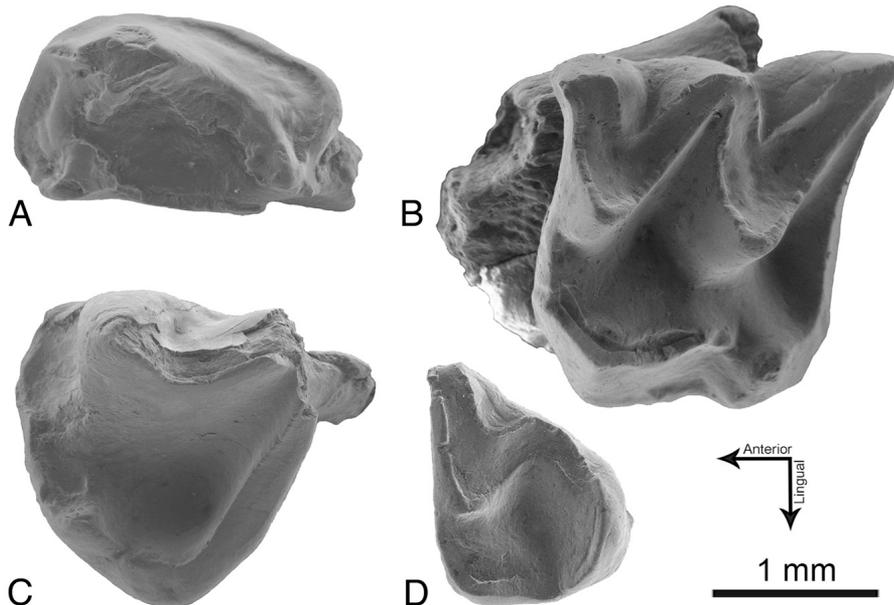


FIGURE 9. Heterosoricidae, gen. et sp. indet. **A**, BAN709, A1 dex (reversed image); **B**, BAN713, M1 sin; **C**, BAN710, P4 sin; **D**, BAN716, M3 dex (reversed image).

Whereas rodents have been widely used for biostratigraphic purposes, insectivores are considered less suitable as biostratigraphic markers due to their longevity (Engesser and Ziegler, 1996). Thus, a biostratigraphic correlation of the assemblage of Banovići based on the findings of the insectivore assemblage is not precise. Comparison with the European insectivore record is more solid than comparison with the Anatolian record, because the European record is better known. In contrast, only two late Oligocene and eight early Miocene insectivore assemblages are known from Anatolia, which hampers correlation.

At the genus level, the Banovići marsupial and insectivores are a mix of genera known from the European late Oligocene–earliest Miocene (MP29–MN3) and Anatolian latest Oligocene–early Miocene (~MP30–MN3). The marsupial *Amphiperatherium* is common in European faunas until the middle Miocene and is not known from Anatolian faunas. *Oligosorex* is present in the European as well as in the Anatolian late Oligocene–early Miocene assemblages (Fig. 10), indicating wide distribution. *Geotrypus* occurs earlier in Europe than in Anatolia, and *Desmanodon* occurs earlier in Anatolia. The erinaceine *Suleimania* is only known from Anatolia. Considering the probable presence of *Srinitium* and *Crosidosorex* as well, a similarity to European assemblages is

more prominent. This is in contrast to the rodents, which were interpreted as being more similar to the Anatolian assemblages (De Bruijn et al., 2013).

Because of the low quantity and poor preservation of the fossils, identification to species level is, in most cases, uncertain. The marsupial *Amphiperatherium exile* is known from European late Oligocene assemblages, and the talpids *Suleimania ruemkae* and *Desmanodon zieglerei* are known from the latest Oligocene until the early Miocene of Anatolia. The absence of certain insectivores, such as *Galerix* and the dimylids, is best explained by the small sample size of the insectivores in the Banovići assemblage, although it is possible that this absence is related to the period until the end of MN2, when these taxa were not present in European assemblages (Van den Hoek Ostende, 2001c; Ziegler, 2005).

This assemblage contains a mix of genera known from the late Oligocene–early Miocene of Europe (MP29–MN3) and Anatolia (~MP30–MN3). This age is thus not as precise as the correlation of the Banovići rodent assemblage to top MP30/base MN1 (De Bruijn et al., 2013). The magnetostratigraphic dating of a lateral equivalent of the fossil-bearing level in an adjacent quarry indicates an age of 24 Ma (De Leeuw et al., 2011), which supports the correlation to MP30.

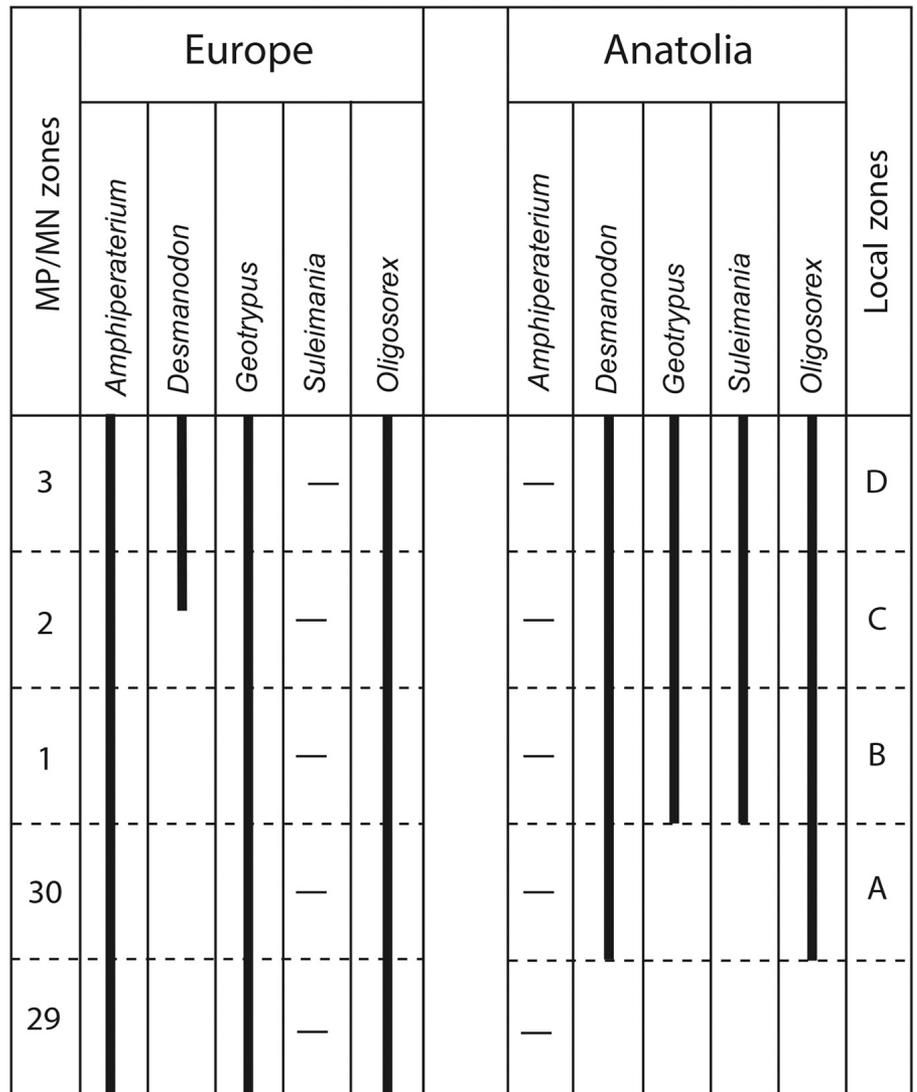


FIGURE 10. Stratigraphic ranges of the marsupial and four insectivore genera recognized in Banovići, which are known from Europe and Anatolia. The stratigraphic ranges are relative to the European MP/MN scheme and the preliminary Anatolian zonation (Schmidt-Kittler et al., 1987; De Bruijn et al., 1992; Werner, 1994; Theocharopoulos, 2000; Fortelius, 2003; Koufos, 2003; Reumer and Wessels, 2003; Únay et al., 2003a, 2003b).

Biogeography

Correlation of the Anatolian mammal assemblages with the European ages remains difficult due to a lack of data from the area between Anatolia and central Europe. The small-mammal fauna of Banovići provides data from an area where Oligocene–early Miocene small mammals are hardly known and can therefore help to interpret faunal similarities between Europe and Anatolia during this time slice. Furthermore, there is little known about insectivores from the (late) Oligocene of Anatolia, because there are almost no assemblages from that time period. Lack of data on insectivores and marsupials in the Dinaride region hampers a straightforward interpretation of the origin and migrations of these small mammals during the late Oligocene.

The dimylid-like talpid *Suleimania* has thus far never been found outside of the early Miocene localities of Anatolia. It is plausible that *Suleimania* was an Asian immigrant, as proposed by Van den Hoek Ostende (2001c), that migrated via Anatolia to Bosnia and Herzegovina during the late Oligocene.

In Europe, the talpid *Desmanodon* had its first occurrence in Spain (Navarette del Rio, MN2b; Van den Hoek Ostende, 1997, 2003). In Anatolia, the oldest occurrence of *Desmanodon* is from the latest Oligocene (Kargı1; Van den Hoek Ostende, 1997), indicating a large area of distribution in the latest Oligocene.

The genera *Geotrypus* and *Oligosorex* all occur in the late Oligocene in Anatolia as well as in Europe (Engesser, 1975; Brunet et al., 1981; Fig. 10). The first two genera are already present in Europe during MP28, and the presence of these genera in the Banovići assemblage supports the proposal of Van den Hoek Ostende (2001c) that these insectivores migrated from western Europe into Anatolia via the Dinaride region during the late Oligocene.

Paleoecology Based on Insectivores from Banovići

The Talpidae ($n = 74$; ~58%) dominate the Banovići insectivore assemblage ($n = 128$) in number of specimens, followed by the Soricidae ($n = 40$; ~31%). The Talpidae are represented by three genera and the Soricidae also by three (of which one is a well-identified genus). The Heterosoricidae are rare ($n = 13$; ~10%), and the Erinaceidae with only one specimen are even more rare.

Insectivores are opportunistic feeders living on a wide range of small invertebrates, which are especially numerous in the topsoil of forests. The importance of the presence of those invertebrates for insectivores can be inferred from the foraging habits of present-day shrews and moles. Because litter decomposers (e.g., worms, wood lice, centipedes, and insects) are an important food source for insectivores, a larger diversity of insectivores is expected in wooded areas than in grasslands (Van den Hoek Ostende, 2001c).

Reumer (1995) studied the evolution of shrews and found that humid paleoclimates stimulated the evolution of shrews. This agrees with the current maximum in shrew diversity in the wet tropics of Africa. Additionally, Van den Hoek Ostende (2001c) concluded that the early Miocene insectivores of Anatolia had a higher diversity in humid environments than in the more open, arid environments. Furió et al. (2011) studied the nestedness of the insectivore faunas in western Europe along a latitudinal gradient and concluded that the diversity of insectivores was higher in the northern more humid regions than in the southern dryer regions.

Considering these assumptions and the relatively high diversity of Soricidae (40 specimens representing four species) in the Banovići assemblage, the climate conditions in the Banovići region were probably humid at the time. The diversity of Talpidae was also relatively high (74 specimens representing four

species), which likewise indicates humid conditions in the Banovići region.

The ecological preferences of some fossil insectivores can be inferred from the way of life of their present-day relatives; however, several of the Banovići insectivore species are members of extinct families, or subfamilies, such as the Heterosoricidae and the Crocidosoricinae. The extant erinaceines inhabit diverse habitats; some erinaceines inhabit very dry environments such as the desert, whereas others prefer more humid conditions in forests (Ziegler, 2005). However, ecological preferences can be deduced from other sources such as depositional environment and skeletal structure of fossil relatives. Doukas (1986) assumed that *Heterosorex ruemkae*, found in the lignite mine of Aliveri, was a forest dweller, based on the sedimentary facies of the locality and on the high percentage of forest dwellers in the small-mammal fauna. The majority of the faunas of Anatolia, in which *Dinosorex* has been found, were also recovered from beds between lignites (Van den Hoek Ostende, 2001c). *Lusorex tashanensis* Storch and Qiu, 2004, is so far the only heterosoricid for which a postcranial skeleton is known. Segments of the hind limbs appear to suggest fossorial habits, which indicates the need for soft and rather humid soils. Heterosoricidae are therefore considered to have lived in humid conditions (Storch and Qiu, 2004).

The way of life of fossil moles can mainly be detected by the morphology of the humerus. *Talpa*, the only extant talpid burrower, spends most of its life underground and needs soils with a constant degree of humidity where the tunnels do not collapse. *Talpa* digs tunnels, making use of its overdeveloped forelimbs with stout humeri. Because other burrowers (e.g., *Geotrypus* and *Proscapanus*) have similar morphological adaptations as those of *Talpa*, a similar burrowing style, and thus a similar need for moist environments is expected for these burrowers (Furió et al., 2011). Moles with a slender humerus are considered to have been non-fossorial (e.g., *Desmaninae*, *Myxomygale*; Van den Hoek Ostende, 2001c). Thus, the discovery of *Geotrypus* sp. in the Banovići assemblage indicates a moist environment for the Banovići region.

The morphology of the humerus of *Desmanodon* indicates a fossorial lifestyle, but not so strongly adapted to digging as *Talpa* or *Proscapanus* (Engesser, 1980; Prieto, 2010). Van den Hoek Ostende (1997, 2001c) states that the humerus of *Desmanodon* resembles the humerus of the extant mole *Scapanulus*. Schwermann and Thompson (2014) state that *Scapanulus* is clearly not strongly fossorial based on the relatively elongated humerus and other manus characteristics.

The diversity of Crocidosoricinae in Europe decreased considerably after MN4, which was partly related to a pronounced decrease in humidity around the MN4/MN5 transition, but mostly to the drop in temperature in MN5 (Reumer, 1994). The surviving Crocidosoricinae are mainly found in southern regions, which leads to the assumption that Crocidosoricinae were warmth-loving shrews adapted to the warm climates of the early Miocene of Europe (Reumer, 1994; Van den Hoek Ostende, 2001c).

Combining the data, the Banovići insectivores indicate the presence of a humid and warm environment with moist soils and nearby dryer areas.

CONCLUSIONS

Despite the relatively small sample size, the diversity of the insectivore and marsupial assemblage from Banovići is quite high, with nine genera in four insectivore families and one marsupial. The composition of the insectivore assemblage is a mix of European as well as Anatolian genera, whereas the only marsupial species is only known from Europe. Biostratigraphic interpretation based on the insectivores and marsupials is uncertain due to their longevity. Correlation to a late Oligocene–early

Miocene time frame is most plausible, considering the presence of the talpids *Suleimania* aff. *ruemkae* and *Desmanodon* aff. *ziegleri*; this fits in the MP30/MN1 age assignment of the rodent assemblage.

Because of the high diversity of insectivores in the Banovići assemblage, we interpret that the Banovići Basin had a humid environment during the late Oligocene. This is supported by the presence of *Geotrypus* and the heterosoricid that exhibited a fossorial habitus or preferred humid environments.

ACKNOWLEDGMENTS

This study is a contribution to the Austrian FWF Project P18519-B17: 'Mollusk Evolution of the Neogene Dinaride Lake System.' We are indebted to M. Milivojević (NHMB) for support in the field and laboratory. A. E. de Bruijn (Huizen, The Netherlands), G. Höck, and O. Mandić (Natural History Museum, Vienna, Austria) were of great help in the field, and E. Šišić (Rudnici mrkog uglja Banovići) made sampling and sediment processing in the coal mine possible. Furthermore, we thank A. Bosma (Utrecht University, The Netherlands), L. W. van den Hoek Ostende (Naturalis, The Netherlands), and J. W. F. Reumer (Utrecht University, The Netherlands) for their help and suggestions. The comments of the reviewers, L. W. van den Hoek Ostende and T. Mörs, are greatly appreciated and improved the manuscript.

LITERATURE CITED

- Blainville, H. M. D. D. E. 1839. Osteographie des Mammifères. Tome I, Livraison 6-H, Insectivores. J. B. Baillière et Fils, Paris, 155 pp.
- Brunet, M., M. Hugueney, and Y. Jehenne. 1981. Cournon-les-Soumèroux: un nouveau site à vertébrés d'Auvergne; sa place parmi les faunes de L'Oligocène supérieur d'Europe. *Geobios* 14:323–359.
- Crochet, J.-Y. 1974. Les Insectivores des Phosphorites du Quercy. *Palaeovertebrata* 6:109–159.
- Crochet, J.-Y. 1975. Diversité des insectivores Soricidés du Miocène inférieur de France. *Colloques Internationaux du Centre National de la Recherche Scientifique* 218:631–652.
- Crochet, J.-Y. 1980. Les Marsupiaux du Tertiaire d'Europe. *Éditions de la Fondation Singer-Polignac*, Paris, 279 pp.
- Crochet, J.-Y. 1995. Le Garouillas et les sites contemporains (Oligocene, MP 25) des phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertèbres. 4. Marsupiaux et insectivores. *Palaeontographica, Abteilung A* 236:39–75.
- De Bruijn, H., and C. G. Rümke. 1974. On a peculiar mammalian association from the Miocene of Oschiri (Sardinia). I and II. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 77:44–79.
- De Bruijn, H., Z. Marković, and W. Wessels. 2013. Late Oligocene rodents from Banovići (Bosnia and Herzegovina). *Palaeodiversity* 6:63–105.
- De Bruijn, H., R. Daams, G. Daxner-Höck, V. Fahbusch, L. Ginsburg, P. Mein, P., and J. Morales. 1992. Report of the RCMNS working group on fossil mammals, Reischensburg 1990. *Newsletters on Stratigraphy* 26:65–118.
- De Leeuw, A., O. Mandić, H. de Bruijn, Z. Marković, J. Reumer, W. Wessels, E. Šišić, and W. Krijgsman. 2011. Magnetostratigraphy and small mammals of the late Oligocene Banovići Basin in NE Bosnia and Herzegovina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310:400–412.
- Doben-Florin, U. 1964. Die Spitzmäuse aus dem Alt-Burdigalium von Wintershof-West bei Eichstätt in Bayern. *Abhandlungen der Bayerische Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche Klasse NF* 117:1–82.
- Doukas, C. S. 1986. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece) Part 5. The Insectivores. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, B* 89:15–38.
- Doukas, C. S., and C. D. Theocharopoulos. 1999. Smaller mammals from the Oligocene of Kyprinos (Thrace, N. Greece); pp. 133–145 in J. W. F. Reumer, and J. de Vos (eds.), *Elephants Have a Snorkel! Papers in Honour of Paul Y. Sondaar*. *Deinsea: Annual of the Natural History Museum Rotterdam* 7.
- Doukas, C. S., and L. W. van den Hoek Ostende. 2006. Insectivores (Erinaceomorpha, Soricomorpha; Mammalia) from Karydiá and Komotini (Thrace, Greece; MN 4/5). *Beiträge zur Paläontologie* 30:109–131.
- Engesser, B. 1975. Revision der europäischen Heterosoricinae (Insectivora, Mammalia). *Eclogae Geologicae Helvetiae* 68:649–672.
- Engesser, B. 1980. Insectivora und Chiroptera (Mammalia) aus dem Neogen der Türkei. *Schweizerische Paläontologische Abhandlungen* 102:47–149.
- Engesser, B., and G. Storch. 2008. Latest Oligocene Didelphimorphia, Lipotyphla, Rodentia and Lagomorpha (Mammalia) from Oberleichtersbach, Rhön Mountains, Germany. *Courier Forschungsinstitut Senckenberg* 260:185–251.
- Engesser, B., and R. Ziegler. 1996. Didelphids, insectivores, and chiropterans from the later Miocene of France, Central Europe, Greece and Turkey; pp. 156–167 in R. L. Bernor, V. Fahlbush, and H. -W. Mittman (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York.
- Filhol, H. 1879. Étude des mammifères fossils de Saint-Gérard-le-Puy. *Annales des Sciences Géologiques* 10:1–253.
- Fischer von Waldheim, G. 1814. *Zoognosia Tabulis synopticis illustrata*. Vol. 3. Nicolai S. Vsevolozsky, Moscow, 694 pp.
- Fortelius, M. (coordinator). 2003. Neogene of the Old World Database of Fossil Mammals (NOW). University of Helsinki, Helsinki, Finland. Available at www.helsinki.fi/science/now/. Accessed December 1, 2016.
- Furió, M., J. van Dam, and F. Kaya. 2014. New insectivores (Lipotyphla, Mammalia) from the Late Miocene of the Sivas Basin, Central Anatolia. *Bulletin of Geosciences* 89:163–181.
- Furió, M., I. Casanovas-Vilar, and L. W. van den Hoek Ostende. 2011. Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304:219–229.
- Gervais, P. 1848–52. *Zoologie et paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivantes et fossiles de la France*. Arthus Bertrand, Paris, Tome 1, 271 pp., Tome II, 146 pp.
- Gill, T. N. 1872. Arrangement of the families of mammals, with analytical tables. Prepared for the Smithsonian Institution. *Smithsonian Miscellaneous Collections* 230:1–198.
- Hordijk, K., A. Bosma, H. de Bruijn, J. van Dam, C. Geraedts, L. W. van den Hoek Ostende, J. W. F. Reumer, and W. Wessels. 2015. Biostratigraphical and palaeoecological implications of the small mammal assemblage from the late early Miocene of Montalvos 2, Teruel Basin, Spain. *Palaeobiodiversity and Palaeoenvironments* 95(3):32–346.
- Hugueney, M. 1972. Les Talpidés (Mammalia, Insectivora) de Coderet-Bransat (Allier) et l'évolution de cette famille au cours de l'Oligocène supérieur et du Miocène inférieur d'Europe. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon, Notes et Mémoires* 50:1–81.
- Hugueney, M. 1976. Un stade primitive dans l'évolution des Soricinae (Mammalia, Insectivora): *Srinitium marteli* nov. gen. nov. sp. de Oligocène moyen de Saint-Martin-de-Castillon (Vaucluse). *Comptes rendus de l'Académie des sciences, Paris D* 282:981–984.
- Hugueney, M., and O. Maridet. 2011. Early Miocene soricids (Insectivora, Mammalia) from Limagne (Central France): new systematic comparisons, updated biostratigraphic data and evolutionary implications. *Geobios* 44:225–236.
- Hutchison, J. H. 1974. Notes on type specimens of European Miocene Talpidae and a tentative classification of old world Tertiary Talpidae (Insectivora; Mammalia). *Geobios* 7:211–256.
- Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society, London* 43:649–662.

- Klietmann, L., D. Nagel, M. Rummel, and L. W. van den Hoek Ostende. 2014. *Amphiperatherium* and Erinaceidae of Petersbuch 28. Bulletin of Geosciences 89:1–20.
- Koufos, G. D. 2003. Late Miocene mammal events and biostratigraphy in the Eastern Mediterranean; pp. 343–371 in J. W. F. Reumer, and W. Wessels (eds.), Distribution and Migration of Tertiary Mammals in Eurasia. Deinsea: Annual of the Natural History Museum Rotterdam 10.
- Kretzoi, M. 1959. New names for Soricid and Arvicolid homonyms. Vertebrata Hungarica 1:247–249.
- Lavocat, R. 1951. Révision de la faune de mammifères Oligocène d'Auvergne et du Velay. Édition Science et Avenir, Paris, 153 pp.
- Linnaeus, C. 1758. Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th edition. Laurentius Salvius, Stockholm, 824 pp.
- Marković, Z., and M. Milivojević. 2010. The Neogene small mammals from Serbia collection – Methods and results. Bulletin of Natural History Museum in Belgrade 3:121–130.
- Meyer, H. von. 1846. Mittheilungen an Professor Bronn gerichtet. Neues Jahrbuch für Mineralogie, Geognosie und Petrefaktenkunde 1846:462–476.
- Parker, T. J., and W. A. Haswell. 1897. A Text-Book of Zoology. Volume 2. MacMillan and Company, London, 683 pp.
- Pomel, A. N. 1848. Études sur les carnassiers insectivores (extrait). Seconde partie, Classification des insectivores. Archive des Sciences Physiques et Naturelles Genève 9:244–251.
- Pomel, A. M. 1853. Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire, et surtout dans la vallée de son affluent principal, l'Allier. Baillière, Paris, 193 pp.
- Prieto, E. 2010. The Middle Miocene mole *Desmanodon crocheti* sp. nov. (Talpidae, Mammalia): the last representative of the genus in the North Alpine foreland basin. Paläontologische Zeitschrift 84:217–225.
- Prieto, E., M. Gross, C. Böhmer, and M. Böhme. 2010. Insectivores and bat (Mammalia) from the late Middle Miocene of Gratkorn (Austria): biostratigraphic and ecologic implications. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 258:107–119.
- Reumer, J. W. F. 1984. Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. Scripta Geologica 73:1–171.
- Reumer, J. W. F. 1987. Redefinition of the Soricidae and Heterosoricidae (Insectivora, Mammalia) with the description of the Crocidosoricinae, a new subfamily of the Soricidae. Revue de Paléobiologie 6:189–192.
- Reumer, J. W. F. 1994. Phylogeny and distribution of the Crocidosoricinae (Mammalia: Soricidae); pp. 345–356 in J. F. Merritt, G. L. Kirkland, and R. K. Rose (eds.), Advances in Biology of Shrews. Carnegie Museum of Natural History, Special Publication 18.
- Reumer, J. W. F. 1995. The evolution of shrews (Mammalia, Soricidae): a key role for humidity. Geobios 18:367–372.
- Reumer, J. W. F., and W. Wessels (eds.). 2003. Distribution and Migration of Tertiary Mammals in Eurasia. Deinsea: Annual of the Natural History Museum Rotterdam 10, 576 pp.
- Rümke, C. G. 1985. A Review of Fossil and Recent Desmaninae (Talpidae, Insectivora). Utrecht Micropaleontological Bulletin, Special Publication 4, 242 pp.
- Schmidt-Kittler, N., M. Godinot, J. L. Franzen, J. J. Hooker, S. Legendre, M. Brunet, and M. Vianey-Liaud. 1987. European reference levels and correlation tables; pp. 13–32 in N. Schmidt-Kittler (ed.), International Symposium on Mammalian Biostratigraphy and Palaeoecology of the European Paleogene, Mainz, 18–21 February 1987. Münchner Geowissenschaftliche Abhandlungen, A 10.
- Schwermann, A. H., and T. Martin. 2012. A partial skeleton of *Geotrypus antiquus* (Talpidae, Mammalia) from the Late Oligocene of the Enspel fossilagerstätte in Germany. Paläontologische Zeitschrift 86:409–439.
- Schwermann, A. H., and R. S. Thompson. 2014. Extraordinarily preserved talpids (Mammalia, Lipotyphla) and the evolution of fossoriality. Journal of Vertebrate Paleontology. doi: 10.1080/02724634.2014.934828.
- Storch, G., and Z. Qiu. 2004. First complete heterosoricine shrew: a new genus and species from the Miocene of China. Acta Palaeontologica Polonica 49:357–363.
- Theocharopoulos, K. D. 2000. Late Oligocene-middle Miocene *Democricetodon*, *Spanocricetodon* and *Karydomys* n. gen. from the eastern Mediterranean area. Gaia 8:1–116.
- Tobien, H. 1939. Die Insektenfresser und Nagetiere aus der aquitanen Spaltenfüllung bei Tomerdingen (Ulmer Alb). Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 36:159–180.
- Trouessart, E. L. 1879. Catalogue des mammifères vivants et fossiles. Insectivores. Revue et Magasin de Zoologie Pure et Appliquée, Paris 3:219–285.
- Ünay, E., H. de Bruijn, and G. Saraç. 2003a. The Oligocene rodent record of Anatolia: a review; pp. 531–538 in J. W. F. Reumer and W. Wessels (eds.), Distribution and Migration of Tertiary Mammals in Eurasia. Deinsea: Annual of the Natural History Museum Rotterdam 10.
- Ünay, E., H. de Bruijn, and G. Saraç. 2003b. A preliminary zonation of the continental Neogene of Anatolia based on rodents; pp. 539–548 in J. W. F. Reumer and W. Wessels (eds.), Distribution and Migration of Tertiary Mammals in Eurasia. Deinsea: Annual of the Natural History Museum Rotterdam 10.
- Van den Hoek Ostende, L. W. 1989. The Talpidae (Insectivora, Mammalia) of Eggingen Mittelhart (Baden-Württemberg, F. R. G.) with special reference to the *Paratalpa-Desmanodon* lineage. Stuttgarter Beiträge zur Naturkunde 152B:1–29.
- Van den Hoek Ostende, L. W. 1992. Insectivore faunas of the Lower Miocene of Anatolia. Part 1. Erinaceidae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 94:437–467.
- Van den Hoek Ostende L.W. 1995a. Insectivore faunas from the Lower Miocene of Anatolia—Part 2: *Dinosorex* (Heterosoricidae). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 98:1–18.
- Van den Hoek Ostende, L. W. 1995b. Insectivore faunas from the lower Miocene of Anatolia. Part 3: Dimylidae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 98:19–38.
- Van den Hoek Ostende, L. W. 1997. Insectivore faunas from the lower Miocene of Anatolia. Part 4. The genus *Desmanodon* (Talpidae) with the description of a new species from the Lower Miocene of Spain. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 100:27–65.
- Van den Hoek Ostende, L. W. 2001a. Insectivore faunas from the lower Miocene of Anatolia. Part 5: Talpidae. Scripta Geologica 122:1–45.
- Van den Hoek Ostende, L. W. 2001b. Insectivore faunas from the lower Miocene of Anatolia. Part 6: Crocidosoricinae (Soricidae). Scripta Geologica 122:47–81.
- Van den Hoek Ostende, L. W. 2001c. Insectivore faunas from the lower Miocene of Anatolia. Part 8: stratigraphy, palaeoecology, palaeobiogeography. Scripta Geologica 122:101–122.
- Van den Hoek Ostende, L. W. 2003. Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) from the Ramblian of the Daroca-Calamocha area. Coloquios de Paleontología 1:281–310.
- Vasileiadou, K., and G. D. Koufos. 2005. The micromammals from the Early/Middle Miocene locality of Antonios, Chalkidiki, Greece. Annales de Paléontologie 91:197–225.
- Vasileiadou, K., and N. Zouros. 2012. Early Miocene micromammals from the Lesvos Petrified Forest (Greece): preliminary results. Palaeobiology and Palaeoenvironment 92:249–264.
- Viret, J., and H. Zapfe. 1951. Sur quelques soricidés miocènes. Eclogae Geologicae Helveticae 44:411–426.
- Von Koenigswald, W. 1970. *Peratherium* (Marsupialia) im Ober-Oligozän und Miozän von Europa. Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen Neue Folge Heft 144, Munich, 79 pp.
- Waddell, P. J., N. Okada, and M. Hasegawa. 1999. Toward resolving the interordinal; relationships of placental mammals. Systematic Biology 48:1–5.
- Werner, J. 1994. Beiträge zur Biostratigraphie der Unteren Süsswasser-Molasse Süddeutschlands: Rodentia und Lagomorpha (Mammalia) aus den Fundstellen der Ulmer Gegend. Stuttgarter Beiträge zur Naturkunde, Serie B 200:1–220.
- Ziegler, R. 1985. Talpiden (Mammalia, Insectivora) aus dem Orleanium und Astaracium Bayerns. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 25:131–175.

- Ziegler, R. 1989. Heterosoricidae und Soricidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde* 154B:1–73.
- Ziegler, R. 1990a. Talpiden (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde* 167B:1–81.
- Ziegler, R. 1990b. Didelphidae, Erinaceidae, Metacondontidae und Dimylidae (Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde* 158B:1–99.
- Ziegler, R. 1998. Marsupialia und Insectivora (Mammalia) aus den oberoligozänen Spaltenfüllungen Herrlingen 8 und Herrlingen 9 bei Ulm (Baden-Württemberg). *Senckenbergiana lethaea* 77:101–143.
- Ziegler, R. 1999. The Insectivora; pp. 49–52 in E. G. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, Munich.
- Ziegler, R. 2005. Erinaceidae and Dimylidae (Lipotyphla) from the Late Middle Miocene of South Germany. *Senckenbergiana lethaea* 85:131–152.
- Ziegler, R. 2009. Soricids (Soricidae, Mammalia) from Early Oligocene fissure fillings in South Germany – and a phylogenetic analyses of the Heterosoricinae. *Palaeodiversity* 2:321–342.

Submitted December 15, 2016; revisions received July 24, 2017; accepted July 25, 2017.

Handling editor: Thomas Martin