

# Late Oligocene rodents from Banovići (Bosnia and Herzegovina)

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## Abstract

The family Muridae dominates the Banovići (Bosnia and Herzegovina) rodent assemblage in diversity as well as in number of specimens. The glirids are the second in importance and the sciurids are only represented by few specimens. The composition of the assemblage is on species level quite unique and on genus level more similar to assemblages from the Earliest Miocene of Anatolia than to assemblages from the Late Oligocene and Early Miocene of Western Europe. In the latter area the murid genera *Deperetomys*, *Mirrabella* and *Eumyarion* are absent. The species of these genera from Banovići combine primitive and derived features and seem to represent the oldest member of their genus or even family, and do not fit in previously reconstructed evolutionary trends. The evolutionary history of the Spalacinae seems to be much more complex than thought so far. Theridomyidae and Eomyidae, typical for Late Oligocene Western European rodent assemblages, are absent in the Banovići assemblage as well as in the Anatolian ones. The Banovići assemblage is in this aspect also more similar to Anatolian rodent assemblages than to European ones. Newly named species are *Bransatoglis bosniensis*, *Deperetomys magnus*, *Eumyarion margueritae*, and in a new genus, *Vetusspalax progressus*. This small mammal study was combined with a magnetostratigraphic investigation of the sedimentary infill of the Banovići basin in Bosnia and Herzegovina. The age correlation of the fauna as well as the magnetostratigraphic data indicate an infill of the Banovići basin between 24–22 Ma. The rodent fauna is from the base of the basin infill, just below the major coal seam, and of an age of ~ 24 Ma.

**Key words:** Bosnia and Herzegovina, Dinarides, Oligocene, Miocene, rodents, systematics, biostratigraphy, biogeography.

## 1. Introduction

### 1.1. Late Oligocene rodents of Europe

Terrestrial faunal exchange between Western Europe and Anatolia is poorly understood despite the good records of Late Oligocene and Early Miocene Rodentia from Western Europe and Anatolia (BARBERÁ et al. 1994; GARCÉS et al. 1996; KRIJGSMAN et al. 1996a, b; DAAMS et al. 1999; VAN DAM et al. 2001; ÜNAY et al. 2003a, b).

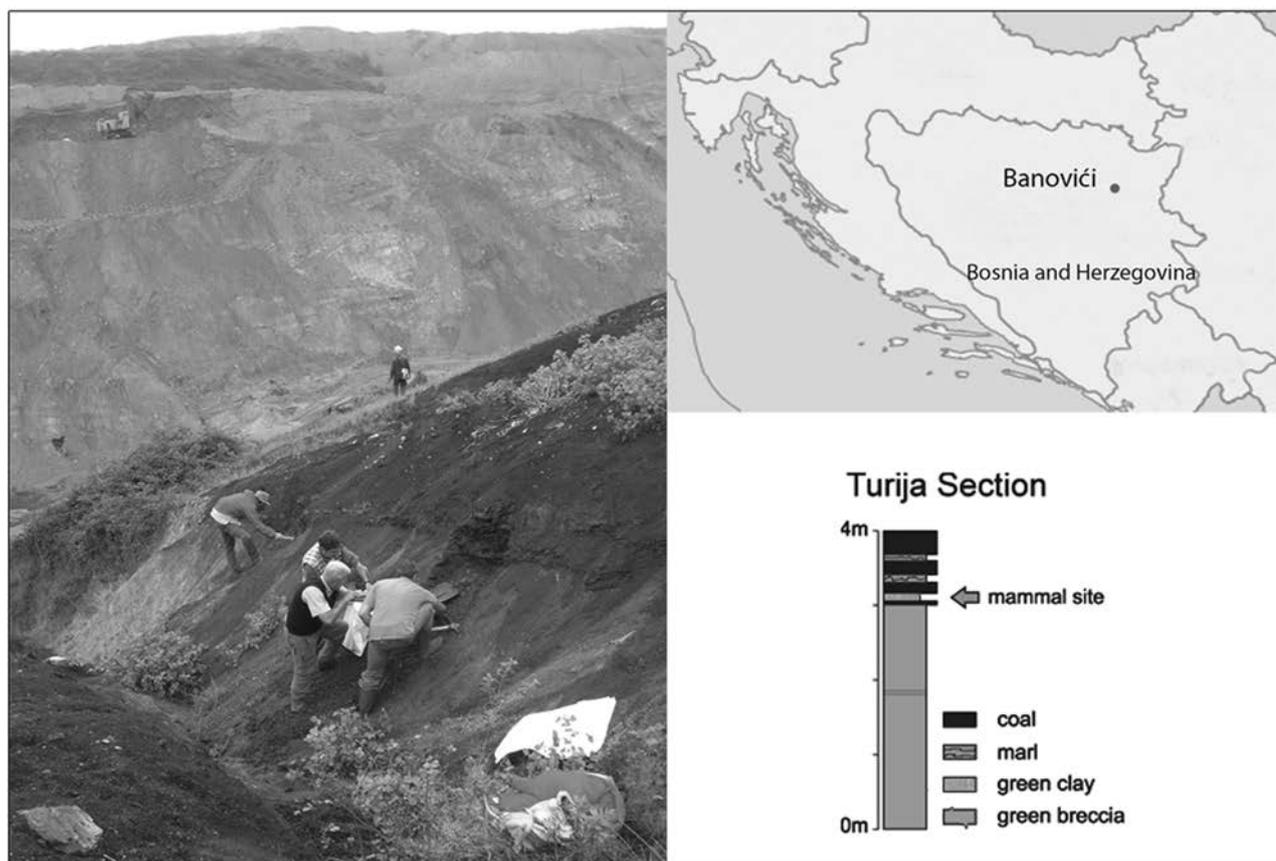
Faunal comparisons by MARIDET et al. (2007) clearly show that many Late Oligocene rodent species are distributed throughout Western Europe and are thus very useful in large-distance correlation. It appears that a high faunal similarity existed in Western Europe in the late Oligocene and earliest Miocene, except for the rodent faunas from southern Germany which are slightly different (MARIDET et al. 2007). The compositions of the rodent faunas changed considerably in the late Early Miocene and the difference between the southWestern part of Europe and the north-eastern part increases. Many new rodent species appear that are considered to be immigrants from the east. However, it is still not clear from where and by which route the new species reached Western Europe.

Marine fauna from the western part of the Paratethys, showing periods of endemic development, indicate that

the Paratethys was often disconnected from the Mediterranean (MANDIC et al. 2011), and that land connections in the southern part of the Paratethys must have existed, enabling terrestrial faunal exchange between western Europe and Anatolia.

In the area between Europe and Anatolia only a few Late Oligocene – Early Miocene rodent faunas are known: In Thrace only two Late Oligocene rodent assemblages (ÜNAY 1989; DOUKAS & THEOCHAROPOULOS 1999), and a few from the Early Miocene (KLEINHOFMEIJER & DE BRUIJN 1985; DOUKAS 2003; KOUFOS 2003; VASILEIADOU & KOUFOS 2005; VASILEIADOU & ZOUROS 2012). Apart from an unpublished Oligocene fauna from Ugljevik (BIH), only late Early Miocene assemblages are known from Serbia (MN4 and MN5; MARKOVIĆ 2003, 2009).

The Late Oligocene rodent assemblage from Banovići (BIH) enables us to extend our knowledge of the distribution of rodents in this area and helps to better understand the faunal exchange between western Europe and the eastern Mediterranean area. This small mammal fauna was discovered in 2008 during interdisciplinary research carried out in this region (project of O. MANDIC). Data from lithostratigraphy, biostratigraphy (Rodentia) and magnetostratigraphy were combined, and provide the age framework of the lake sediments from the Banovići basin (DE LEEUW et al. 2011).



**Fig. 1.** Picture of the mammal locality Banovići, Turija section, in the open-pit coalmine Banovići, map with the location of Banovići within Bosnia and Herzegovina, and a stratigraphic column of the section. The mammal site, a 20 cm thick lignitic clay bed which contains limestone nodules, is just below the main coal layers.

DE LEEUW et al. (2011) used the Banovići rodent fauna for correlating the sediments of the Banovići Basin to the GPTS and only briefly discussed the assemblage. In this paper the rodent fauna, with several new species, is described in detail and its biostratigraphic significance and biogeographic implications are discussed. The lagomorphs, insectivores and marsupials will be published in a separate paper.

## 1.2. Geology

The geological setting, with emphasis on the regional stratigraphic and paleogeographic development the basin infill, is described in detail in DE LEEUW et al. (2011). The small mammal locality is situated in the Banovići basin, a Dinaride intramontane basin in the north-western part of Bosnia and Herzegovina. The basin was formed during the Late Eocene–Oligocene on the north eastern margin of the Dinarides (TARI & PAMIĆ 1998), when the northward movement of the African plate induced uplift of the Dinarides and sediments from this new high were deposited.

The infill of the Banovići basin consists of 320 meters of Oligocene to Miocene lacustrine sediments.

The fossiliferous layer of greenish clay with very thin lignite layers is situated just below the main coal seam in the Turija opencast mine near Banovići (Fig. 1).

### Abbreviations

BAN	code for the Banovići locality, Bosnia and Herzegovina
Country codes:	BIH – Bosnia and Herzegovina; ESP – Spain; FR – France; GER – Germany; NL – The Netherlands; TUR – Turkey
MNHW	Museum of Natural History Vienna, Austria
NHMB	Natural History Museum Belgrade, Serbia
UU	Utrecht University, The Netherlands

Abbreviations for measurements and descriptions: N – number of specimens; R – range of measurements; L – length; W – width; sin – sinistral; dex – dextral.

### Acknowledgements

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## 2. Material and methods

The fossils were collected from a 20 cm thick lignitic clay bed with limestone nodules that is located just below the main coal layer in the Turija opencast mine near Banovići (BIH). Two tons of sediment were washed and sieved in the field over 0.5 mm sieves. The residue was treated with chemicals in the laboratory of Utrecht, washed and sieved and subsequently sorted, mounted and measured. The Banovići assemblage contains 295 identifiable fossil rodent molars, of which 207 first and second molars. The measurements and are given in mm and were taken with an Ortholux microscope with mechanical stage and measuring clocks, with a precision of 0.01 mm. All specimens are figured as left ones. If the original is from the right side its number is underlined on the plates.

Lower case letters refer to the lower dentition, upper case letters refer to the upper dentition.

Detailed data on the geographical distributions and bio-chronological ranges of the species mentioned are given in Appendix 1. The collection is stored in the Department of Earth Sciences, Utrecht University. In the future, the collection from Banovići will be housed in the Museum of Natural History in Vienna.

## 3. Systematic palaeontology

Order Rodentia BOWDICH, 1821

Family Sciuridae FISCHER DE WALDHEIM, 1817

Genus *Palaeosciurus* POMEL, 1853

Species included: *Palaeosciurus feignouxi* POMEL, 1853; *Palaeosciurus fissurae* (DEHM, 1950); *Palaeosciurus goti* VIANEY-LIAUD, 1974; *Palaeosciurus sutteri* ZIEGLER & FAHLBUSCH, 1986; *Palaeosciurus ultimus* MEIN & GINSBURG, 2002; and *Palaeosciurus* nov. sp. FEJFAR & KAISER, 2005.

Remarks. – The type of *Palaeosciurus feignoux* (POMEL, 1853), from Langy (France) is missing, Montaigne-le-Blin (France) is now considered as the reference assemblage (WERNER 1994).

*Palaeosciurus* aff. *feignouxi* (POMEL, 1853)

Pl. 1, Figs. 1–6

.2011 *Palaeosciurus* aff. *feignouxi* (POMEL, 1853). – DE LEEUW et al., p. 405, fig. 4.1–4.3.

Occurrences: *Palaeosciurus feignouxi*: Germany MN1–3; France MN1–2; Spain MP30–MN2; Switzerland MN2; Turkey Zone B and C (~MN1–2). *Palaeosciurus* sp. (cf. *feignouxi*): Germany MN1.

Comparison material: *Palaeosciurus feignouxi*, Montaigne-le-Blin (FR), collection UU; *Palaeosciurus feignouxi*, Eggingen (Germany, WERNER 1994); *Palaeosciurus feignouxi*, Montaigne-le-Blin (France, WERNER 1994); *Palaeosciurus* sp. (cf. *feignouxi*), Ulm-Westtangente (Germany, WERNER 1994); *Palaeosciurus* aff. *goti*, Herrlingen 8&9 (Germany, ZIEGLER 1994); *Palaeosciurus goti*, Oberleichtersbach (Germany, ENGESSER & STORCH 2008); *Palaeosciurus* sp., Coderet (France, HUGUENEY 1969); *Palaeosciurus feignouxi*, Kilçak 3a (Turkey), collection UU.

Locality: Banovići (Bosnia and Herzegovina).

Material and measurements: 8 complete specimens (Pl. 1, Figs. 1–6; Tab. 1; Figs. 2–3). Catalogue numbers: BAN410–419.

Description. – D4. The shape of the occlusal surface of the D4 is sub-triangular. The parastyl has an unusually long (for the Sciuridae) lingual extension that reaches the base of the rather small pointed protocone. The protoconule is absent in both specimens, but one has a metaconule. The enamel surface of both teeth is slightly rugose.

M1<sup>o</sup>2. The anteroloph of the M1<sup>o</sup>2 is stronger than the posteroloph as in all species of *Palaeosciurus*. The sub-parallel protoloph and metaloph are devoid of conules. The lingual part of the M1<sup>o</sup>2 is wide, but the hypocone is incorporated into the endo/posteroloph. The mesostyl is either developed as an anterior spur of the metacone, a posterior spur of the paracone or as a small individual cusp. The enamel surface is rugose in one specimen, but smooth in the others.

M3. The occlusal surface of the M3 is sub-triangular and the posterior part of this tooth is not separated from the protocone by a notch. The transverse protoloph does not bear a protoconule. The enamel surface is somewhat rugose.

m1. The anteroconid of the m1 is rather large. The metaloph is thick but short and does not reach the metaconid. The mesostylid is larger and more individualized than the mesoconid because there is a deep notch between the entoconid and the mesostylid. The enamel surface is rugose.

m2. The lingual side of the single m2 is somewhat damaged. The metalophid is thick and short as in the m1. The mesoconid is rather strong. The enamel surface is slightly rugose.

Discussion. – The small collection of isolated *Palaeosciurus* cheek teeth from Banovići seems at first

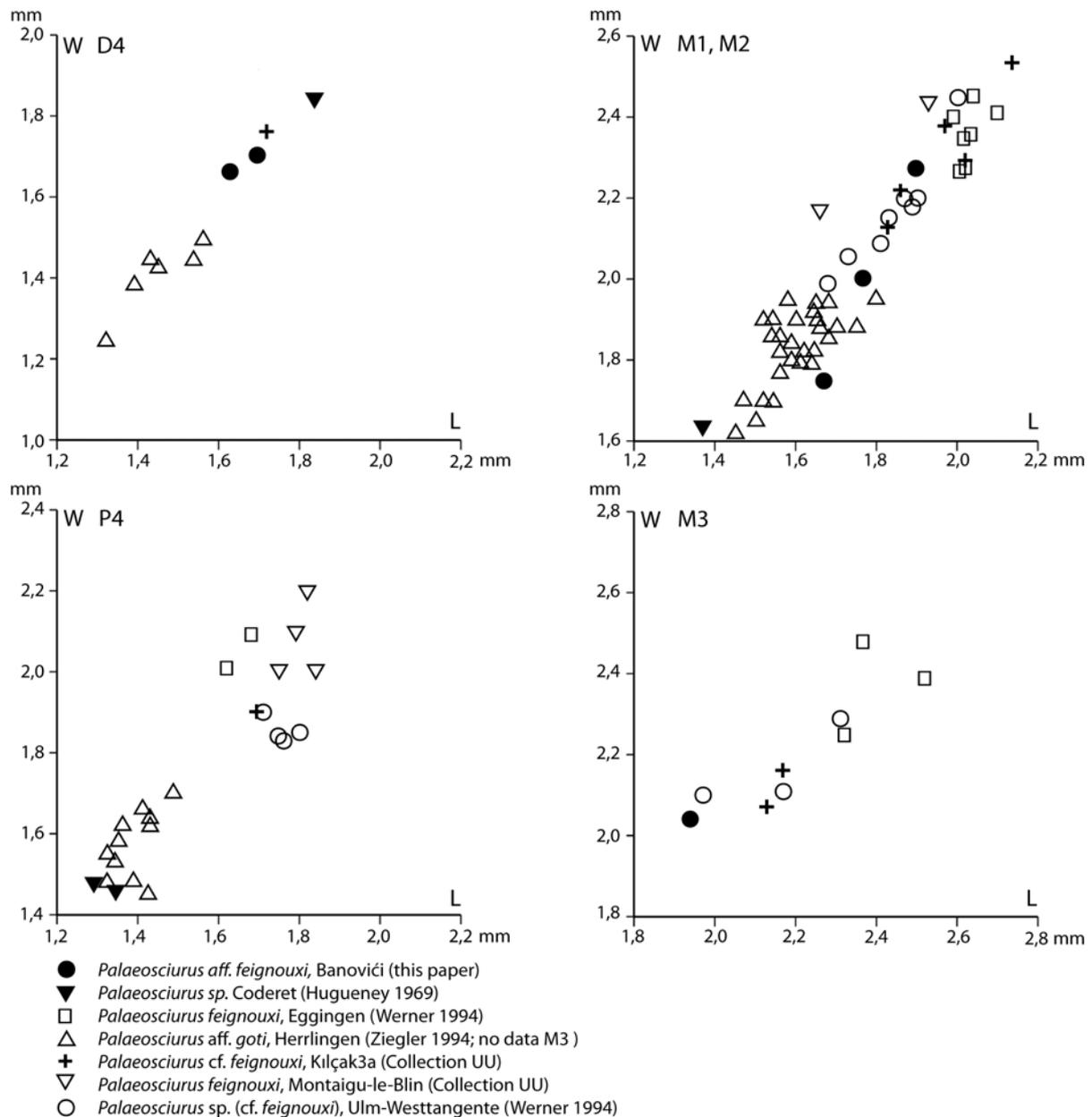
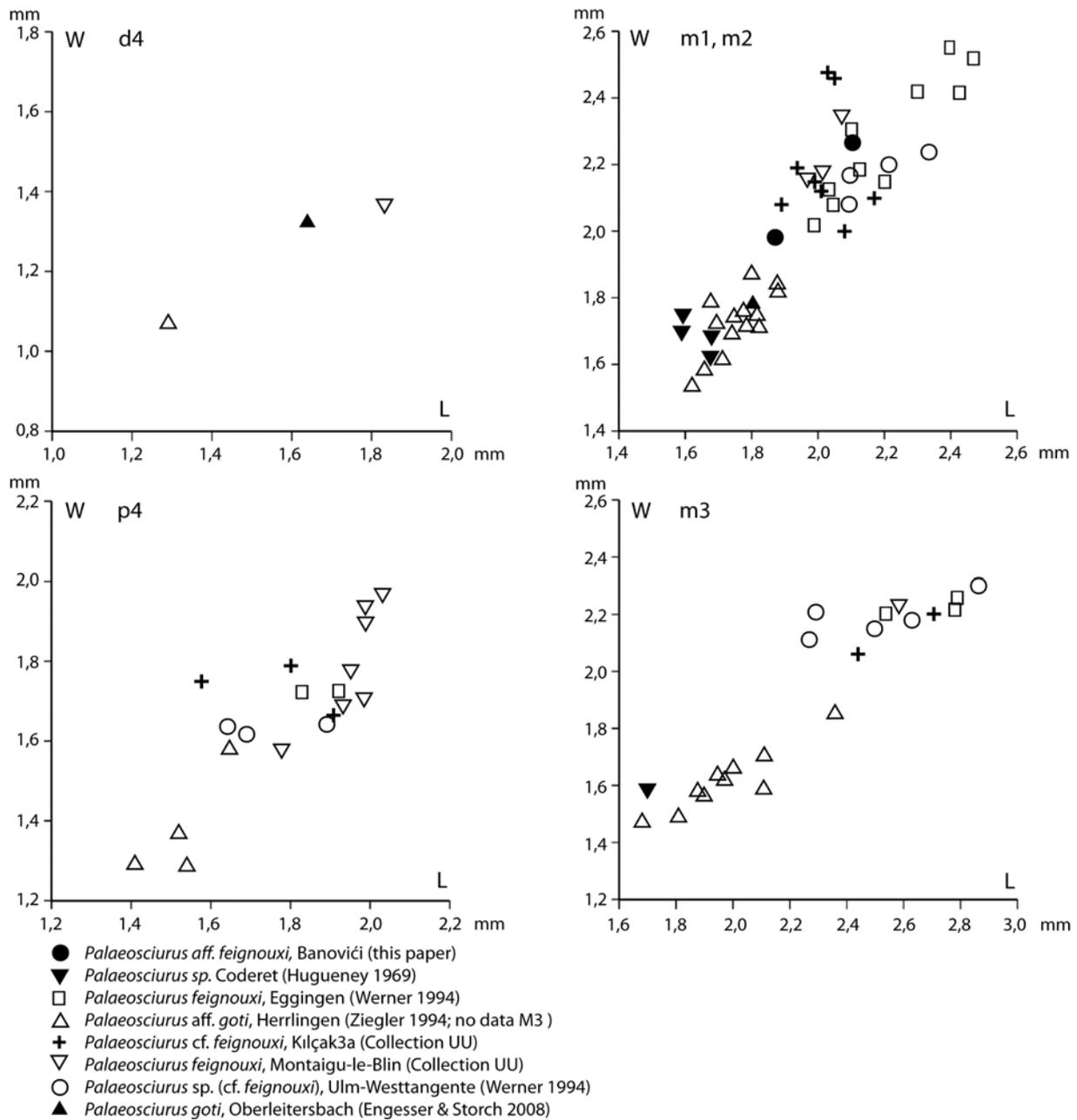


Fig. 2. Scatter diagrams of length and width of the upper molars of *Palaeosciurus aff. feignouxii* POMEL, 1853 from Banovići and of *Palaeosciurus* species from several other localities.

sight to contain two species because of the difference in size among the M1<sup>or</sup>2. In order to get an idea of the size variation within a species of this genus we compared the Banovići material with other samples of *Palaeosciurus* (Figs. 2–3). Since the size variation among the M1<sup>or</sup>2 in all these association is large also, so we tentatively consider the *Palaeosciurus* material from Banovići to belong to one species.

*Palaeosciurus* occurs in many fossil assemblages (see Appendix 1) but only in a few of these all dental elements

are represented. Because of the large variation in size it is often difficult to allocate *Palaeosciurus* molars at species level. Distinctive features are size, relative size of the dental elements, number of roots, shape of the metacone(id) and ornamentation of the incisor. The Oligocene species are smaller than the Miocene species. *Palaeosciurus goti* and *?Palaeosciurus dubius* from the Early Oligocene of France (MP22–24) are the oldest, followed by *Palaeosciurus aff. goti* in Germany (MP28), *Palaeosciurus goti* (MP 30 Germany) and *P. feignouxii* (MP30 France, Spain), so



**Fig. 3.** Scatter diagrams of length and width of the lower molars of *Palaeosciurus* aff. *feignouxii* POMEL, 1853 from Banovići and of *Palaeosciurus* species from several other localities.

there is a long hiatus in the record of *Palaeosciurus*. *Palaeosciurus* aff. *goti* from Herrlingen 8 & 9 seems to represent a new species (ZIEGLER (1994), differing by its smaller milk-teeth and smaller upper fourth premolars.

*P. feignouxii*, *P. fissurae*, *P. sutteri* are, until the late Middle Miocene, common in many European mammal assemblages.

Characteristic differences between *Palaeosciurus goti* and *P. feignouxii* are size and number of roots in the lower

molars. *P. goti* is the smallest species with two roots in the lower molars, whereas *P. feignouxii* is larger and has three roots in the lower molars. *P. feignouxii*, *P. sutteri* and *P. fissurae*, all with three roots in the lower molars, differ in the ornamentation of the incisors and in size of premolars and third molars. Since the roots are often not preserved the number of roots is a problematic characteristic. Moreover, the number of roots may vary within a population. The lower molars of *P. feignouxii* from Montaignu-le-Blin (Fr.) in

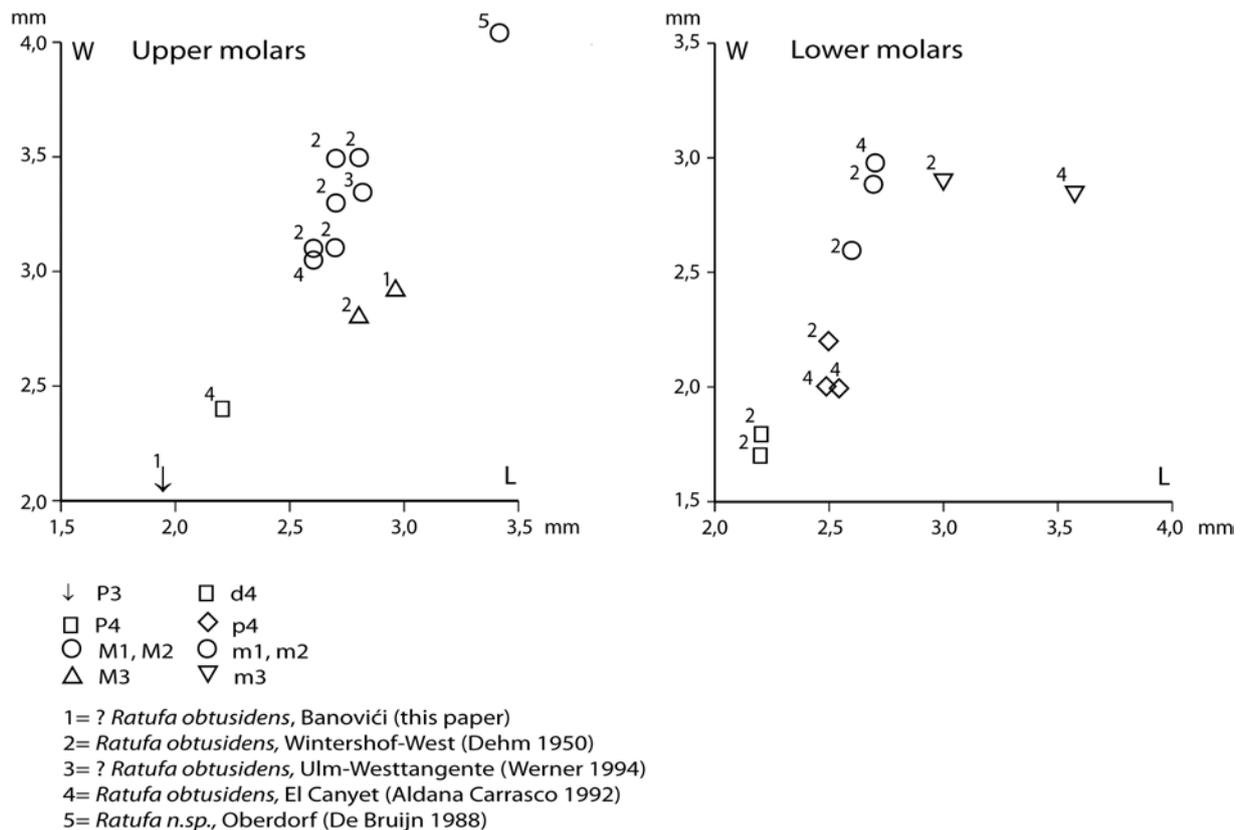


Fig. 4. Scatter diagrams of length and width of ?*Ratufa obtusidens* DEHM, 1950 from Banovići and several other localities.

the UU collection and the lower molars from Kilçak have either two or three roots. Unfortunately, the roots of the two lower molars available from Banovići are not preserved.

*Palaeosciurus* sp. (cf. *feignouxi*) from Ulm-Westtangente, *Palaeosciurus feignouxi* from Kilçak3a and *Paleosciurus* aff. *feignouxi* from Banovići, show an overlap in size with *P. aff. goti* as well with *P. feignouxi* (Figs. 2–4).

Our material from Banovići may represent a new species that is intermediate in size between the smaller *P. goti* and the larger *P. feignouxi*. Given the morphological resemblance of the teeth of all the species of this genus and the paucity of the material from Banovići we do not name this species formally, but allocate this material to *P. aff. feignouxi*.

#### Genus *Ratufa* GRAY, 1867

Extant species: *Ratufa affinis*, *Ratufa bicolor*, *Ratufa indica*, *Ratufa macroura*. Distribution of *Ratufa*: India, Indonesia, Malaysia, Nepal, Sri Lanka (NOWAK 1999; WILSON & REEDER 2005)

Fossil species: *Ratufa maelongensis* MEIN & GINSBURG 1997 (MN4; Li Mae Long, Thailand); *Ratufa yaunmouensis* QI, DONG, ZHENG, ZHAO, GAO, YUE & ZHANG, 2006 (Late Miocene, China).

Fossil species tentatively allocated to *Ratufa* (Early and Middle Miocene species): ?*Ratufa obtusidens* DEHM, 1950 in: WERNER 1994 (MN 2a; Ulm-Westtangente; Germany); *Ratufa obtusidens* DEHM, 1950 (MN3; Wintershof-West, Germany; MN4; El Canyet, Spain); *Ratufa* sp. in: KOWALSKI 1993 (MN5; Belchatów, Poland); *Ratufa* n. sp. DE BRUIJN, 1998 (MN4; Oberdorf, Austria); '*Sciurus*' *giganteus* (= *Ratufa* ? *obtusidens*) in FEJFAR et al. 2003 (MN 3; Tuchariche, Merkur North, Czech Republic); *Ratufa* sp. in: MÖRS, 2002 (MN6; Hambach 6C, Germany).

Remarks. – DEHM (1950) was the first to tentatively refer Early Miocene European material of a large squirrel to the South East Asiatic giant tree squirrel genus *Ratufa*. The shape of the mandible and the low-crowned bunodont cheek teeth of his species *Ratufa obtusidens* corroborate DEHM's conclusion that this material documents a large tree squirrel, but its allocation to *Ratufa* is as questionable now as it was in 1950. Comparison of DEHM's originals from the fissure filling of Wintershof-West (southern Germany) with some isolated *Ratufa* teeth from an unknown Pleistocene fissure filling on Java (Indonesia) in the Utrecht collection (Pl. 1, Fig. 9) and extant material of *Ratufa bicolor* in the collection of the national natural history museum Naturalis in Leiden (the Netherlands) casts doubts on the allocation of the fossil material to *Ratufa*, because the

irregular tubercles that characterize the enamel surface of the Pleistocene and extant giant squirrels from South East Asia are absent in the Early Miocene material.

The increased interest in fossil rodents and the modernization of collecting techniques have resulted in a much better record of fossil rodents than in DEHM's days. Nevertheless new finds of Early Miocene giant tree squirrels remained restricted to a few specimens from Spain, Germany; Austria and Poland, and the M3 and P3 from Bosnia and Herzegovina that is described below. This poor documentation does not allow the reconstruction of the phylogenetic position of these squirrels that had a large geographical range and that were apparently restricted to the European Early Miocene. We therefore think that classification of this group in a new genus would reflect current knowledge better than allocation to either *Ratufa* or *Palaeosciurus*. The latter was suggested by ALDANA-CARRASCO (1992), MEIN & GINSBURG (1997) and COSTEUR et al. (2012). The short, deep mandible and short diastema (see descriptions in DEHM 1950; ALDANA-CARRASCO 1992) suggests tree squirrel affinities rather than ground squirrel affinities, therefore we maintain the traditional allocation of this species to *?Ratufa* for the time being.

*?Ratufa obtusidens* DEHM, 1950  
Pl. 1, Figs. 7–8

.2011 *?Ratufa obtusidens* DEHM, 1950. – DE LEEUW et al., p. 405, Fig. 4.4.

Occurrences and comparison material: *?Ratufa obtusidens*, Wintershof-West (Germany, DEHM 1950); *?Ratufa obtusidens*, El Canyet (Spain, ALDANA CARRASCO 1992); *?Ratufa obtusidens*, Ulm-Westtangente (Germany, WERNER 1994); *?Ratufa* n. sp., Oberdorf (Austria, DE BRUIJN 1998); *?Ratufa obtusidens*, Tuchoriche, Merkur North (Czech Republic, FEJFAR et al. 2003).

Locality: Banovići (Bosnia and Herzegovina).

Material and measurements: 1 P3 (1.19 x 1.25 mm), 1 M3 (2.96 x 2.91 mm). (Pl. 1, Figs. 7–8; Fig. 4). Catalogue numbers: P3, BAN403; M3, BAN401.

Description. – P3. The dental pattern of this oval tooth, which is tentatively identified as a left P3, is difficult to interpret because there is no facet indicating the contact with the P4 on either side. Supposing that our identification is correct the anteroloph is crescent-shaped, the low protoloph and metaloph converge towards the lingual margin of the occlusal surface and the posteroloph is merely a low cingulum.

M3. The shape of the occlusal surface of the M3 is sub-triangular. The anteroloph is long, but low. The low transverse protoloph connects the rather high and pointed paracone with the large low protocone. The metacone is incorporated into the low posteroloph. Posteroloph and ectoloph border the main basin posteriorly and labially.

Discussion. – Although we do not have a cast of the M3 from Wintershof-West for comparison, the M3 from Banovići fits the M1<sup>or</sup>2 from that locality perfectly, so there is no doubt that it represents *?R. obtusidens*. The identity of the P3 remains uncertain, because this tooth is not represented in the type material.

Family Gliridae MUIRHEAD, 1819  
Subfamily Bransatoglirinae DAAMS & DE BRUIJN, 1995

Remarks. – FREUDENTHAL & MARTÍN-SUÁREZ (2007b) revised the classification of the originally monogeneric Bransatoglirinae, distinguishing three genera within this subfamily on the basis of size: *Bransatoglis* HUGUENEY, 1967, *Paraglis* BAUDELLOT, 1970 and *Oligodyromys* BAHLO, 1975. Their thorough analysis shows conclusively that the dental morphology as well as the size of the teeth of the species of the Bransatoglirinae (formerly *Bransatoglis*) shows no major breaks. In the same work they suggest on the basis of the relative size and the shape of the premolars that the genus *Microdyromys* DE BRUIJN, 1966 belongs in the Bransatoglirinae. Our main objection against the classification presented by FREUDENTHAL & MARTÍN-SUÁREZ (2007b) is that this brave effort to express their reconstruction of the phylogenetical relationships among the species of the Bransatoglirinae in a formal classification is bound to lead to long discussions about the generic identity of species and is therefore not in the interest of the stability of nomenclature. We therefore choose not to follow FREUDENTHAL & MARTÍN-SUÁREZ (2007b) and tentatively consider the subfamily to be monogeneric. A long discussion of the problem outlined above is beyond the scope of this paper.

Genus *Bransatoglis* HUGUENEY, 1967

Synonyms: *Paraglis* BAUDELLOT, 1970; *Oligodyromys* BAHLO, 1975.

Species included: *Bransatoglis concavidens* HUGUENEY, 1967 (type) (MP30; Coderet, France); *Bransatoglis spectabilis* (DEHM, 1950) (MN3; Wintershof West, Germany); *Bransatoglis fugax* (HUGUENEY, 1967) (MP30; Coderet, France); *Bransatoglis astaracensis* (BAUDELLOT, 1970) (MN6; Sansan, France); *Bransatoglis bahloi* BOSMA & DE BRUIJN, 1982 (Eocene; Headon Hill 3, Great Britain); *Bransatoglis infralactorensis* (BAUDELLOT & COLLIER, 1982) (MN3; Estrepouy, France); *Bransatoglis mayri* RABEDER, 1984 (MN5; Schönweg, Austria); *Bransatoglis cadeoti* BULOT, 1987 (MN4A; Bezan, France); *Bransatoglis moyai* HUGUENEY & ADROVER, 1990 (MP25; Sineu, Spain); *Bransatoglis sjeni* ÜNAY-BAYRAKTAR, 1989 (Early Oligocene; Kocayarma, Turkey); *Bransatoglis complicatus* ÜNAY, 1994 (MN2; Harami 1, Turkey); *Bransatoglis ingens* (WERNER, 1994) (MN2a; Ulm-Westtangente, Germany); *Bransatoglis parvus* FREUDENTHAL, 1996 (MP21; Olalla 4A, Spain); *Bransatoglis adroveri* HUGUENEY, 1997 (MP23-24; Paguera, Spain); *Bransatoglis attenuatus* PELÁEZ-CAMPOMANES, 2000 (MP21; Aguatón, Spain), and *Bransatoglis bosniensis* n. sp.

*Bransatoglis bosniensis* n. sp.

Pl. 1, Figs. 10–18

Etymology: The species is named after Bosnia.

Holotype: M1 sin., BAN433 (Pl. 1, Fig. 13).

Paratypes: 2 p4 (BAN421–422); 1 m1 (BAN424); 3 m2 (BAN425–427); 1 m3 (BAN429); 1 D4 (BAN431); 2 M1 (BAN432, 434); 2 M3 (BAN438, 440).

Measurements of the holotype: 1.77 x 1.27 mm.

Type locality: Banovići (Bosnia and Herzegovina).

Type level: Late Oligocene (MP 30).

Comparison material: Same as species included.

Material and measurements: 13 specimens (10 complete) (Pl. 1, Figs. 10–18; Tab. 2; Figs. 5–6). Catalogue numbers BAN421–422; BAN424–427; BAN429; BAN431–432; BAN434; BAN438; BAN440.

Occurrences: Late Oligocene (MP 30), Bosnia and Herzegovina.

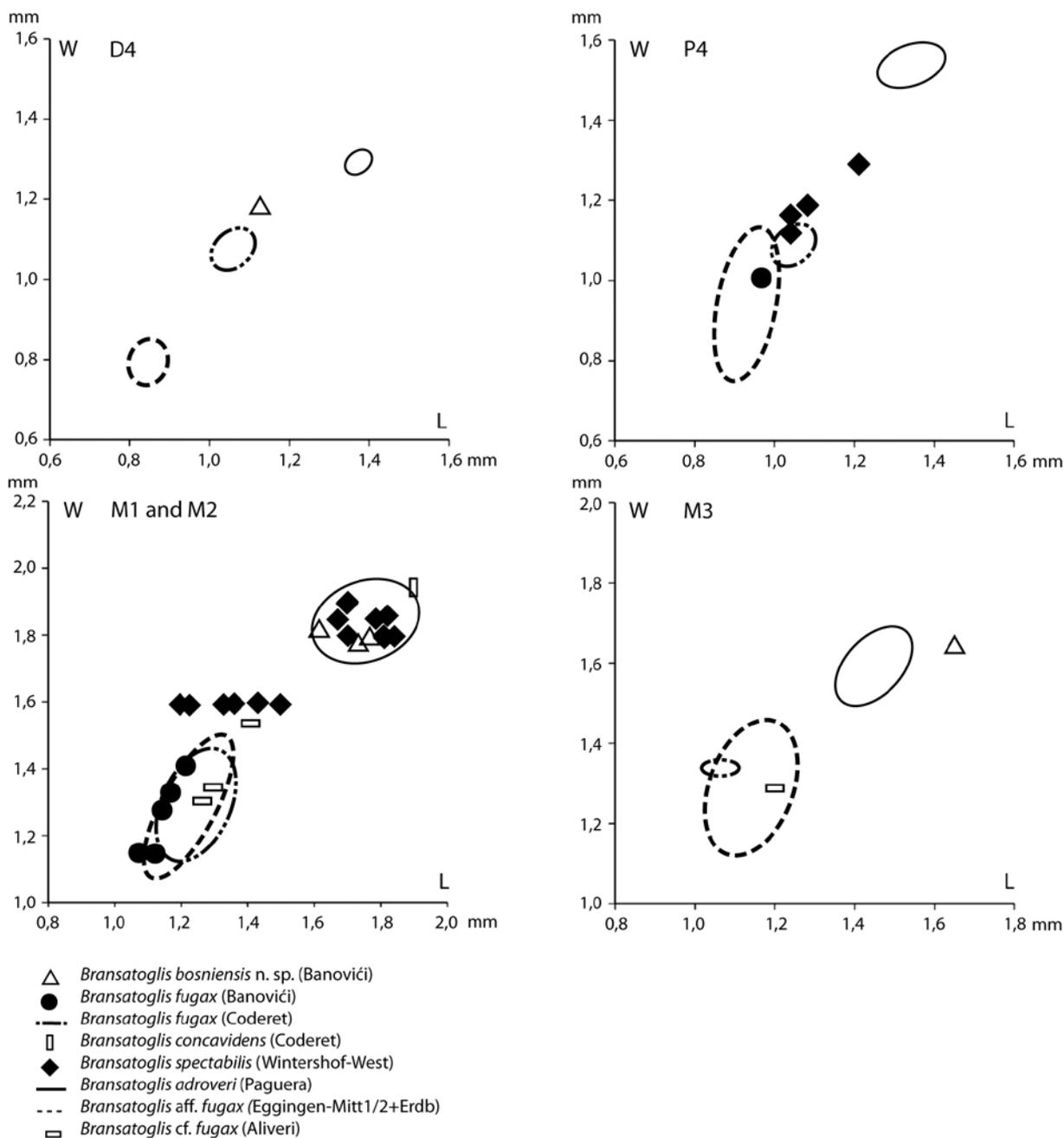
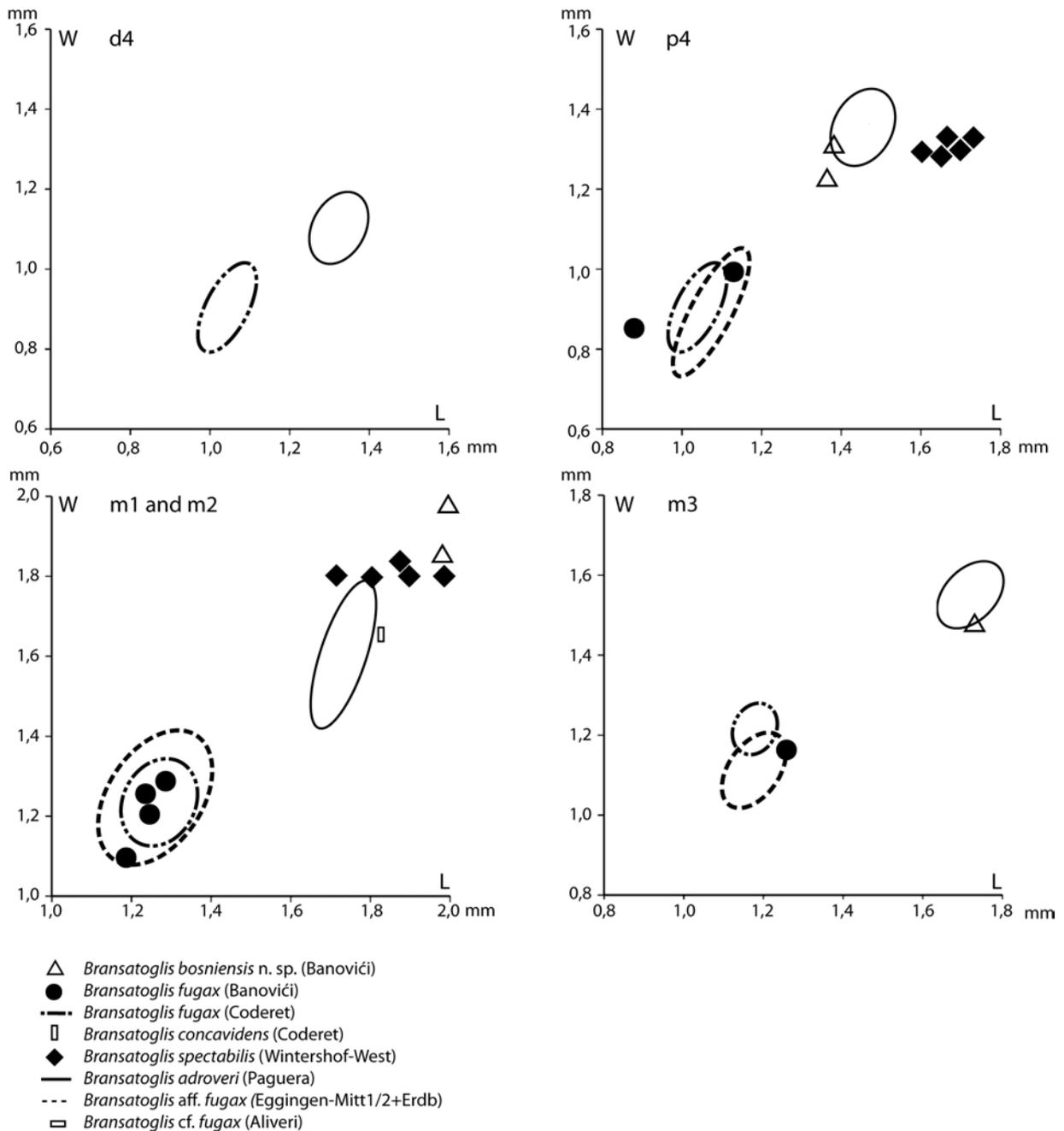


Fig. 5. Scatter diagrams of length and width of the upper molars of *Bransatoglis bosniensis* n. sp. from Banovići, and of several *Bransatoglis* species from other localities.

**Diagnosis.** – *Bransatoglis bosniensis* has about the same size as *B. concavidens* HUGUENEY, 1967 and *B. spectabilis* (DEHM, 1950). The occlusal surface of the M1<sup>or</sup>2 is concave and shows ten or eleven ridges. The occlusal surface of the m1 and m2 is less concave than in the M1<sup>or</sup>2 and shows nine to twelve ridges. All lower molars have three extra ridges between the mesolophid and the posterolophid.

**Differential diagnosis.** – *Bransatoglis bosniensis* is much larger than all the Oligocene species of the genus except *B. concavidens*. *Bransatoglis bosniensis* is also larger than the Miocene species *B. complicatus*, *B. infralactorensis* and *B. astaracensis*. *B. bosniensis* is smaller than *B. cadeoti* and *B. mayri*. The only species that are of about the same size as *B. bosniensis* are *B. adroveri*, *B. concavidens* and *B. spectabilis*. These species have a



**Fig. 6.** Scatter diagrams of length and width of the lower molars of *Bransatoglis bosniensis* n. sp. from Banovići, and of several *Bransatoglis* species from other localities.

dental pattern with seven ridges in the m1-2 and eight to ten ridges in the M1-2. In *B. bosniensis* these numbers are ten to eleven respectively nine to twelve. The lower molars of *B. bosniensis* differ from those of *B. adroveri*, *B. concavidens* and *B. spectabilis* by having three extra ridges between the mesolophid and the posterolophid instead of only one. *Bransatoglis bosniensis* is clearly distinguishable by its much larger size from *Bransatoglis fugax*, which is also present in this assemblage.

**Description.** – D4. The relatively long anteroloph of the D4 is connected to the paracone and reaches the base of the protocone. The protoloph and the metaloph converge towards the distinct protocone. The anterior centroloph is longer and wider than the posterior centroloph, but does not reach the protocone. The long posteroloph is not firmly connected to the protocone.

M1<sup>or</sup>2. The dental pattern of the M1<sup>or</sup>2 shows much variation (Pl. 1, Figs. 11–13). The ridges may be interrupted or join adjacent ones. Basically the occlusal pattern consists of the four sub-parallel main ridges, a long extra ridge between the anteroloph and the protoloph, two extra ridges between the protoloph and the long anterior centroloph that reaches the endoloph and an extra ridge between the posterior centroloph and the metaloph.

M3. The occlusal surface of the complete M3 is concave and shows a very complex pattern, because many ridges are interrupted. The four main ridges are still identifiable. The incomplete posterior centroloph is connected to the endoloph, but the anterior centroloph is ending free. If all the, sometimes very narrow short ridges, are included in our count, the total number is twelve.

p4. The dental pattern of the p4 is simple in comparison to that of the molars. It consists of the four main ridges, one extra ridge between the anterolophid and the metalophid and one extra ridge between the mesolophid and the posterolophid.

m1. The concave occlusal surface of the only complete m1 in the collection shows a very complex pattern due to the presence of connections between the main ridges and extra ridges (Pl. 1, Fig. 16). We recognize three extra ridges between the anterolophid and the metalophid, one extra ridge on either side of the centrolophid and three extra ridges between the mesolophid and the posterolophid.

m2. The dental pattern of the m2 is, except for the presence of only two extra ridges in the anterior valley, very similar to that of the m1. Notable is the presence of three extra ridges between the mesolophid and the posterolophid.

m3. The dental pattern of the m3 differs from that of the m1 and m2 by having only one extra ridge in the anterior valley. The three extra ridges between the mesolophid and the posterolophid are preserved. Apparently the reduction of the number of extra ridges from the m1 through the m3 takes place in the valley between the anterolophid and the metalophid.

**Discussion.** – The three extra ridges between the mesolophid and the posterolophid in the m1 clearly distinguish the lower molars of *B. bosniensis* from those of *B. concavidens* and *B. spectabilis*. Data in the literature suggest that *Bransatoglis spectabilis*, and *B. concavidens* are very similar in size and morphology. Whether or not this is the case can only be established by direct comparison of the type materials with the rich sample of *B. concavidens* from southern Germany described by WERNER (1994). However, it is of interest that the stratigraphical range of *B. spectabilis* would cover MP30 to MN3 in case of synonymy. WERNER (1994: 95) explicitly comments that, in spite of the complexity of the dental pattern of this species, it shows very little variation. Given this stability of the dental pattern in *B. concavidens* we conclude that the more complex teeth from Banovići represent a different species.

*Bransatoglis fugax* HUGUENEY, 1967  
Pl. 2, Figs. 1–12

.2011 *Bransatoglis fugax* HUGUENEY, 1967. – DE LEEUW et al., p. 405, fig. 4.5–4.12.

Occurrences: *Bransatoglis fugax*: MP 30–MN1, MN4; *Bransatoglis cf. fugax*: MP27–MN1, MN4; *Bransatoglis aff. fugax* MP28–30.

Comparison material: *Bransatoglis fugax*, LNFM (France, AGUILAR 1977); *Bransatoglis fugax*, Plaisan (France, AGUILAR 1977); *Bransatoglis fugax*, Oberleitersbach (Germany, ENGESSER & STORCH 2008); *Bransatoglis cf. fugax*, Aliveri (Greece, VAN DER MEULEN & DE BRUIJN 1982); *Bransatoglis aff. fugax*, Eggingen-Mitt1/2+Erdb. (Germany, WERNER 1994).

Locality: Banovići (Bosnia and Herzegovina).

Material and measurements: 14 specimens (Pl. 2, Figs. 1–12; Tab. 3; Figs. 5–6). Catalogue numbers BAN441–445; BAN447; BAN449; BAN451–456; BAN458–459.

**Description.** – P4. The occlusal surface of the rather large P4 is oval. Its pattern consists of the four main ridges, a long anterior centroloph, a shorter posterior centroloph and one indistinct extra ridge between the protoloph and the anterior centroloph.

M1<sup>or</sup>2. Three out of five M1<sup>or</sup>2 seem to be M1. The pattern of these consists of the four main ridges, a long anterior centroloph that reaches the complete endoloph, a shorter posterior centroloph, one extra ridge between the protoloph and the anterior centroloph and another between the posterior centroloph and the metaloph. Two of the M1 are rather worn. In these it is difficult to establish whether or not there were additional ridges outside the trigon, but it seems there were none. In the only fresh specimen there is a low additional ridge between the anteroloph and the protoloph. This element is present in the two M2. The pattern of these M2 is more irregular than that of the M1.

M3. Both M3 are damaged on their labial side. The pattern of one is much more complex than that of the other.

The simple one shows the four main ridges, a long posterior centroloph that reaches the endoloph, a shorter anterior centroloph and probably an extra ridge between the posterior centroloph and the metaloph. The more complex M3 has moreover an additional ridge between the anteroloph and the protoloph and one on the labial side between the centrolophs.

p4. The rather large p4 shows the four main ridges and one extra ridge in the anterior as well as in the posterior valley.

m1. The two m1 share a pattern consisting of the four main ridges and an extra ridge in the anterior as well as in the posterior valley. The development of the centrolophid differs between these two specimens. In one it is interrupted in the middle, but very long and connected to the metaconid and the protoconid, in the other it is much shorter and neither connected to the metaconid, nor to the protoconid. This last m1 has a short additional ridge in the posterior valley.

m2. The dental pattern of the m2 consists of the four main ridges, a long centrolophid that reaches the protoconid in one of the two specimens and an extra ridge in the anterior as well as in the posterior valley.

m3. The m3 is as long as the m2. Apart from the somewhat shorter centrolophid the pattern is the same as in the m2.

**Discussion.** – The material of *Bransatoglis fugax* from Banovići resembles that from the Late Oligocene type locality Coderet-Bransat better than the rich material of *B. aff. fugax* from the Early Miocene of southern Germany (WERNER 1994). A feature that has not been reported from either of these assemblages is the occurrence of an extremely long centrolophid as in one m1 and one m2 from Banovići. Comparison of *B. fugax* specimens from Banovići with the teeth of that species from the Early Miocene of Aliveri (VAN DER MEULEN & DE BRUIJN 1982) shows that the latter are somewhat larger.

#### Subfamily Dryomyinae DE BRUIJN, 1967

**Remarks.** – Traditionally the Dryomyinae include the genera *Dryomys* PALLAS, 1778, *Eliomys* WAGNER, 1840, *Graphiurus* SMUTS, 1832, *Microdyromys* DE BRUIJN, 1966, *Glirulus* THOMAS, 1906, *Paraglrulus* ENGESSER, 1972, and *Graphiurops* BACHMAYER & WILSON, 1980. Species of these genera share dental features such as a moderately concave occlusal surface of the cheek teeth, extra ridges narrower than the main ridges and the presence of a complete endoloph in the M1<sup>o</sup>2. The rapidly improved fossil record during the last decades has raised doubts among specialists whether or not the Dryomyinae are a clade. FREUDENTHAL & MARTÍN-SUÁREZ (2007b), for instance, suggested that the genus *Microdyromys*, traditionally considered to be the core of the Dryomyinae (DAAMS & DE BRUIJN 1995), belongs

to the Bransatoglririnae. On the other hand the improved information on the variation within large assemblages of single species tends to blur the difference between genera such as *Microdyromys*, *Glirulus* and *Paraglrulus*, making the identification of these genera on the basis of small samples problematic.

#### Genus *Microdyromys* DE BRUIJN, 1966

**Species included:** *M. praemurinus* FREUDENBERG, 1941; *M. complicatus* DE BRUIJN, 1966; *M. koenigswaldi* DE BRUIJN, 1966 (?= *M. orientalis* WU, 1986); *M. monspeliensis* AGUILAR, 1977; *M. legidensis* DAAMS, 1981; *M. sinuosis* ALVAREZ SIERRA & GARCÍA MORENO, 1986; *M. hildebrandti* WERNER, 1994; *M. puntarronensis* FREUDENTHAL & MARTÍN SUÁREZ, 2007a; *M. remmertii* GARCÍA-PAREDES, PELÁEZ-CAMPOMANES & ÁLVAREZ-SIERRA, 2010.

#### *Microdyromys* cf. *monspeliensis* AGUILAR, 1977

Pl. 2, Figs. 13–24

.2011 *Microdyromys* cf. *monspeliensis* AGUILAR, 1977. – DE LEEUW et al., p. 405, fig. 4.13–4.20.

**Occurrences:** *Microdyromys monspeliensis*: MP30–MN2; *Microdyromys* cf. *monspeliensis*: MP30.

**Locality:** Banovići (Bosnia and Herzegovina).

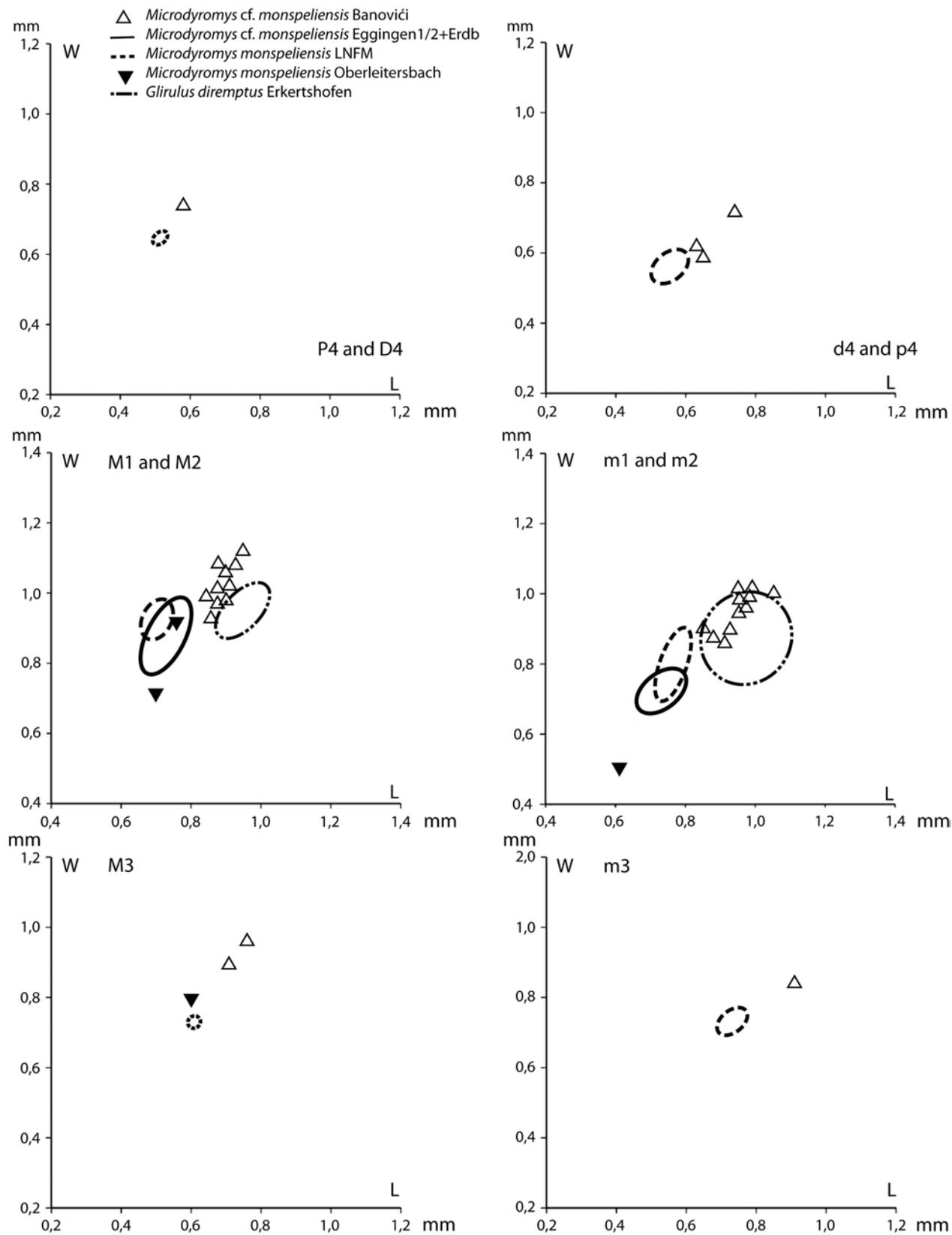
**Material and measurements:** 28 specimens (Pl. 2, Figs. 13–24; Tab. 4; Fig. 7). Catalogue numbers: BAN461; BAN463; BAN465–467; BAN471–489.

**Comparison material:** *Bransatoglis fugax*, LNFM (France, AGUILAR 19779; *Bransatoglis fugax*, Plaisan (France, AGUILAR 19779; *Bransatoglis fugax*, Oberleitersbach (Germany, ENGESSER & STORCH 20089; *Bransatoglis* cf. *fugax*, Aliveri (Greece, VAN DER MEULEN & DE BRUIJN 19829; *Bransatoglis* aff. *fugax*, Eggingen-Mitt1/2+Erdb. (Germany, WERNER 19949.

**Description.** – The enamel of all the cheek teeth extends far below the crowns, so the roots are situated on a small enamel-free area.

P4. The occlusal surface of the P4 has an oval circumference. The anteroloph is low and short. The protoloph and metaloph converge towards the protocone. The anterior centroloph is long, but the posterior one is absent. The metaloph and the posteroloph are connected labially as well as lingually.

M1<sup>o</sup>2. Seven out of the ten teeth in this category are probably M1. These teeth show a rather simple pattern consisting of the four main ridges, a long anterior centroloph, a shorter and weaker posterior centroloph that is often not connected to the metacone and a short extra ridge in the valley between the protoloph and the anterior centroloph. Two out of these seven M1 have an indistinct additional extra ridge in the anterior valley. Two of the three teeth identified as M2 have basically the same pattern as the M1, but the third is much more complex and does therefore not fit in the morphological variation expected in one species. The long extra ridges in the anterior and posterior valley have the modal morphology seen in *Glirulus diremptus* (MAYR, 1979).



**Fig. 7.** Scatter diagrams of length and width of the upper and lower molars of *Microdyromys cf. monspeliensis* from Banovići and Eggingen (Ger), of *Microdyromys monspeliensis* from LNFM (Fr.) and Oberleitersbach (Ger.) and of *Glirulus diremptus* from Erkerthofen (Ger.).

M3. The dental pattern of one of the two M3 is not clear due to wear. In the other specimen the transverse protoloph and metaloph are long, but the metaloph and posteroloph are short and oblique. The posterior centroloph is longer than the anterior centroloph and there is one extra ridge between the posterior centroloph and the metaloph.

p4. The dental pattern of the three p4 shows the four main ridges and an indistinct extra ridge in the posterior basin. The centrolophid is present in one specimen only. The p4 has one root.

m1. The m1 shows the four main ridges, a rather long centrolophid, which is not attached to the metaconid in two of the four specimens, and one extra ridge in the anterior as well as in the posterior valley. The m1 has two roots.

m2. The dental pattern of the m2 is basically the same as in the m1. In three of the seven specimens there is a very weak additional ridge. The position of this additional ridge varies. The m2 has two roots.

m3. The only m3 has a rather complex dental pattern. Its centrolophid is very long and reaches the labial border of the occlusal surface. In addition to the anterior and posterior extra ridge there is a weak ridge between the centrolophid and the metalophid and in the posterior valley. The m3 has three roots.

**Discussion.** – The assemblage of these small glirid teeth from Banovići is morphologically rather heterogeneous, but since there are intermediates between the extremes and there is no size difference between the simple and complex morphotypes, we consider them to represent one species. Since many specimens have the same size and morphology as *Microdyromys monspeliensis* we tentatively assign the assemblage to that species. The majority of the specimens is indistinguishable from the type material of *Microdyromys monspeliensis*, but some teeth show extra ridges that do not occur in the material from La Nouvelle Faculté de Médecine (MN1, AGUILAR 1977). In this respect the sample from Banovići is very similar to the collections from Eggingen-Mittelhart 1 and 2 and Eggingen-Erdbeerhecke (all MP30) described by WERNER (1994). The dental pattern of the M2 and the m3 figured on Plate 2 (Figs. 15, 24) are in fact reminiscent of those of *Glirulus diremptus* (MAYR, 1979), which suggests that the assemblages from Banovići and southern Germany possibly document populations that are transitional between *Microdyromys* and *Glirulus*.

Family Muridae ILLIGER, 1811

Subfamily incertae sedis

Genus *Deperetomys* MEIN & FREUDENTHAL, 1971

**Species included:** *Deperetomys hagni* (type species) (FAHLBUSCH, 1964); *Deperetomys intermedius* (DE BRUIJN et al., 1987); *Deperetomys anatolicus* DE BRUIJN et al., 1993; *Deperetomys magnus* n. sp.

**Occurrences:** *Deperetomys hagni*: Germany, Switzerland MN7–8; *Deperetomys intermedius*: Turkey Zone C (MN2); *Deperetomys anatolicus*: Turkey Zone B–C (MN1–2); *Deperetomys* sp.: Turkey Zone B–D (MN1–3).

**Remarks.** – *D. hagni* seems to be synonymous with *Cricetodon rhodanicus* DEPÉRET, 1887, which is known by the holotype M1 only (FAHLBUSCH in DE BRUIJN et al. 1993). Since this specimen comes from an unknown fissure near La Grive St. Alban (old collection) we do not synonymize the well documented *D. hagni* with the insufficiently known *D. rhodanicus* (see also PRIETO 2012) but consider the latter a nomen dubium.

Most, if not all, rodent specialists have classified *Deperetomys* in the Cricetodontinae sensu stricto. This opinion is supported by the occurrence in *Deperetomys* and *Cricetodon* of the same derived microstructure in the lower incisors (type 10, in KALTHOFF 2000). However, *Eumyarion* and *Enginia*, genera that are generally considered to be phylogenetically not closely related to *Cricetodon* and *Deperetomys*, share the same enamel structure. This suggests that this very characteristic enamel may have developed independently in different groups of Muridae.

Comparison of the cheek teeth of *D. magnus* with those of the dominant, but not yet described, cricetid from the Late Oligocene lignite deposit of Ugljevik, Bosnia and Herzegovina, shows that the dental pattern of the one may easily be derived from the other. Since this rodent, which teeth suggest affinities with the genus *Enginia*, is very different from the time equivalent *Cricetodon*, we conclude that *Deperetomys* and *Cricetodon* are probably not closely related, but acquired similar dentitions through convergent evolution. This interpretation is not entirely new, because it was suggested on other grounds by DE BRUIJN et al. in 1993, but we did not have any clue to the ancestry of *Deperetomys* at the time. The comparison of the dentitions of the cricetid from the Late Oligocene of Ugljevik, *Enginia gertcheki* DE BRUIJN & VON KOENIGSWALD, 1994 and *Deperetomys magnus* suggests that *Enginia* and *Deperetomys* share the same ancestor. One branch seems to have developed a dentition suggesting an exclusively herbivorous diet: *Enginia*, while the other acquired dental characters suggesting a mixed, probably more insectivorous, diet: *Deperetomys*.

Problem remains that, if the above reconstruction is correct, the systematic position of *D. anatolicus* is not understood, because it is much smaller than the other members of the genus. Pending new information we classify *Deperetomys* and *Enginia* as subfamily *incertae sedis*.

*Deperetomys magnus* n. sp.

Pl. 3, Figs. 25–27, Pl. 4, Figs. 1–8a

**Etymology:** Magnus means large in Latin.

**Holotype:** M1 dext., BAN121 (Pl. 4, Figs. 1, 1a)

**Paratypes:** 2 M1 (BAN122–123), 6 M2 (BAN122, 124, 126–130), 7 M3 (BAN131–134, 137–139), 6 m1 (BAN101–104, 117–118), 6 m2 (BAN105–109, 119), 4 m3 (BAN111–113, 115).

**Type locality:** Banovići, Bosnia and Herzegovina.

**Type level:** Late Oligocene.

**Measurements of the holotype:** 3.60 x 3.37 mm.

**Material and measurements:** 34 specimens (28 complete) (Pl. 3, Figs. 25–27, Pl. 4, Figs. 1–8a; Tab. 5; Fig. 8).

**Comparison material:** *Deperetomys hagni*, Giggerhausen (Germany, FAHLBUSCH 19649; *Deperetomys hagni*, Anwil (Switzerland, ENGESSER 19729; *Deperetomys hagni*, Kleineisenbach (Germany, DE BRUIJN et al. 1993); *Deperetomys intermedius*, Harami 1 (Turkey, DE BRUIJN et al. 1987); *Deperetomys anatolicus*, Kargı2; Kilcak 0" & 3a,b (Turkey, DE BRUIJN et al. 1993); *Enginia gertcheki*, Keseköy (Turkey, DE BRUIJN & VON KOENIGSWALD 1994); *Enginia djanpolati*, Kargı2; Kilcak 0" & 3a,b; Keseköy (Turkey, DE BRUIJN & VON KOENIGSWALD 1994). Catalogue numbers: BAN101–109; BAN111–113; BAN115; BAN117–119; BAN122–124; BAN126–134; BAN137–139.

**Diagnosis.** – *D. magnus* is a large *Deperetomys*. The anteroloph of the M1 has two sub-equal cusps. The ectoloph of the M1 and M2 is often incomplete. The mesoloph in the M1 is formed by the posterior arm of the protocone and variable in length. In the M3 the mesoloph is invariably long and reaches the labial outline of the occlusal surface. The metaloph of the M1 and of all except one M2 is directed posteriorly and connected to the posteroloph. The strong metaloph of the M3 is directed slightly forwards and connected to the anterior side of the hypocone.

The posterior arm of the protoconid and the mesolophid are both present in all except one m1. The lingual tips of these ridges are often connected, enclosing a small pit. The ectomesolophid is weaker from m1 through m3. A free-ending posterior arm of the hypoconid is present in some m1 only. In the others this ridge is fused with the posterolophid, which bears a rather strong hypoconulid.

**Differential diagnosis.** – *Deperetomys magnus* is the largest species of the genus. The size difference with the other rather large species, *D. intermedius* and *D. hagni*, is more pronounced in the second and third molars than in the M1/m1. The dental pattern of *D. magnus* resembles that of the much smaller *D. anatolicus*, except for the anterocone of the M1, which is more clearly bifid in *D. magnus*. Moreover, the posteroloph of the M2 and M3 and the metacone and metaloph of the M3 are not reduced in *D. magnus*.

The pattern of the lower molars of *D. magnus* is more primitive than in the other species of *Deperetomys*. The characteristic X-pattern in the m1, formed by the connec-

tions between protoconid/entoconid and between hypoconid/metaconid, is developed in one of the six specimens from Banovići only. In the others the posterior arm of the protoconid and the mesolophid are separate ridges. This primitive configuration is preserved in many m2 and some m3. The m3 of *D. magnus* is on average longer than the m2 and as long as the m1. In the other species of the genus the m3 is relatively smaller.

**Description.** – M1. Among the two and half M1 there is considerable variation in the development of the ectolophs. In the holotype and the broken specimen the ectoloph is weak and situated on the labial outline of the occlusal surface, while the posterior spur of the paracone is short and the anterior spur of the metacone is absent. In the third specimen the posterior spur of the paracone and the anterior spur of the metacone are strong and connected to the long mesoloph, forming a complete ectoloph. The strong anterior arm of the protocone (protolophule) is connected to the middle of the anterocone.

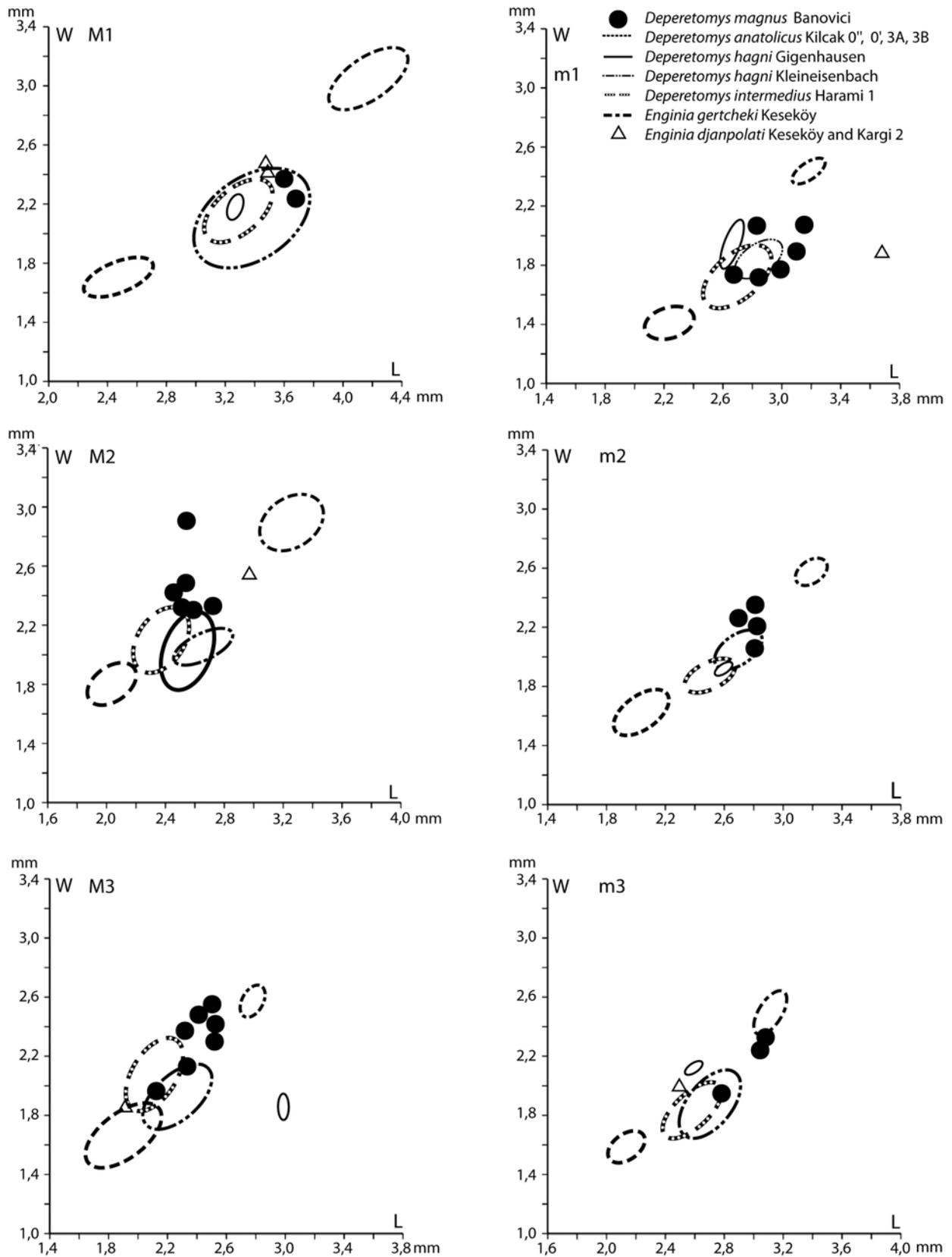
M2. Among the nine M2 there is a similar morphological variation as among the M1. Six M2 have a short posterior spur of the paracone, miss the anterior spur of the metacone and have a short mesoloph. The three other M2 have strong, burgee-shaped, spurs of the paracone and metacone that are connected to a long mesoloph, forming a complete ectoloph. The lingual branch of the anteroloph of the M2 is rather strong, which seems to be characteristic for the genus.

M3. Five of the seven M3 are large and hardly reduced posteriorly. In these the metaloph is strong and the posteroloph is separated from the metacone by a notch, while the mesoloph is long and reaches the labial outline of the occlusal surface. The two other M3 are more reduced posteriorly and the posteroloph is connected to the metacone. The posterior spur of the paracone is strong in all the seven M3.

m1. The unicuspid anteroconid of the m1 is symmetrical and situated on the longitudinal axis of the occlusal surface. The weak metalophid is connected to the anterolophid in four m1, in the other two it is directed more forwards and connects directly to the anteroconid. Five of the six m1 have a posterior arm of the protoconid as well as a rather long mesolophid. These two ridges often meet in the central basin. In one m1 these ridges seem to be fused. All the m1 have a rather well-developed hypoconulid. The ectomesolophid varies in length.

m2. The lingual branch of the anterolophid is high and encloses the anterosinusid. Four out of the six m2 have a strong posterior arm of the protoconid as well as a short mesolophid. In the other two m2 the posterior arm of the protoconid is long, but the mesolophid absent. The ectomesolophid is weak or absent.

m3. The relatively large m3 is similar to the m2. All the specimens have a strong posterior arm of the protoconid



**Fig. 8.** Scatter diagrams of length and width of the upper and lower molars of *Deperetomys magnus* n. sp. from Banovići and of relevant species from several other localities.

nid that may connect to the metaconid. Only one m3 has a short mesolophid as well as the posterior arm of the protoconid. The ectomesolophid is absent.

**Discussion.** – *Deperetomys magnus* is the largest and probably oldest member of the genus. Although there remains uncertainty about the identification of primitive and derived dental characteristics in Muridae because of parallel and convergent evolution in this very diverse family, we interpret the large, unreduced M3/m3 of *D. magnus* as primitive and the incipient development of the X-pattern formed by the protoconid/entoconid and hypoconid/metaconid connections in the m1 as derived.

#### Subfamily Eumyarioninae ÜNAY-BAYRAKTAR, 1989

**Genera included:** *Eumyarion* THALER, 1966; *Mirrabella* DE BRUIJN et al., 2007.

**Remarks.** – The allocation of *Mirrabella* to the Eumyarioninae is based on general resemblance of the dental pattern of *Mirrabella* and *Eumyarion* only, and is therefore tentative. The presence of true Eumyarioninae in China has never been proven, and *Alloeumyarion* from China (QIU 2010) is not included in this subfamily.

#### Genus *Mirrabella* DE BRUIJN, VAN DEN HOEK OSTENDE & DONOVAN, 2007

**Synonym:** *Mirabella* DE BRUIJN, ÜNAY, SARAÇ & KLEIN HOFMEIJER, 1987.

**Species included:** *Mirrabella tuberosa* (DE BRUIJN et al., 1987), type species; *Mirrabella anatolica* (DE BRUIJN & SARAÇ, 1992); *Mirrabella crenulata* (DE BRUIJN et al., 1992b); *Mirrabella hansoullii* (DOUKAS & THEOCHAROPOULOS, 1999).

**Occurrences:** *Mirrabella tuberosa*: Greece MN4, Turkey zone E (MN4); *Mirrabella* cf. *tuberosa*: Germany, MN4; Switzerland, MN4; *Mirrabella anatolica*: Turkey zone B and C (MN1–2); *Mirrabella crenulata*: Turkey zone D (MN3); *Mirrabella hansoullii*: Greece (Late Oligocene).

#### *Mirrabella* aff. *anatolica* (DE BRUIJN & SARAÇ, 1992) Pl. 2, Figs. 25–29

.2011 *Mirrabella* aff. *anatolica* (DE BRUIJN & SARAÇ, 1992). – DE LEEUW et al., p. 405, Fig. 4.21–4.23.

**Material and measurements:** 13 specimens (12 complete) (Pl. 2, Figs. 25–29; Tab. 6; Fig. 9). Catalogue numbers: BAN141–143; BAN145–147; BAN151–157.

**Comparison material:** *Mirrabella tuberosa*, Aliveri (Greece, DE BRUIJN et al. 1987); *Mirrabella anatolica*, Harami 1 (Turkey, DE BRUIJN & SARAÇ 1992); *Mirrabella crenulata*, Kesköy (Turkey, DE BRUIJN et al. 1992b); *Mirrabella hansoullii*, Kypirinos (Greece, DOUKAS & THEOCHAROPOULOS 1999).

**Description.** – M2. The lingual branch of the anteroloph of the rather robust M2 is absent. The proto-

phule 1 and 2 fuse in three out of four specimens at the longitudinal axis of the occlusal surface. In the fourth specimen the straight protolophule 1 and 2 reach the paracone independently. The paracone has a strong posterior spur, which is separated from the long mesoloph by a deep notch. The labial part of the mesoloph bends posteriorly and is connected to the metacone. The hypocone and the metacone are connected by a strong transverse metaloph in three M2, in the fourth specimen this connection is double. The posteroloph is connected to the base of the metacone.

M3. The occlusal surface of the M3 is almost round. The lingual sinus of the strongly reduced M3 is not developed and the hypocone is incorporated into the posteroloph. The protoloph, mesoloph and metaloph are narrow, and may be incomplete.

m1. The small anteroconid of the rather robust m1 is connected to the protoconid by the anterolophulid and to the metaconid by the metalophid 1. The metalophid 2 seems to be formed by the posterior arm of the protoconid. The endolophid is complete. The long mesolophid is connected to the endolophid. The strong, but narrow, hypolophid reaches the longitudinal ridge anterior of the hypoconid in two specimens, in the third it connects to the hypocone. The posterior arm of the hypoconid is long in the only unworn m1, in the two others it is fused into the posterolophid. The posterolophid ascends to the tip of the entoconid. The ectomesolophid is weak or absent.

m2. The labial branch of the anterolophid is weak. The straight metalophid is directed only slightly forwards and connects to the anterolophulid. The long mesolophid and posterior arm of the protoconid are connected by a short longitudinal ridge. The straight transverse hypolophid inserts on the anterior side of the hypoconid. The posterior arm of the hypoconid is long in the unworn specimen, in the two others it is incorporated into the posterolophid. The posterolophid ascends to the tip of the entoconid. The ectomesolophid is absent.

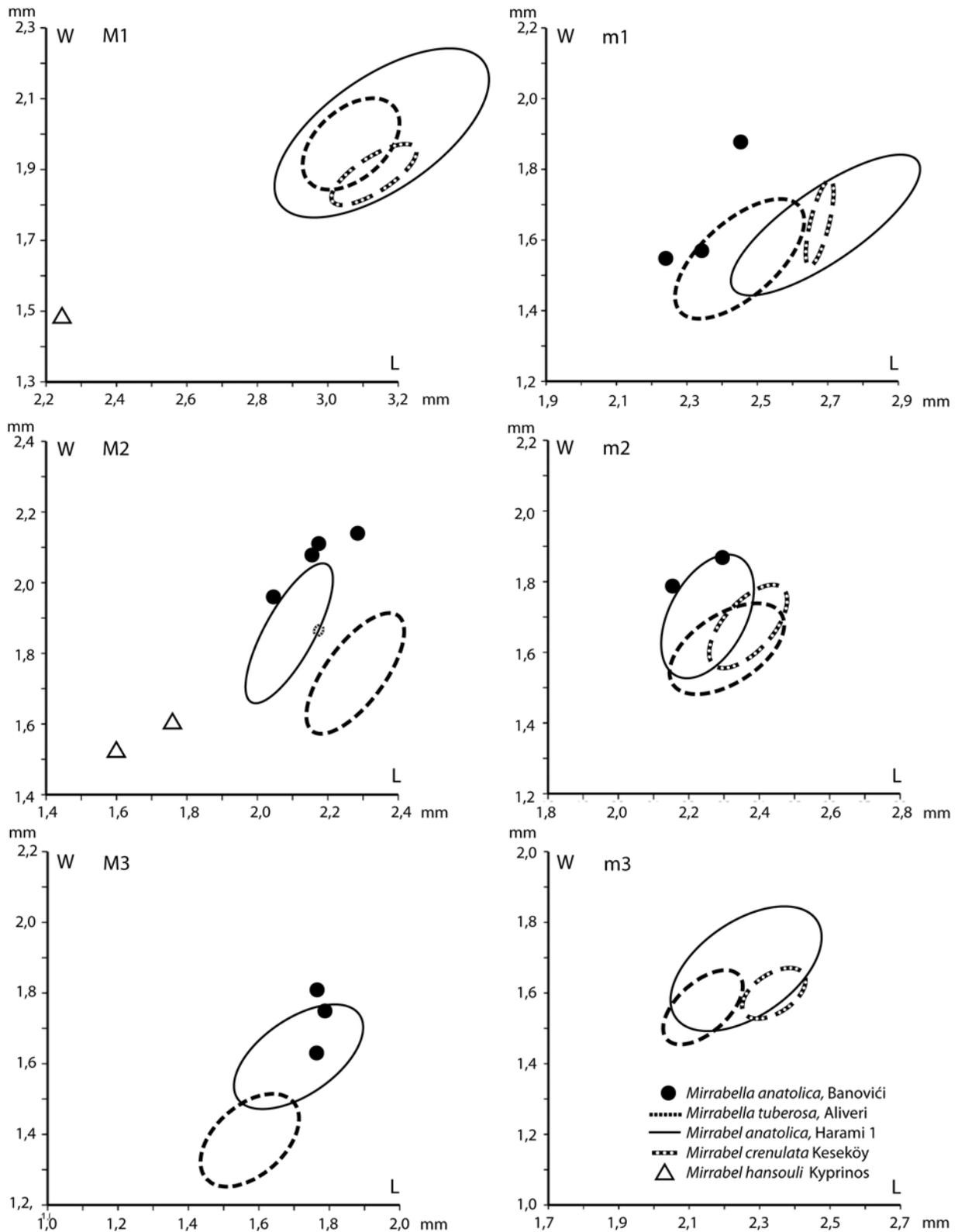
**Discussion.** – The teeth from Banovići resemble those of *M. anatolica*, but are more robust. Moreover, they differ from the type material of that species in a number of details. These differences are:

M2. Lingual branch of the anteroloph is almost absent. Metaloph 1 and 2 not interrupted. Metaloph not connected to the posterior spur of the paracone, but forming a loop that ascends to the metacone. Metaloph transverse and sometimes double.

M3. Dental pattern more reduced. M3 smaller relative to the M2. Lingual sinus hardly indicated.

m1. Posterior arm of the protoconid connected to the metaconid. Hypolophid narrow, straight and complete. Ectomesolophid weak or absent.

m2. Metalophid narrow, straight and complete. Posterior arm of the protoconid and mesolophid connected by a short longitudinal ridge. Ectomesolophid absent.



**Fig. 9.** Scatter diagrams of length and width of the upper and lower molars of *Mirabella* aff. *anatolica* from Banovići, *M. anatolica* from Harami 1 (Tur.), *Mirabella crenulata* from Keseköy (Tur.), *Mirabella tuberosa* from Aliveri (Gr.) and *Mirabella hansouli* from Kyprinos (Gr.).

The differences between the material from Banovići and the type material of its closest relative *M. anatolica* do not leave any doubt that it documents a different species. The material from Bosnia shows a number of primitive murid characteristics that are modified in the species from Anatolia, yet these teeth are more robust and the M3 is more reduced. The material does therefore not fit the evolutionary trend reconstructed on the basis of the various species from Anatolia and Greece. We refrain from formally naming the species from Banovići, because not all the tooth positions are represented in our collection and the variation in dental pattern is inadequately known.

#### Genus *Eumyarion* THALER, 1966

Species included: *Eumyarion medius* (LARTET, 1851); *Eumyarion weinfurteri* (SCHAUB & ZAPPE, 1953); *Eumyarion latior* (SCHAUB & ZAPPE, 1953); *Eumyarion bifidus* (FAHLBUSCH, 1964); *Eumyarion leemanni* (HARTENBERGER, 1965a); *Eumyarion carbonicus* DE BRUIJN & SARAÇ, 1991; *Eumyarion montanus* DE BRUIJN & SARAÇ, 1991; *Eumyarion microps* DE BRUIJN & SARAÇ, 1991; *Eumyarion* aff. *microps* DE BRUIJN & SARAÇ, 1991; *Eumyarion intercentralis* DE BRUIJN & SARAÇ, 1991; *Eumyarion orhani* DE BRUIJN, MAYDA, VAN DEN HOEK OSTENDE, KAYA & SARAÇ, 2006; *Eumyarion* sp. in ÜNAY et al. (2003b).

Remarks. – The geologically oldest finds of cheek teeth that have been allocated to *Eumyarion* sp. are from the locality Kargi 2 (Oligo/Miocene boundary interval, local zone B (ÜNAY et al. 2003b) in Anatolia, while the oldest species based on adequate collections: *E. carbonicus* and *E. microps* were described from Harami 1 (zone C) (DE BRUIJN & SARAÇ 1991). Although these species have a much more primitive dental pattern than the type species *E. medius* their allocation to the genus *Eumyarion* has not been in doubt so far. The allocation of the new species from Banovići to *Eumyarion* is uncertain because we noticed that similar *Eumyarion* species from the Early Miocene of Anatolia, *E. carbonicus* and *E. microps* (DE BRUIJN & SARAÇ 1991) show a strong resemblance to species from the Early Oligocene of Spain that have been allocated to *Atavocricetodon* by FREUDENTHAL (1996). This raises the question of how to distinguish these two genera. However, a detailed analysis of the possible generic identity of *Eumyarion* and *Atavocricetodon* is beyond the scope of this paper. We decided to follow DE BRUIJN & SARAÇ (1991) for the time being and allocate the material from Banovići to *Eumyarion*.

#### *Eumyarion margueritae* n. sp. Pl. 3, Figs. 1–12

Etymology: This species is named after our colleague Dr. MARGUERITE HUGUENEY (Lyon) acknowledging her work on fossil rodents.

Holotype: M1 sin., BAN231 (Pl. 3, Fig. 2).

Paratypes: 8 M1 (BAN232–233, 236–240), 13 M2 (BAN241–249, 251–254), 9 M3 (BAN261–264, 266–270), 8 m1 (BAN201–206, 208–210), 8 m2 (BAN211–213, 215–219), 9 m3 (BAN221–225, 227–230).

Type locality: Banovići (Bosnia and Herzegovina).

Type level: Late Oligocene.

Measurements of holotype: 2.23 x 1.38 mm.

Material and measurements: 55 specimens (53 complete). (Pl. 3, Figs. 1–12; Tab. 7; Fig. 10). Catalogue numbers: BAN201–206; BAN208–213; BAN215–219; BAN221–225; BAN227–230; BAN232–233; BAN236–249; BAN251–254; BAN261–264; BAN266–270.

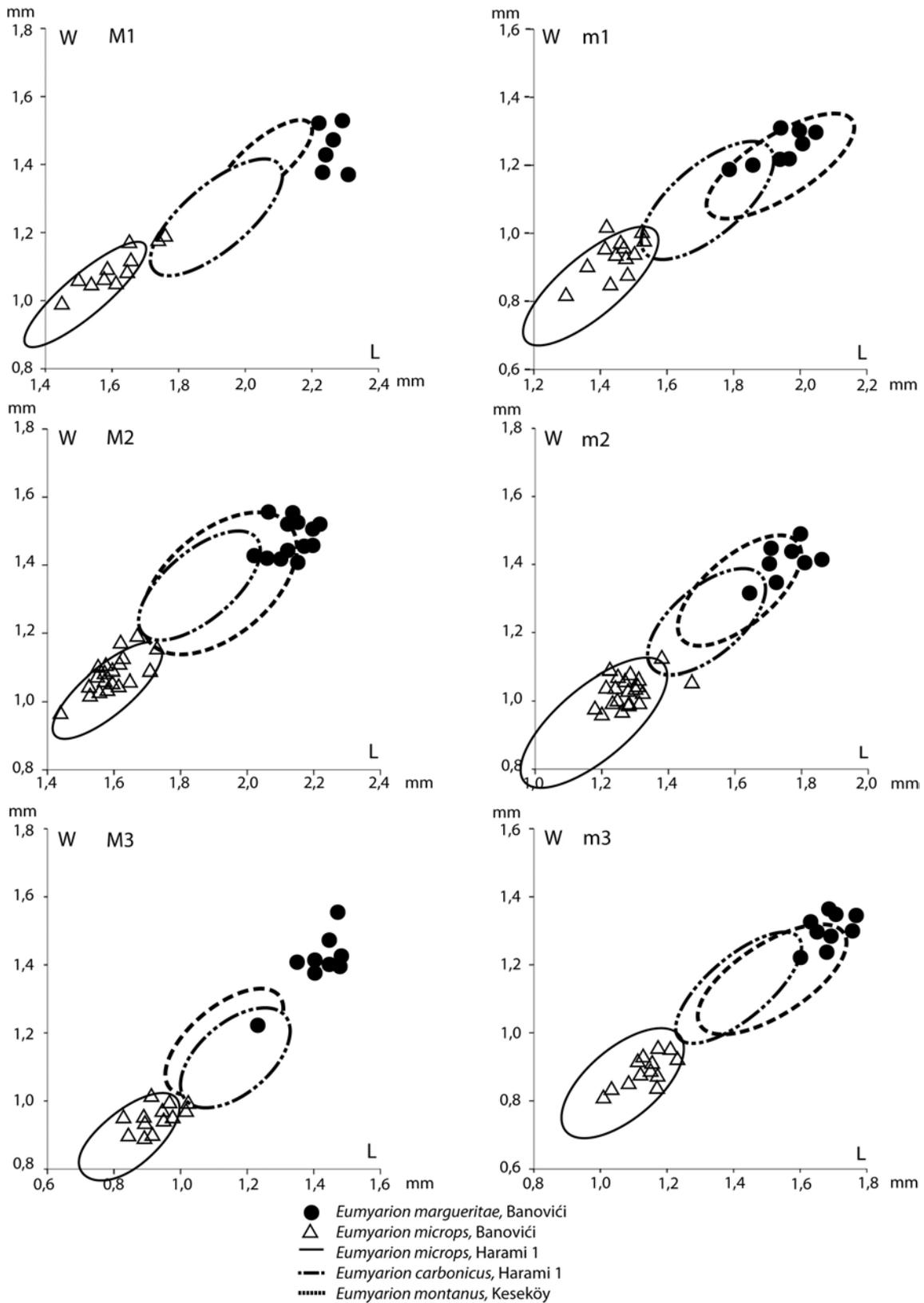
Comparison material: Same as species included.

Diagnosis. – The anteroloph of the M1 is crescent-shaped and has a rather labial position. The short protoloph (anterior arm of the protocone) forms a weak connection between the protocone and the paracone of the M1. The protolophule 1 and 2 of the M2 are usually well developed, but either one may be absent. The lingual and labial branches of the M2 are strong. The posterior spur of the paracone of the M1 and M2 shows much variation, in some specimens it is long and burgee-shaped, in others it is short or almost absent. The posterior arm of the hypoconid is short or absent in the m1 and m2, always absent in the m3.

Differential diagnosis. – Among the primitive *Eumyarion* species, which have slender, “not inflated”, cusps *E. margaritae* is on average somewhat larger than *E. carbonicus* and *E. montanus*, but there is overlap in size. The M1 and m1 of *E. margueritae* are shorter relative to the M2 and m2 of the latter two species. The crescent-shaped anterocone, weak protoloph and usually strong paracone spur of the M1 makes this tooth readily distinguishable from the M1 of all other *Eumyarion* species. The M2 with its strong lingual branch of the anteroloph, often double protolophule and strong posterior spur of the paracone is quite characteristic also. The short posterior arm of the protoconid that is connected to the metaconid in the m1 is a characteristic that is shared with *E. carbonicus* and *E. montanus*, but these species have much stronger posterior arms of the hypoconid in all lower molars.

Description. – M1. The anterocone of the M1 is crescent-shaped has a long labial branch, that reaches the paracone, and a much weaker lingual branch. The anterior arm of the protocone is usually short and may be absent. In most specimens this spur is connected to the base of the paracone forming a protolophule 1, but in one M1 it ends free as in *Atavocricetodon*. The complete protolophule 2 inserts on the longitudinal ridge behind the protocone. The length of the posterior spur of the paracone and of the mesoloph shows considerable variation.

M2. The lingual and labial branch of the anteroloph are about equally long. The protolophule 1 and 2 are complete



**Fig. 10.** Scatter diagrams of length and width of the upper and lower molars of *Eumyarion margueritae* n. sp. and *E. microps* from Banovići, *E. microps* and *E. carbonicus* from Harami (Tur.) and *E. montanus* from Keseköy (Tur.).

in seven out of the twelve M2. In the three others the protolophule 1 is present only, while the remaining two M2 have a poorly developed constricted protolophule 2. The length of the posterior spur of the paracone and of the mesoloph is variable as in the M1.

M3. The majority of the M3 show the same pattern as all other *Eumyarion* species: the sinus is closed by a new connection between the protocone and the hypocone and the posterior part is reduced. One specimen has been less affected by this reduction than any *Eumyarion* M3 we have seen (Pl. 3, Fig. 5). In many M3 the metacone is not entirely incorporated into the posteroloph.

m1. The small centrally placed anteroconid is much lower than the protoconid and metaconid, which gives these teeth a slender appearance. The often weak metalophulid 1 connects the metaconid to the anteroconid. The anterior arm of the protoconid shows a good deal of variation: In some m1 it is absent, in others it forms a metalophulid 2 and in still others it forms a rather strong, straight, connection between the protoconid and anteroconid. The short posterior arm of the protoconid connects the protoconid to the base of the metaconid in most specimens. The longitudinal ridge is very low and weak. The mesolophid is short or absent, but the ectomesolophid is present in all m1. The hypolophid inserts on the longitudinal ridge just in front of the hypoconid. The posterior arm of the hypoconid connects the hypoconid and the posterolophid in six out of eight m1. A short, free ending posterior arm of the hypoconid is present in only one specimen and this ridge connects the hypoconid with the entoconid in another (Pl. 3, Fig. 8).

m2. The m2 of *E. margueritae* is not characteristic for this species. The length of the posterior arm of the protoconid and of the mesolophid is very variable. A short free-ending posterior arm of the hypoconid is present in three out of seven m2.

m3. The m3 is relatively long and has, in contrast to the m1 and m2 a well-developed longitudinal ridge and posterior arm of the protoconid. The mesolophid and the posterior arm of the hypoconid are absent in all m3.

*Eumyarion microps* DE BRUIJN & SARAÇ, 1991  
Pl. 3, Figs. 13–24

.2011 *Eumyarion microps* DE BRUIJN & SARAÇ, 1991. – DE LEEUW et al., p. 405, Fig. 4.24–4.29.

Occurrences: *Eumyarion microps* Harami 1 (Zone C, Turkey), *Eumyarion aff microps*, Harami 3 (Zone C, Turkey).

Comparison material: *Eumyarion margueritae*, Banović (Bosnia and Herzegovina); *Eumyarion* sp., Kargı 2 (Turkey, ÜNAY et al. 2003b); *Eumyarion microps*, Harami 1 (Turkey, DE BRUIJN & SARAÇ 1991); *Eumyarion aff microps*, Harami 3 (Turkey, DE BRUIJN & SARAÇ 1991); *Eumyarion carbonicus*, Harami 1 (Turkey, DE BRUIJN & SARAÇ 1991); *Eumyarion montanus*, Keseköy (Turkey, DE BRUIJN & SARAÇ 1991).

Material and measurements: 96 specimens (89 complete) (Pl. 3, Figs. 13–24; Tab. 8; Fig. 10). Catalogue numbers: BAN271–274; BAN281–288; BAN291–295; BAN301–323; BAN331–348; BAN351–357; BAN361–378; BAN381–386; BAN391–397.

Description. – M1. The anterocone of the M1 is wide. In some specimens the anterocone is rounded anteriorly, in others its anterior face is rather flat. In these there is a tendency to divide the anterocone into two cusps. The short anterior arm of the protocone often connects to the base of the paracone, forming a weak protolophule 1. The weak protolophule 2 inserts just behind the protocone. The posterior spur of the paracone is long and burgee-shaped in some M1, but short in others. The mesoloph, which is formed by the anterior arm of the hypocone is of medium length and reaches the posterior spur of the paracone in only one out of fifteen specimens. The metaloph is curved forwards and inserts on the hypocone or on the longitudinal ridge just in front of the hypocone.

M2. The labial branch of the anteroloph is much longer than the lingual branch. The strong protolophule 1 is directed forwards in seventeen of the eighteen M2 and inserts in front of the protocone. In one specimen this ridge is interrupted and a protolophule 2 is developed (Pl. 3, Fig. 15). A very indistinct and incomplete protolophule 2 is present in a few other M2 also. The posterior spur of the paracone is either short or absent. The mesoloph is long and reaches the labial outline of the occlusal surface in five out of eighteen M2. The metaloph is consistently directed forwards and inserts on the anterior arm of the hypocone.

M3. The dental pattern of the M3 is quite variable. The lingual sinus is weak and the new connection between the protocone and the reduced hypocone is present in all specimens. In some M3 remnants of the mesoloph are preserved, in others the mesoloph is absent.

m1. The small pointed anteroconid of the m1 is connected to the metaconid by the short forwards directed metalophulid 1. The labial branch of the anteroconid does not reach the protoconid. The short posterior arm of the protoconid forms a metalophulid 2 in eleven m1, in the two remaining specimens this ridge ends free in the main basin. The mesolophid and ectomesolophid are short or absent. The short transverse hypolophid inserts on the longitudinal ridge in front of the hypocone. The posterior arm of the hypoconid is strong and ends free.

m2. The labial branch of the anterolophid is stronger than the lingual branch. The forwards directed metalophulid 1 inserts on the anterolophulid or on the anterolophid. The posterior arm of the protoconid ends free in eighteen out of twenty specimens, in the remaining two it forms a metalophulid 2. The mesolophid is short and the ectomesolophid is absent.

m3. The anteriorly directed metalophid inserts in some m3 on the anterolophulid, but in others on the anterolophid.

The posterior arm of the protoconid is long in most specimens. The mesolophid and ectomesolophid are absent. The entoconid is incorporated into the complete endolophid. The posterior arm of the hypoconid is absent.

**Discussion.** – The cheek teeth of *E. microps* from Banovići are on average somewhat larger than the ones from the type locality, but there is considerable overlap. There are some subtle differences in dental pattern between the two associations also, but these are all a matter of degree. These differences are:

- The anterior arm of the protocone and the mesoloph of the M1 are shorter.
- The metalophule 1 of the M2 inserts on average more anteriorly and the mesoloph of these teeth is shorter.
- The metalophulid 2, mesolophid and ectomesolophid of the m1 are less well developed.
- The mesolophid of the m2 is on average shorter.

The differences listed above are, considering the large geographical distance between Harami and Banovići, small and do not warrant, in our opinion, the distinction of different species.

#### Subfamily Spalacinae GRAY, 1821

**Genera included:** *Spalax* GÜLDENSTÄDT, 1770 (including *Nannospalax* PALMER, 1903); *Pliospalax* KORMOS, 1932 (including *Sinapospalax* SARICA & SEN, 2003); *Heramys* KLEIN HOFMEIJER & DE BRUIJN, 1985; *Debruijnia* ÜNAY, 1996; *Vetusspalax* n. gen.

**Occurrences of fossil species:** *Pliospalax*: Turkey Zone E–O (MN 4–16); Ukraine MN10; Greece MN14–16; Romania MN15. *Heramys*: Greece MN4. *Debruijnia*: Turkey Zone D–E (MN3–4).

#### Genus *Vetusspalax* nov.

**Etymology:** “Vetus” means old in Latin.

**Type species:** *Vetusspalax progressus* n. sp.

**Comparison material:** Same as *V. progressus*.

**Diagnosis.** – *Vetusspalax* is a small spalacid with semi-hypsodont cheek teeth. The cusps are distinct and higher than the lophs in unworn molars. The dental pattern is complex in unworn molars, but becomes soon simple by wear through fusion of lophs. The small indistinctly bifid anterocone of the M1 is not incorporated into the anteroloph and situated labially. The lingual sinus of the M3 remains open until a late wear stage. The metaconid of the m1 is situated far forward. The tiny anteroconid of the m1 is situated labially of the metaconid. A free ending posterior arm of the hypoconid is present in almost all m1, but has not been observed in the m2 and m3. The m1 and the m3 have about the same length.

**Differential diagnosis.** – *Vetusspalax* is readily distinguishable from *Spalax*, *Pliospalax* and *Heramys*

by the presence of a large number of primitive murid dental characteristics. Most striking among these is that the cusps are not incorporated into the lophs in unworn molars.

*Vetusspalax* differs from *Debruijnia* in having a relatively much narrower and smaller anterocone of the M1. The metaloph of the M1 and M2 is generally connected to the posteroloph in *Vetusspalax*, but to the hypocone in *Debruijnia*. The lingual sinus of the M3 of *Vetusspalax* remains open until a late wear stage, in *Debruijnia* this sinus is usually closed even in fresh teeth. The anteroconid of the m1 is very small and situated labially of the metaconid in *Vetusspalax*, in *Debruijnia* this cusp is larger and less retracted. The free ending posterior arm of the hypoconid of the m1 is shorter in *Vetusspalax* than in *Debruijnia*, while this loph seems to be absent in the m2.

#### *Vetusspalax progressus* n. sp.

Pl. 5, Figs. 1–12

**Etymology:** “Progressus” means to move forwards in Latin.

**Holotype:** M1 sin., BAN181 (Pl. 5, Figs. 1, 1a).

**Paratypes:** 3 M1 (BAN182–184), 8 M2 (BAN185–191, 198), 4 M3 (BAN192–194, 196), 9 m1 (BAN161–169), 4 m2 (BAN171–173, 178), 4 m3 (BAN174–177).

**Type locality:** Banovići (Bosnia and Herzegovina).

**Type level:** Late Oligocene.

**Measurements of the holotype:** 2.25 x 1.72 mm.

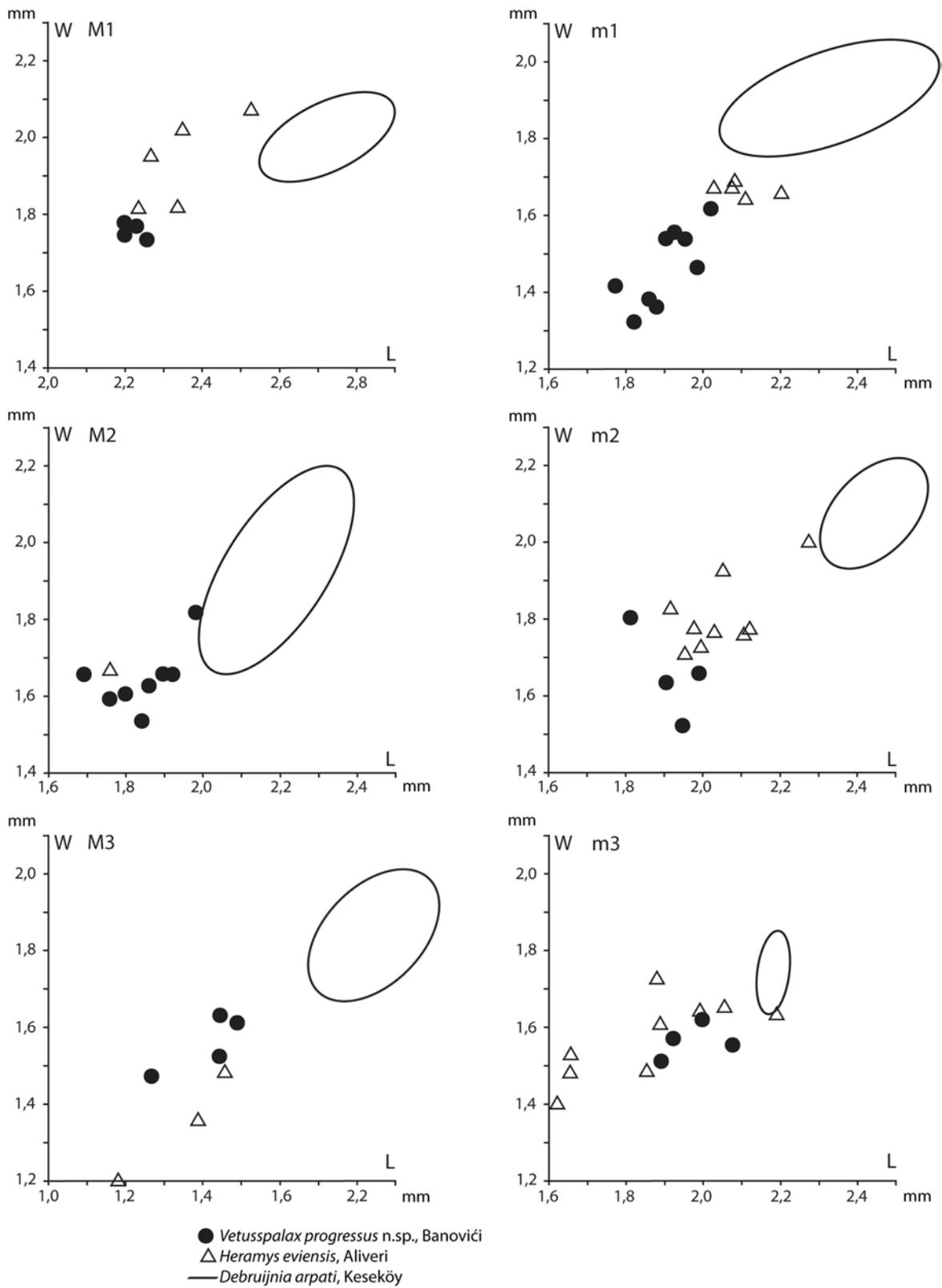
**Material and measurements:** 33 specimens (Pl. 5, Figs. 1–12; Tab. 9; Fig. 11). Catalogue numbers: BAN161–169; BAN171–178; BAN181–194; BAN196; BAN198.

**Comparison material:** *Debruijnia arpati*, Keseköy (Turkey, ÜNAY 1996); *Heramys eviensis*, Aliveri (Greece, KLEIN-HOFMEIJER & DE BRUIJN 1985).

**Diagnosis and differential diagnosis:** Same as for the genus.

**Description.** – M1. The small anterocone of the M1 is indistinctly divided into two cusps and not incorporated into the anteroloph. The forwards directed lingual sinus is deep and extends to close to the crown base. The short protoloph inserts on the longitudinal ridge just behind the protocone. The metaloph is directed posteriorly and connected to the posteroloph in three out of the four M1. In the fourth specimen the metaloph is irregular and connects to the hypocone. The mesoloph is long in two M1 and of medium length in the two others.

M2. The lingual branch of the anteroloph is absent, but the labial branch remains until a very advanced stage of wear. The transverse protoloph connects the paracone to the protocone. The metaloph of five out of seven M2 is directed posteriorly and connected to the posteroloph in five out of the seven M2, in the other two it connects the metacone to the hypocone. The deep lingual sinus reaches almost to the base of the crown. The mesoloph is of medium



**Fig. 11.** Scatter diagrams of length and width of the upper and lower molars of *Vetusspalax progressus* n. sp., *Debruijnina arpati* from Keseköy (Gr.) and *Heramys eviensis* from Aliveri (Tur.).

length. The dental pattern of the M2 becomes much simpler in late wear stages due to fusion of the anteroloph, the protoloph and the mesoloph. The result is an S-pattern formed by the forwards directed lingual sinus and the backwards directed labial sinus. This situation is remarkably similar to that seen in M2 of geologically younger spalacids.

M3. The lingual branch of the anteroloph is absent, but the labial branch is wide and short. The protoloph is directed forwards and connects to the protocone. The posterior part is reduced and the short metaloph fuses with the posteroloph in an early rear stage. The narrow lingual sinus of the M3 is always open. In one specimen the longitudinal ridge is interrupted and the lingual- and labial sinus are confluent.

m1. The very small anteroconid of the m1 is hardly more than a low labial spur of the metaconid. The metaconid is situated more forwards than the protoconid, a very unusual position for any murid. The metaconid and the protoconid are connected by a low, rather irregular, and sometimes incomplete ridge. The posterior arm of the protoconid and the mesolophid meet in the main basin. A short ectomesolophid is present in the majority of the m1. Four out of the seven rather fresh specimens have a free-ending posterior arm of the hypoconid. In worn specimens only two sinusids remain: A lingual one directly behind the metaconid and a labial one between the protoconid and the hypoconid.

m2. The dental pattern of fresh m2 is very similar to that of a number of other semi-hypsodont generalized murids, but the metalophid and the anterolophid are fused and form one ridge. The mesolophid is short. The hypolophid is transverse and inserts on the longitudinal ridge in front of the hypoconid. The free-ending posterior arm of the hypoconid, which is common in the m1, is absent in the m2.

m3. The dental pattern of the m3 has more original murid characteristics than the m2, because the forwards directed metalophid is not fused with the anterolophid until a late wear stage. The posterior arm of the protoconid is long, the mesolophid absent. Worn specimens show an s-pattern through fusion of lophids and the disappearance of the postero-lingual sinusid.

**Discussion.** – The dentition of the small *Vetusspalax progressus* shows a mixture of primitive and derived characteristics. The small bifid, labially situated, anterocone of the M1 and the peculiar metaconid/anteroconid complex of the m1 are interpreted as primitive for Spalacinae and make *Vetusspalax* very different from all other spalacinae. Other primitive characteristics that distinguish *Vetusspalax* are in our opinion that the m1 and m3 have the same length and that the lingual sinus of the M3 is open. In contrast, the posteriorly directed metalophs of the majority of the M1 and M2 and the development of an s-pattern in the M2 and m2 through wear as in geologically younger

members of the subfamily are interpreted as derived.

We conclude therefore that the evolutionary history of the Spalacinae is probably much more complex than has been suggested so far. *Vetusspalax progressus* is the smallest, and probably geologically oldest, member of the Spalacinae, but its phylogenetic position within the subfamily and the identity of the ancestor of the subfamily among the Paleogene Muridae remain unresolved.

#### 4. Comparison of Banovići with Anatolian and Central European rodent faunas

##### Faunal list of Banovići:

##### Order Rodentia

##### Family Sciuridae

- Palaeosciurus* aff. *P. feignouxi* POMEL, 1853
- ?*Ratufa obtusidens* DEHM, 1950

##### Family Gliridae

##### Subfamily Bransatoglirinae

- Bransatoglis bosniensis* n. sp.
- Bransatoglis fugax* HUGUENEY, 1967

##### Subfamily Dryomyinae

- Microdyromys* cf. *monspeliensis* AGUILAR, 1977

##### Family Muridae

##### Subfamily incertae sedis

- Deperetomys magnus* n. sp.

##### Subfamily Eumyarioninae ÜNAY-BAYRAKTAR, 1989

- Mirrabella* aff. *anatolica* (DE BRUIJN & SARAÇ, 1992)
- Eumyarion margueritae* n. sp.

- Eumyarion microps* DE BRUIJN & SARAÇ, 1991

##### Subfamily Spalacinae GRAY, 1821

- Vetusspalax progressus* n. gen. n. sp.

The Muridae, with five species belonging to four genera, dominate the Banovići assemblage in diversity as well as in number of specimens (N=164; 80%). The Gliridae are with three species of two genera the second in importance (N=37; 18%) and the Sciuridae with two genera and two species are rare (N=6; 2%).

The general composition of the assemblage is very similar to the ones from the Early Miocene of Anatolia (Fig. 11; Tab. 1). However, this similarity is clearer on genus level than on species level. Similarities on species level are most marked within the Sciuridae and Gliridae. *Palaeosciurus* aff. *feignouxi* seems to be a new species intermediate in size between the smaller *P. goti* from Germany (MP 30), and the larger *P. feignouxi* from France and Spain (MP30). The Gliridae are represented in the association from Banovići by two species of *Bransatoglis* and a species of *Microdyromys*. *Bransatoglis fugax* is very similar to the type material from Coderet (MP30; France), but differs from *B. aff. fugax* from the Early Miocene of southern Germany (WERNER 1994). *Microdyromys* cf. *monspeliensis* is very similar to the material from Eggingen-Mittelhart 1 and 2 and Eggingen-Erdbeerhecke (all MP30, Germany).

Similarities with Anatolian assemblages at genus level are highest within the Muridae such as the genera *Deperetomys*, *Mirrabella* and *Eumyarion*. These genera are absent from the Late Oligocene and Early Miocene of Western Europe. However, the species of these genera from Banovići do not fit previously reconstructed evolutionary trends. They combine primitive and derived features and seem to represent the oldest member of their genus or even family. Examples are: *Deperetomys magnus*, which is the largest yet probably oldest member of the genus, *Mirrabella* aff. *anatolica* which does not fit the evolutionary trend reconstructed on the basis of the various species from

Anatolia and Greece, and *Vetusspalax progressus* which is the smallest, probably geologically oldest, member of the Spalacinae but has some derived dental characters. This suggests that the evolutionary history of the Spalacinae is much more complex than thought so far.

In Late Oligocene rodent assemblages from Western Europe members of the Theridomyidae and Eomyidae are always present. However, these are absent in the Banovići assemblage as well as in the Anatolian ones. In this aspect the Banovići assemblage is more similar to roughly time equivalent Anatolian rodent assemblages than to European ones.

MP/MN zones	Europe						Anatolia						Local zones
	<i>Palaeosciurus feignouxii</i>	? <i>Ratufa obtusidens</i>	<i>Bransatoglis fugax</i>	<i>Microdyromys</i> cf. <i>monspeliensis</i>	<i>Mirrabella anatolica</i>	<i>Eumyarion microps</i>	<i>Palaeosciurus feignouxii</i>	? <i>Ratufa obtusidens</i>	<i>Bransatoglis fugax</i>	<i>Microdyromys</i> cf. <i>monspeliensis</i>	<i>Mirrabella anatolica</i>	<i>Eumyarion microps</i>	
3		█		█	—	—		—	—	—			D
2	█	█		█	—	—		—	—	—	█	█	C
1	█		█	█	—	—	█	—	—	—	█	█	B
30	█		█	█	—	—		—	—	—			A

Fig. 12. Six out of the ten rodent species recognized in Banovići are known from Europe and/or Anatolia; the stratigraphical ranges are relative to the European MP/MN scheme and the preliminary Anatolian zonation (DE BRUIJN et al. 1992a; FORTELIUS 2010; KOUFOS 2003; REUMER & WESSELS 2003; SCHMIDT-KITTLER et al. 1987; THEOCHAROPOULOS 2000; ÜNAY et al. 2003a, b; WERNER 1994).

## 5. Biogeography

The resemblance of the Banovići rodent assemblage and the ones from Anatolia indicate that the Dinaride region was stronger connected to Anatolia during the Late Oligocene than to Western Europe.

The presence of Gliridae in the Late Oligocene of Western Europe, the Dinaride region and Anatolia indicate a distribution event. However, the absence of Theridomyidae and Eomyidae in the Dinaride region and in Anatolia indicate that such a faunal exchange was highly selective and restricted.

The combination of primitive and derived features in several species from Banovići, some representing the oldest member of their genus, suggests that this part of the Dinaride region was intermittently an isolated area with its own typical evolutionary development of rodents.

## 6. Age of the assemblage

A straightforward correlation with the western European sequence is difficult due to the absence in Banovići of the Eomyidae and Theridomyidae. The Eomyidae are well represented in Western Europe in the Late Oligocene and Early Miocene, and are good markers in the biostratigraphy. The Theridomyidae are dominant in Western Europe until the Late Oligocene, and then rapidly diminish in diversity and abundance to become extinct in the Early Miocene, this coincides with the appearance and rapid distribution of Lagomorpha all over Western Europe (ENGESSER & STORCH 2008).

Correlation of the Banovići assemblage to more eastern areas is problematic since the Oligocene/Miocene rodent fauna from the east coast of the Paratethys (BENDUKIDZE et al. 2009) appears to be very different.

Six out of the ten rodent species recognized in Banovići are known from Europe and/or Anatolia. Figure 12 gives the stratigraphical ranges of these species relative to the European MP/MN scheme and the preliminary Anatolian zonation (ÜNAY et al. 2003a, b).

The best fit of the assemblage from Banovići is with MP30 in Europe and zone B in Anatolia. This correlation is further supported by the presence of the new *Bransatoglis* species, which resembles *B. concavidens* (MP30), the new *Deperetomys* species which is more primitive than *D. intermedius* from zone C, *Eumyarion margueritae* that resembles *E. carbonicus* from zone C and the new spalacid that is in many respects more primitive than the hitherto oldest spalacid *Debruijnina arpatii* from the zone D.

On the basis of the rodent fauna we conclude that the Banovići assemblage is older than locality Harami 1 (Turkey, zone C), which has been correlated to chron C6Bn.2n of the magnetic polarity time scale by KRIJGSMAN et al. (1996b). The rodent assemblage from Banovići seems to

be of about the same age or somewhat younger than that from Coderet (France), Late Oligocene (MP30; HUGUENEY 1969; SCHMIDT-KITTLER et al. 1987). We interpret the Banovići assemblage as top MP30/base MN1, even though the absence of similar faunas, the lack of Eomyidae and the presence of new species hamper exact correlation.

Magnetostratigraphy of the Grivice section, 6 km east of the Turija section, in combination with the biostratigraphical age of the Banovići assemblage correlates the sediments of the Banovići basin to the C6Cr to C6Cn.2n interval of the GPTS. This correlation (DE LEEUW et al. 2011) indicates that the infill of the basin started shortly after 24 Ma and lasted until ~23 Ma.

## 7. References

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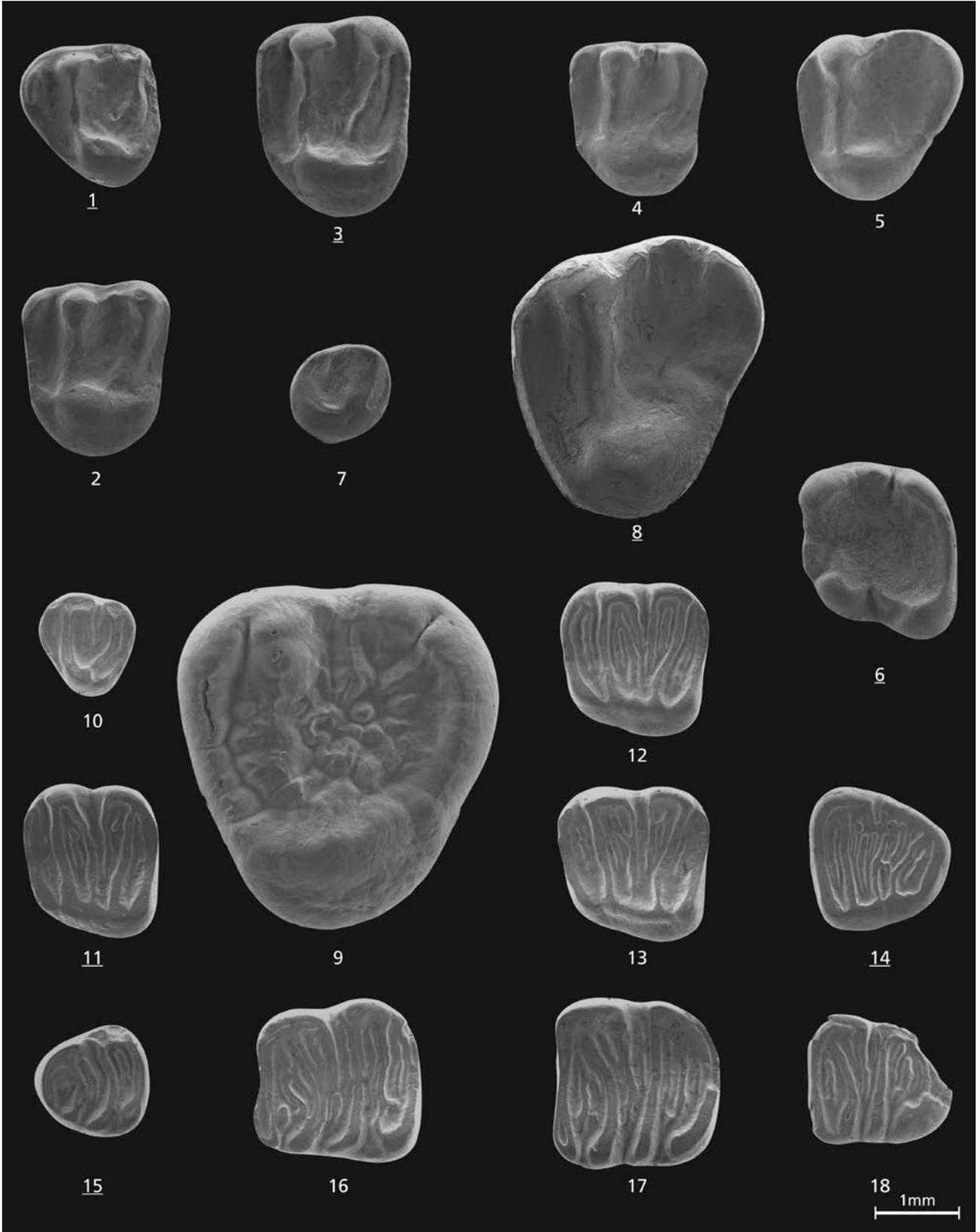
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**Plate 1**

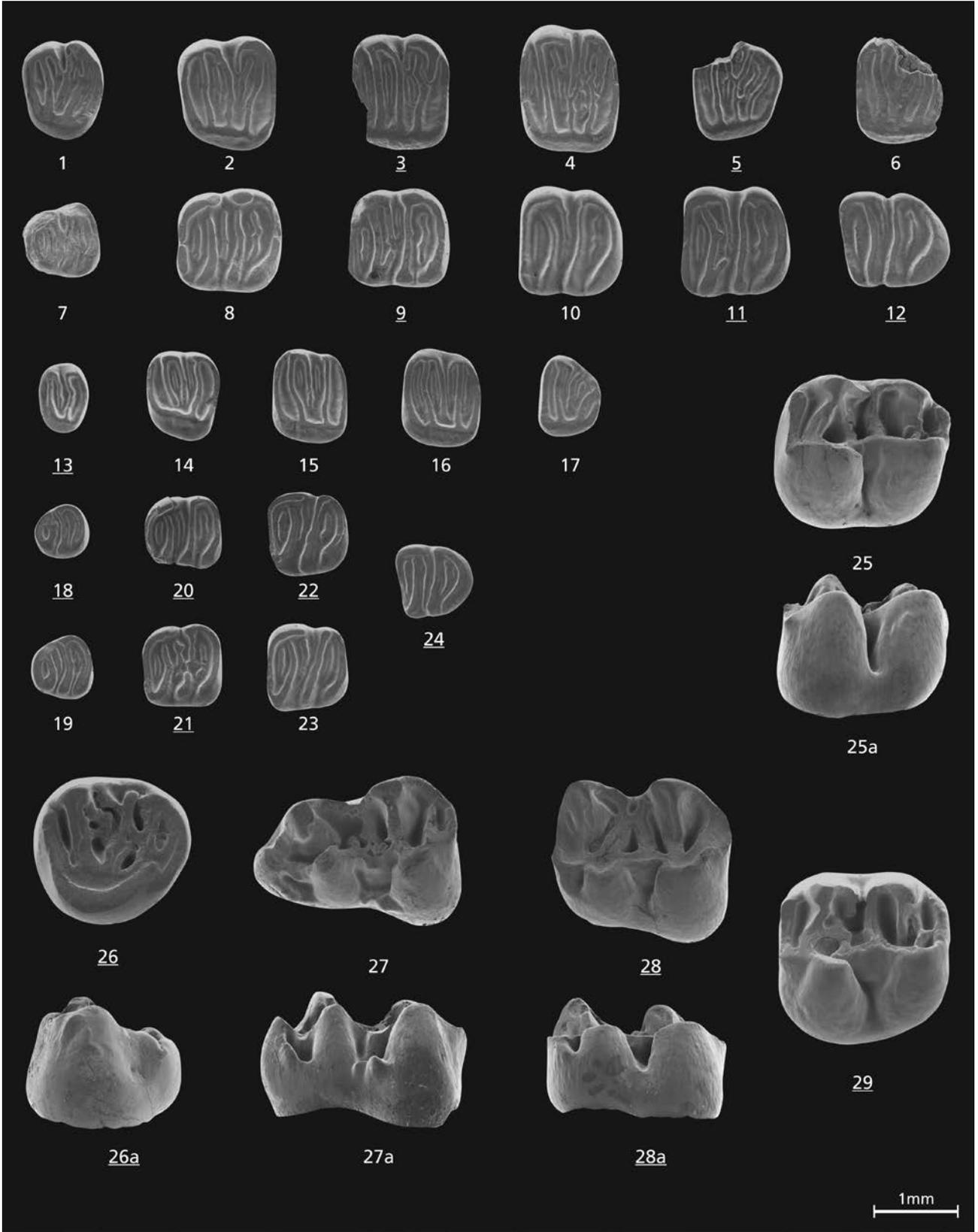
*Palaeosciurus* aff. *feignouxi*.

**Fig. 1.** D4; BAN413 dex, **Figs. 2-4.** M1-2; BAN417sin, BAN415dex, BAN416sin, **Fig. 5.** M3; BAN419sin, **Fig. 6.** m1; BAN411dex. *?Ratufa obtusidens*. **Fig. 7.** P3; BAN403?, **Fig. 8.** M3; BAN401dex. *Bransatoglis bosniensis* n. sp. **Fig. 10.** D4; BAN431sin, **Figs. 11-12.** M1; BAN434dex, BAN432, **Fig. 13.** M1 holotype; BAN433sin, **Fig. 14.** M3; BAN438dex, **Fig. 15.** p4; 421BANdex, **Fig. 16.** m1; BAN424sin, **Fig. 17.** m2; BAN427sin, **Fig. 18.** m3; BAN429sin. All from Banovići (Bosnia and Herzegovina). *Ratufa bicolor*. **Fig. 9.** M3sin, Utrecht Pleistocene collection; fissure filling on Java (Indonesia). – Scale bar is 1 mm. Underlined numbers are inverse.



**Plate 2***Bransatoglis fugax*

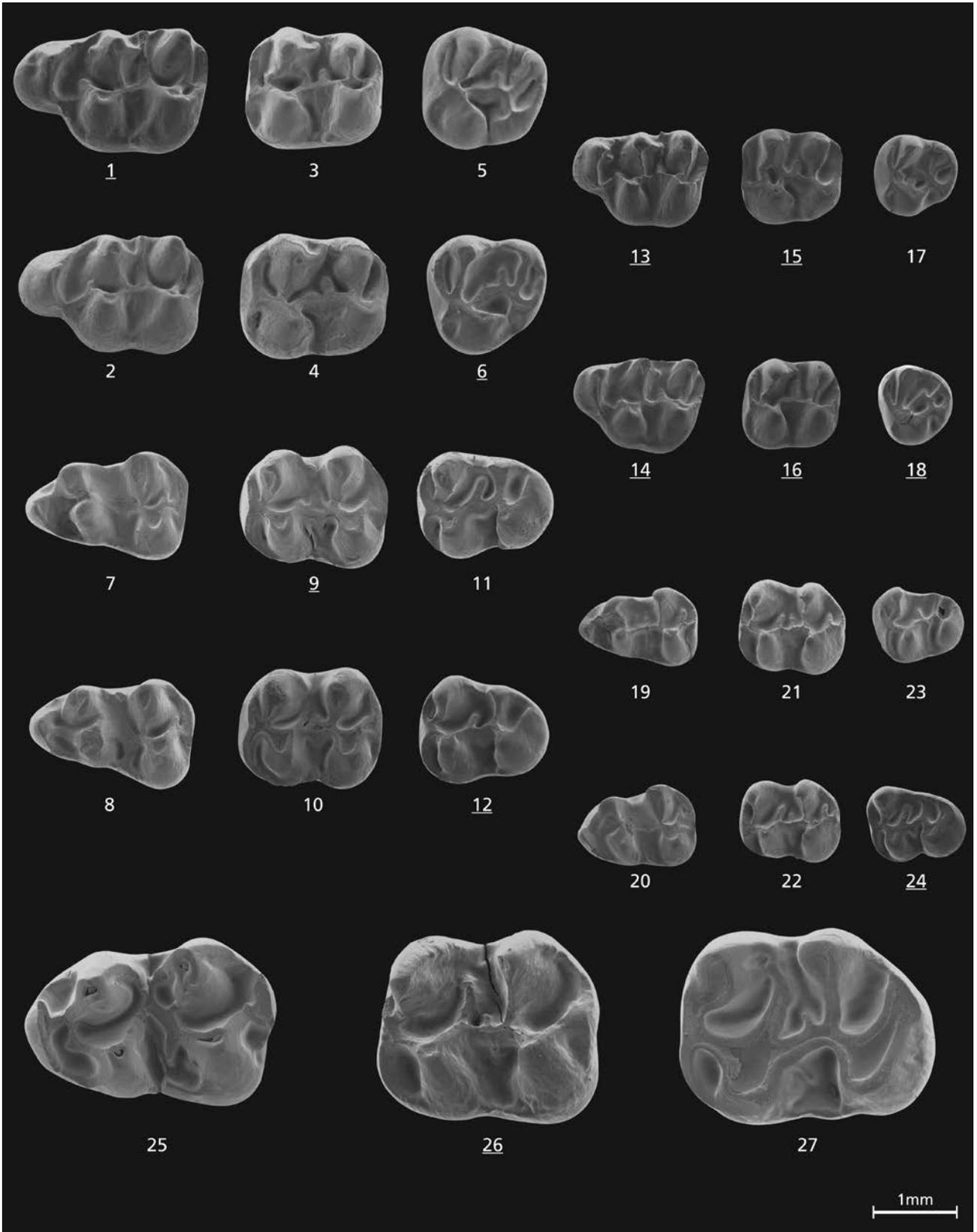
**Fig. 1.** P4; BAN451dex, **Fig. 2.** M1; BAN452sin, **Figs. 3–4.** M2; BAN456dex, BAN455sin, **Figs. 5–6.** M3; BAN459dex, BAN458sin, **Fig. 7.** p4; BAN441sin, **Figs. 8–9.** m1; BAN443sin, BAN442dex, **Figs. 10–11.** m2; BAN444sin, BAN445dex, **Fig. 12.** m3; BAN-447dex. *Microdyromys* cf. *monspeliensis*. **Fig. 13.** P4; BAN461dex, **Figs. 14–16.** M1-2; BAN482sin, BAN487sin, BAN486sin, **Fig. 17.** M3; BAN489sin, **Figs. 18–19.** p4; BAN471dex, BAN472sin, **Figs. 20–21.** m1; BAN474dex, BAN473dex, **Figs. 22–23.** m2; BAN-479dex, 475sin, **Fig. 24.** m3; BAN480dex. *Mirabella* aff. *anatolica*. **Figs. 25, 25a, 29.** M2; BAN153sin, BAN154dex, **Figs. 26, 26a.** M3; BAN157dex, **Figs. 27–27a.** m1; BAN141sin, **Figs. 28–28a.** m2; BAN147dex. All from Banovići (Bosnia and Herzegovina). Lingual view in Fig. 25a, 26a, and labial view in 27a, 28a. – Scale bar is 1 mm. Underlined numbers are inverse.



**Plate 3**

*Eumyarion margueritae* n. sp.

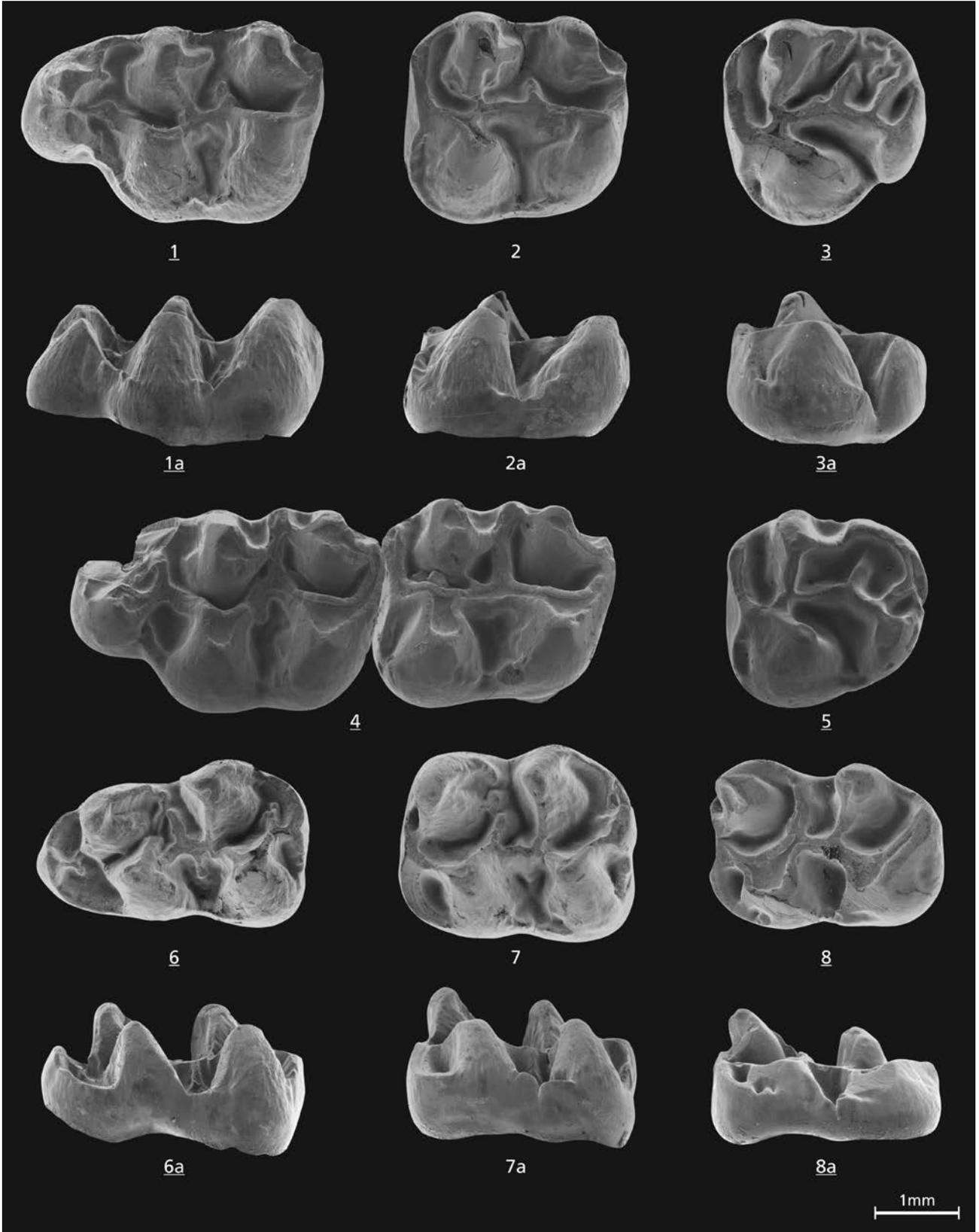
**Fig. 1.** M1; BAN237dex. **Fig. 2.** M1 holotype; BAN231sin. **Figs. 3–4.** M2; BAN241sin, BAN245sin, **Figs 5–6.** M3; BAN268sin, BAN-261dex, **Figs. 7–8.** m1; BAN201sin, BAN209dex, **Figs. 9–10.** m2; BAN219dex, BAN211sin, **Figs. 11–12.** m3; BAN221sin, BAN-230dex. *Eumyarion microps*. **Figs. 13–14.** M1; BAN351dex, BAN356dex, **Figs. 15–16.** M2; BAN273dex, BAN371dex, **Figs. 17–18.** M3; BAN383sin, BAN391dex, **Figs. 19–20.** m1; BAN281sin, BAN284sin, **Figs. 21–22.** m2; BAN301sin, BAN305sin, **Figs. 23–24.** m3; BAN321sin, BAN331dex. *Deperetomys magnus*. **Fig. 25.** m1; BAN101sin. **Fig. 26.** m2; BAN107dex, **Fig. 27.** m3; BAN111sin. All from Banovići (Bosnia and Herzegovina). – Scale bar is 1 mm. Underlined numbers are inverse.



**Plate 4**

*Deperetomys magnus* n. sp.

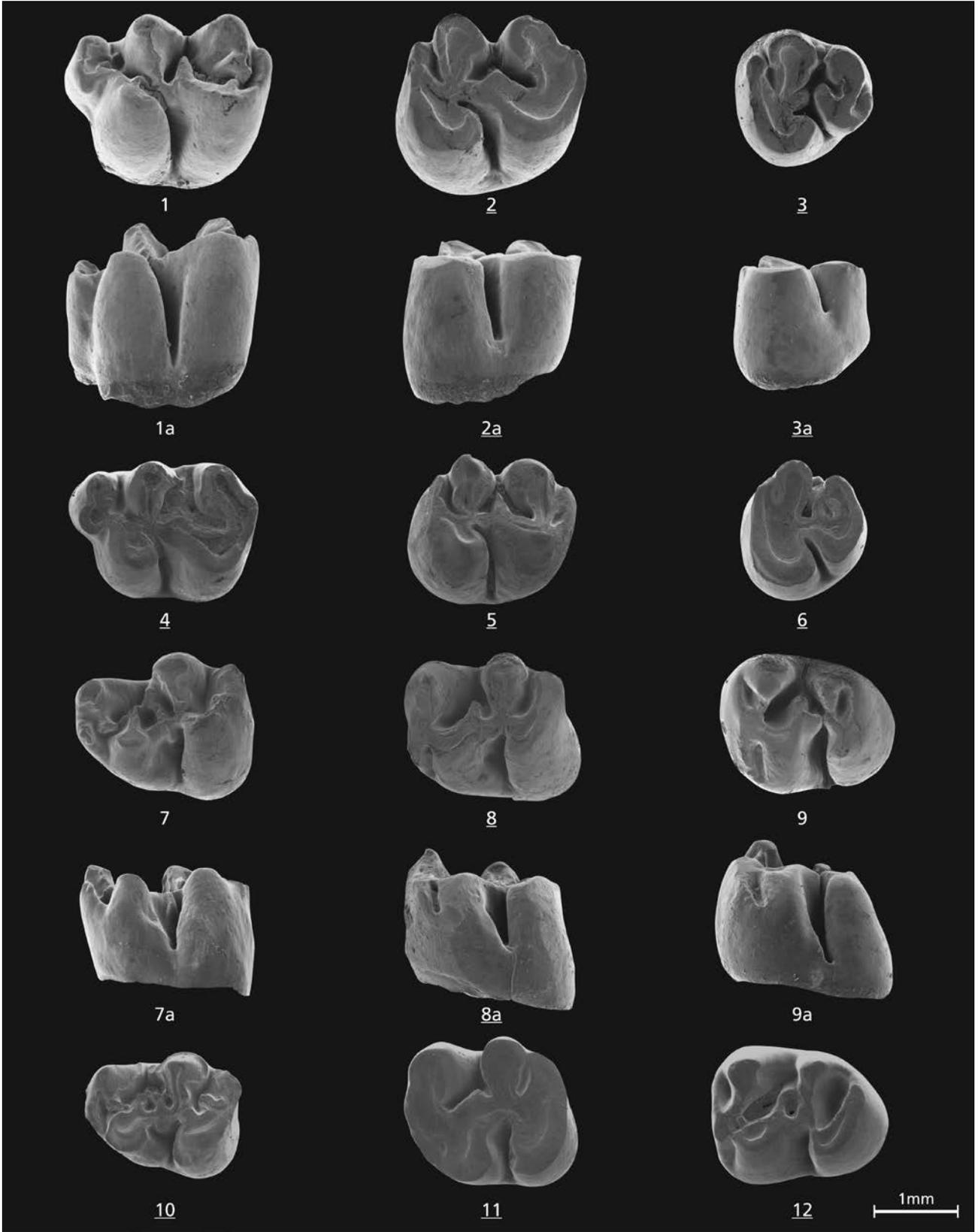
**Figs. 1, 1a.** M1 holotype; BAN121dex, **Figs. 2, 2a.** M2; BAN126sin, **Figs. 3, 3a.** M3; BAN131dex, **Fig. 4.** M1–M2 (same individual); BAN122dex, **Fig. 5.** M3, BAN132dex, **Figs. 6, 6a.** m1; BAN101dex, **Figs. 7, 7a.** m2; BAN107sin, **Figs. 8, 8a.** m3; BAN111dex. All from Banovići (Bosnia and Herzegovina). Lingual view in Fig. 1a, 2a, 3a and labial view in 6a, 7a, 8a. – Scale bar is 1 mm. Underlined numbers are inverse.



**Plate 5**

*Vetusspalax progressus* n. gen. n. sp.

**Figs. 1, 1a.** M1; holotype; BAN181sin, **Figs. 2, 2a.** M2; BAN191dex, **Figs. 3, 3a.** M3; BAN192dex, **Fig. 4.** M1; BAN184dex, **Fig. 5.** M2; BAN188dex, **Fig. 6.** M3; BAN196dex, **Figs. 7, 7a.** m1; BAN161sin, **Figs. 8, 8a.** m2; BAN171dex, **Figs. 9, 9a.** m3; BAN174sin, **Fig. 10.** m1; BAN164dex, **Fig. 11.** m2; BAN172dex, **Fig. 12.** m3; BAN175dex. All from Banovići (Bosnia and Herzegovina). Lingual view in Fig. 1a, 2a, 3a and labial view in 7a, 8a, 9a. – Scale bar is 1 mm. Underlined numbers are inverse.



## Appendix I. – Detailed data on the occurrences of the mentioned species.

Genus	species	Locality	MN/MP unit	Reference
<i>Palaeosciurus</i>	<i>feignouxi</i>	Coderet	MP30	HUGUENEY 1969
<i>Palaeosciurus</i>	<i>feignouxi</i>	Eggingen	MP30	WERNER 1994
<i>Palaeosciurus</i>	<i>feignouxi</i>	Santa Cilia	MP30	ÁLVAREZ-SIERRA et al. 1990
<i>Palaeosciurus</i>	<i>feignouxi</i>	Kılçak 3a	Zone B	This paper
<i>Palaeosciurus</i>	<i>feignouxi</i>	Cluzel	MN2a	HUGUENEY 1974
<i>Palaeosciurus</i>	<i>feignouxi</i>	Montaigu-le-Blin	MN2a	Collection UU / WERNER 1994
<i>Palaeosciurus</i>	<i>feignouxi</i>	Saint-Gérard-le-Puy	MN2a	VIANEY-LIAUD 1974
<i>Palaeosciurus</i>	sp. (cf. <i>feignouxi</i> )	Ulm-Westtangente	MN2a	WERNER 1994
<i>Palaeosciurus</i>	<i>goti</i>	Aubrelong 1	MP21	VIANEY-LIAUD 1974
<i>Palaeosciurus</i>	<i>goti</i>	La Plante 2	MP22	VIANEY-LIAUD 1974
<i>Palaeosciurus</i>	<i>goti</i>	Mas-de-Got	MP22	VIANEY-LIAUD 1974
<i>Palaeosciurus</i>	<i>goti</i>	Mège	MP22	VIANEY-LIAUD 1974
<i>Palaeosciurus</i>	<i>goti</i>	Pech Crabit	MP23	VIANEY-LIAUD 1974
<i>Palaeosciurus</i>	<i>goti</i>	Roqueprune 2	MP23	VIANEY-LIAUD 1974
<i>Palaeosciurus</i>	<i>goti</i>	Oberleitersbach	MP30	ENGESSER & STORCH 2008
<i>Palaeosciurus</i>	aff. <i>goti</i>	Herrlingen 8	MP28	ZIEGLER 1994
<i>Ratufa</i>	<i>maelongensis</i>	Li Mae Long	MN4	MEIN & Ginsburg 1997
? <i>Ratufa</i>	<i>obtusidens</i>	Ulm Westtangente	MN2a	WERNER 1994
? <i>Ratufa</i>	<i>obtusidens</i>	Tuchoriche	MN3	FEJFAR et al. 2003
? <i>Ratufa</i>	<i>obtusidens</i>	Wintershof west	MN3	DEHM 1950
? <i>Ratufa</i>	<i>obtusidens</i>	El Canyet	MN4	ALDANA CARRASCO 1992
? <i>Ratufa</i>	<i>obtusidens</i>	Hambach 6C	MN6	MÖRS 2002
? <i>Ratufa</i>	sp.	Oberdorf	MN4	DE BRUIJN 1998
? <i>Ratufa</i>	sp.	Belchatów B	MN5	KOWALSKI 1997
<i>Bransatoglis</i>	<i>adroveri</i>	Paguera	MP23-24	HUGUENEY 1997
<i>Bransatoglis</i>	<i>complicatus</i>	Harami 1	Zone C	ÜNAY 1994
<i>Bransatoglis</i>	<i>complicatus</i>	Kılçak 3 b, 0", 3A	Zone B	ÜNAY 1994
<i>Bransatoglis</i>	<i>concauidens</i>	Coderet	MP30	HUGUENEY 1969
<i>Bransatoglis</i>	<i>fugax</i>	Coderet	MP30	HUGUENEY 1969
<i>Bransatoglis</i>	<i>fugax</i>	LNFM France	MN1	AGUILAR 1977
<i>Bransatoglis</i>	<i>fugax</i>	Oberleitersbach	MP30	ENGESSER & STORCH 2008
<i>Bransatoglis</i>	<i>fugax</i>	Plaisan	MN1	AGUILAR 1977
<i>Bransatoglis</i>	aff. <i>fugax</i>	Eggingen-Mittelhart1/2 + Erdbeerhecke	MP30	WERNER 1994
<i>Bransatoglis</i>	cf. <i>fugax</i>	Aliveri	MN4	VAN DER MEULEN & DE BRUIJN 1982
<i>Bransatoglis</i>	<i>spectabilis</i>	Wintershof-West	MN3	DEHM 1950
<i>Glirulurus</i>	<i>direptus</i>	Affalterbach	MN5	MAYR 1979
<i>Microdyromys</i>	<i>monspeliensis</i>	LNFM France	MN1	AGUILAR 1977
<i>Microdyromys</i>	<i>monspeliensis</i>	Oberleitersbach	MP30	ENGESSER & STORCH 2008
<i>Microdyromys</i>	cf. <i>monspeliensis</i>	Eggingen-Mittelhart1/2 + Erdbeerhecke	MP30	WERNER 1994

## Appendix I. (Continued)

Genus	species	Locality	MN/MP unit	Reference
<i>Deperetomys</i>	<i>anatolicus</i>	Kılçak 0", 3 A, 3B	Zone B-C	DE BRUIJN et al. 1993
<i>Deperetomys</i>	<i>hagni</i>	Anwil	MN 7/8	ENGESSER 1972
<i>Deperetomys</i>	<i>hagni</i>	Giggenhausen	MN7/8	FAHLBUSCH 1964
<i>Deperetomys</i>	<i>hagni</i>	Kleineisenbach	MN 7/8	DE BRUIJN et al. 1993
<i>Deperetomys</i>	<i>hagni</i>	Petersbuch 48	MN 7/8	PRIETO 2012
<i>Deperetomys</i>	<i>hagni</i>	Mörgen	MN 7/8	SEEHUBER 2009
<i>Deperetomys</i>	<i>intermedius</i>	Harami 1	Zone C	DE BRUIJN et al. 1993
<i>Enginia</i>	<i>djanpolati</i>	Keseköy	Zone D	DE BRUIJN & VON KOENIGSWALD 1994
<i>Enginia</i>	<i>gertcheiki</i>	Keseköy	Zone D	DE BRUIJN & VON KOENIGSWALD 1994
<i>Enginia</i>	<i>beckerplateni</i>	Kargi 2	Zone B	DE BRUIJN & VON KOENIGSWALD 1994
<i>Mirrabella</i>	<i>anatolica</i>	Harami 1	Zone C	DE BRUIJN & SARAÇ 1992
<i>Mirrabella</i>	<i>crenulata</i>	Keseköy	Zone D	DE BRUIJN et al. 1992b
<i>Mirrabella</i>	<i>hansoulii</i>	Kyprinos	Late Oligocene	DOUKAS & THEOCHAROPOULOS 1999
<i>Mirrabella</i>	<i>tuberosa</i>	Aliveri	MN4	DE BRUIJN et al. 1987
<i>Mirrabella</i>	<i>tuberosa</i>	Kaplangı	Zone E	ÜNAY et al. 2003
<i>Mirrabella</i>	<i>cf. tuberosa</i>	Reimbach	MN4	DE BRUIJN & SARAÇ 1992; DE BRUIJN et al. 2007
<i>Mirrabella</i>	<i>cf. tuberosa</i>	Reiden-Sertel	MN4?	DE BRUIJN & SARAÇ 1992
<i>Eumyarion</i>	<i>carbonicus</i>	Harami 1	Zone C	DE BRUIJN & SARAÇ 1991
<i>Eumyarion</i>	<i>microps</i>	Harami 1	Zone C	DE BRUIJN & SARAÇ 1991
<i>Eumyarion</i>	<i>aff. microps</i>	Harami 3	Zone C	DE BRUIJN & SARAÇ 1991
<i>Eumyarion</i>	<i>montanus</i>	Keseköy	Zone D	DE BRUIJN & SARAÇ 1991
<i>Eumyarion</i>	<i>sp.</i>	Kargi 2	Zone B	ÜNAY et al. 2003
<i>Eumyarion</i>	<i>orhanie</i>	Sabuncubeli	Zone C	DE BRUIJN et al. 2006
<i>Debruijnia</i>	<i>arpai</i>	Keseköy	Zone D	ÜNAY 1996
<i>Heramys</i>	<i>eviensis</i>	Aliveri	MN4	KLEIN HOFMEIJER & DE BRUIJN 1985

Table 1. Measurements (in mm) of *Palaeosciurus* aff. *feignouxi* (POMEL, 1853).

	Length			Width	
	range	mean	N	mean	range
D4	1.63–1.69	1.66	2	1.70	1.68–1.72
M1 <sup>or</sup> 2	1.66–1.90	1.78	3	2.01	1.75–2.27
M3		1.94	1	2.04	
m1		1.87	1	1.98	
m2		2.10	1	2.27	

**Table 2.** Measurements (in mm) of *Bransatoglis bosniensis* n. sp.

	Length		N	Width	
	range	mean		mean	range
D4		1.15	1	1.18	
M1 <sup>or</sup> 2	1.62–1.80	1.73	3	1.78	1.77–1.79
M3	1.56–1.65	1.61	2/1	1.65	
p4	1.37–1.39	1.38	2	1.28	1.22–1.33
m1		1.98	1	1.85	
m2	1.75–1.99	1.86	3/1	1.97	
m3		1.74	1	1.48	

**Table 3.** Measurements (in mm) of *Bransatoglis fugax* HUGUENEY, 1967.

	Length		N	Width	
	range	mean		mean	range
P4		0.97	1	1.01	
M1 <sup>or</sup> 2	1.10–1.21	1.16	5	1.26	1.15–1.41
M3		1.08	1/1	1.23	
p4	0.88–1.13	1.01	2	0.93	0.86–1.00
m1	1.22–1.24	1.23	2	1.15	1.10–1.20
m2	1.23–1.31	1.27	2	1.26	1.25–1.29
m3		1.27	1	1.14	

**Table 4.** Measurements of *Microdyromys cf. monspeliensis* AGUILAR, 1977.

	Length		N	Width	
	range	mean		mean	range
P4		0.58	1	0.74	
M1 <sup>or</sup> 2	0.85–0.95	0.89	10	1.02	0.93–1.12
M3	0.71–0.76	0.74	2	0.93	0.89–0.96
p4	0.63–0.74	0.67	3	0.64	0.59–0.72
m1	0.88–0.99	0.93	4	0.94	0.86–1.02
m2	0.85–1.05	0.96	7	0.95	0.90–1.00
m3		0.91	1	0.84	

**Table 5.** Measurements (in mm) of *Deperetomys magnus* n. sp.

	Length		N	Width	
	range	mean		mean	range
M1	3.60–3.68	3.64	2/3	2.28	2.23–2.27
M3	2.54–2.76	2.56	8/6	2.48	2.32–2.85
p4	2.14–2.52	2.38	7	2.35	1.99–2.56
m1	2.64–3.15	2.92	6	1.87	1.75–2.05
m2	2.63–2.80	2.75	6/4	2.22	2.19–2.27
m3	2.75–3.04	2.94	3/4	2.18	1.96–2.27

**Table 6.** Measurements (in mm) of *Mirrabella* aff. *anatolica* (DE BRUIJN & SARAÇ, 1992).

	Length		N	Width	
	range	mean		mean	range
M1			0		
M2	2.04–2.28	2.16	4	2.07	1.96–2.14
M3	1.76–1.79	1.77	3	1.73	1.63–1.81
m1	2.24–2.45	2.34	3	1.67	1.55–1.88
m2	2.15–2.29	2.23	3/2	1.83	1.79–1.87
m3			0		

**Table 7.** Measurements (in mm) of *Eumyarion margueritae* n. sp.

	Length		N	Width	
	range	mean		mean	range
M1	2.22–2.31	2.26	6/8	1.47	1.37–1.53
M2	1.62–1.82	1.72	13	1.45	1.30–1.55
M3	1.21–1.48	1.41	9	1.41	1.22–1.56
m1	1.79–2.05	1.95	8	1.26	1.19–1.31
m2	1.64–1.86	1.75	8	1.40	1.31–1.48
m3	1.60–1.76	1.69	9	1.30	1.22–1.35

**Table 8.** Measurements (in mm) of *Eumyarion microps* DE BRUIJN & SARAÇ 1991.

	Length		N	Width	
	range	mean		mean	range
M1	1.45–1.75	1.61	11/17	1.11	0.99–1.19
M2	1.04–1.33	1.20	20/19	1.08	0.96–1.18
M3	0.83–1.02	0.92	13	0.95	0.90–1.01
m1	1.31–1.53	1.45	13	0.93	0.82–1.02
m2	1.18–1.47	1.28	20	1.02	0.96–1.12
m3	1.01–1.23	1.13	13	0.89	0.81–0.95

**Table 9.** Measurements (in mm) of *Vetusspalax progressus* n. sp.

	Length		N	Width	
	range	mean		mean	range
M1	2.20–2.25	2.22	4	1.75	1.72–1.79
M2	1.69–1.99	1.85	8	1.64	1.52–1.83
M3	1.27–1.50	1.42	4	1.52	1.35–1.63
m1	1.77–2.02	1.90	9	1.46	1.31–1.61
m2	1.81–2.10	1.96	4	1.64	1.50–1.80
m3	1.88–2.09	1.97	4	1.55	1.50–1.59

