

New data on the earliest European ruminant (Mammalia, Artiodactyla): A revision of the fossil mandible from Rusce in the Pčinja basin (late Eocene, Southeastern Serbia)

Bastien Mennecart, Predrag Radović, and Zoran Marković

ABSTRACT

A fragmented right branch of a ruminant mandible from Rusce (Pčinja basin, Serbia) was originally published in the first half the twentieth century as *Micromeryx flourensianus*, a small ruminant common in the middle Miocene of Europe. Based on this determination, sedimentary filling of the Pčinja basin was considered to be of late Miocene age. However, later paleobotanical and micromammalian studies pointed to a late Eocene age for these deposits. The redescription and discussion of the ruminant fossil mandible from Rusce led to the conclusion that the specimen may belong to a small species of Bachitheriidae, probably to *Bachitherium thraciensis*. This ruminant was originally only known from late Eocene strata in Bulgaria. The peculiar late Eocene faunal composition from the Balkans (e.g., rodents, perissodactyls, and ruminants) confirms that the “Balkanian High” was a distinct paleobiogeographical province from that of Western Europe until the *Bachitherium* dispersal event, which occurred during the early Oligocene ca. 31 Mya.

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Keywords: *Bachitherium*; paleobiogeography; Balkans; Grande-Coupure; *Bachitherium* dispersal event

Submission: 30 April 2018 Acceptance: 18 October 2018

Mennecart, Bastien, Radović, Predrag, and Marković, Zoran. 2018. New data on the earliest European ruminant (Mammalia, Artiodactyla): A revision of the fossil mandible from Rusce in the Pčinja basin (late Eocene, Southeastern Serbia). *Palaeontologia Electronica* 21.3.38A 1-12. <https://doi.org/10.26879/883>
palaeo-electronica.org/content/2018/2339-eocene-ruminant-from-rusce

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INTRODUCTION

Ruminants are currently one of the most diverse clades of large herbivorous mammals with more than 200 species described from all over the world, and the reasons for their success may be linked to their complex stomach and the unique ruminating process (Groves and Grubb, 2011). However, very little is known about their origin. The first ruminant diversification event occurred in Asia during the middle Eocene (Archaeomerycidae and Lophiomerycidae) and then in North America (Leptomerycidae and Hypertragulidae) (Webb, 1998; Métais and Vislobokova, 2007). In contrast, recent studies confirm that ruminants reached Western Europe during the Oligocene Grande-Coupure dispersal event (Mennecart, 2012; Mennecart and Métais, 2015) and Africa during the early Miocene (Van der Made, 1999; Cote, 2010). Only scarce remains of Eocene large mammals are known from Eastern Europe and Western Asia, in contrast to the very abundant fossil record from Central Asia (mainly China and Mongolia) and Western Europe. Recent revisions of *Perissodactyla* from the Balkans highlighted the existence of a quite diversified latest Eocene Rhinoceroidea fauna with Asian affinities (Mennecart et al., 2018) including the newly described *Sellamynodon zimborensis* (Tissier et al., 2018). However, no members of this fauna survived the Eocene-Oligocene boundary (Mennecart et al., 2018). While data on Eocene micromammals from the Balkan Peninsula are becoming more and more extensive (Marković et al., 2013, 2018; de Bruijn et al., 2018; Wessels et al., 2018; van der Weerd et al., 2018), ruminants are currently known only by one mandible found in a borehole in Sladun, Bulgaria (late Bartonian or early Priabonian; Mennecart et al., 2018). The recent description of this oldest ruminant from Europe (*Bachitherium thracensis* Mennecart, Geraads, Spassov, and Zagorchev, 2018) led to a new scenario for the pattern of dispersal events between Asia and Europe (Mennecart et al., 2018). Furthermore, this fossil is the only pre-Grande-Coupure ruminant known so far from Europe (Mennecart, 2012; Mennecart et al., 2018).

An additional ruminant fossil mandible comes from Rusce (i.e., between the villages Rusce and Buštranje), a village in the municipality of Vranje (Southeastern Serbia), and it was originally described by Laskarev (1939). He attributed the specimen to the moschid species *Micromeryx flourensianus* Lartet, 1851, mainly based on the small size of the specimen. However, the site is located within the Pčinja basin, well known for its Eocene,

and possibly Oligocene, sedimentary fillings (de Bruijn et al., 2018). Thus, the mandible from Rusce most certainly comes from pre-Neogene deposits. Since the genus *Micromeryx* first appeared during the early Miocene (oldest fossil known is middle Orléanian or MN4, see Alaburić and Radović, 2016; the origin of the Moschidae is estimated to the earliest Miocene, see Sánchez et al., 2015 and Mennecart et al., 2017), Laskarev's taxonomical attribution of the specimen from Rusce seems highly unlikely. Unfortunately, the whereabouts of the original fossil are currently unknown. Nevertheless, considering the extremely poor fossil record of Paleogene ruminants from this part of Europe, we decided to re-examine the specimen based on the detailed published descriptions, measurements, photographs, and drawings (Laskarev, 1939).

Here we reassess the ruminant fossil specimen from Rusce. The new taxonomical attribution, associated to the Balkano-Anatolian late Eocene faunas, may confirm the "*Bachitherium* dispersal event" scenario as a southern dispersion toward Western Europe during the earliest Oligocene, latter than the Eocene-Oligocene transition Grande-Coupure dispersal event through a northern pathway.

GEOLOGICAL SETTING

The Pčinja basin is located near the city of Vranje in southeastern Serbia, within Proterozoic and Palaeozoic metamorphic crystalline complexes of the Serbo-Macedonian Massif (Dimitrijević, 1997; Figure 1). The basin extends from Vranje-Bujanovac in the northwest into the Pčinja River valley in the southeast, over a distance of about 14 km (Terzin et al., 1977). It is filled with poorly exposed Eocene and few Oligocene sediments (up to 1500 m thick), which overlie Proterozoic crystalline rocks, Proterozoic and Palaeozoic granites, and Senonian rocks at places. As summarized by Dimitrijević and Dimitrijević (1981), Dimitrijević (1997), and de Bruijn et al. (2018), the basin fill consists of the following units. It begins with a unit (up to 750 m thick) of subaerially deposited Lepčince pyroclastics (tuffs and tuffites), found only along the eastern border of the basin. These are followed by an 80–300 m thick succession of pink to reddish pyroclastics with intercalated conglomerates deposited in ephemeral and braided streams (i.e. Koćurica Formation). The Koćurica Fm grades upward into 70–250 m thick grey non marine clastics (conglomerates, sandstones, siltstones, clays) known as the Vražja Crkva Forma-

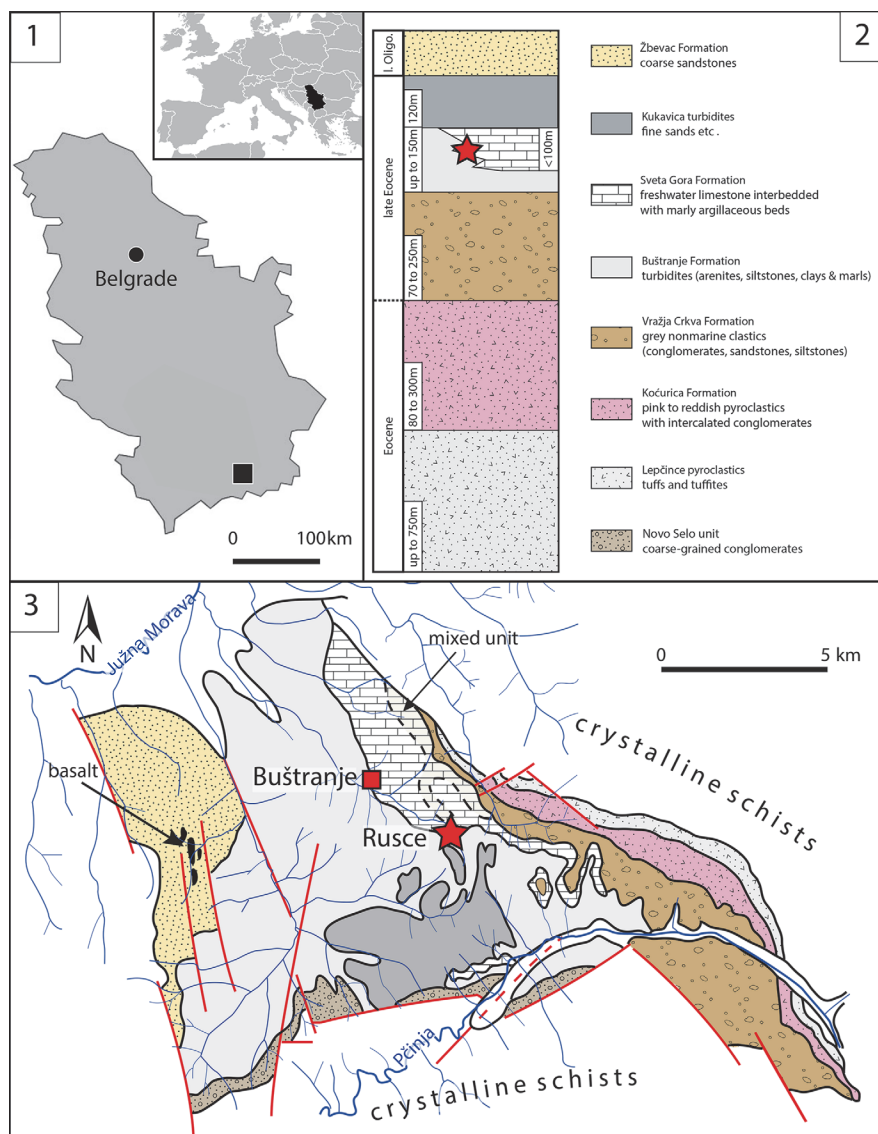


FIGURE 1. Geographical and geological setting of the Rusce locality. **1.** Location of the Pčinja basin (black square) in Serbia; **2.** Simplified lithologic section of the Pčinja basin with the approximate stratigraphic position of the Rusce Eocene ruminant (red star); **3.** Simplified geological map of the Pčinja basin with the location of Rusce (red star: Rusce Eocene ruminant locality; red square: Buštranje Eocene mammal locality).

tion. The Buštranje Formation represents a turbiditic succession (arenites, silt, clays, and marls) up to 150 m thick, occurring nearly all over the Pčinja area. This succession resulted from a deepening of the depositional environment and bears spectacular traces of mass transport (i.e., slumping). In the southern central parts of the basin, the Buštranje Fm is followed by 120 m thick Kukavica turbidites, which represent the uppermost member in this region. Developed only on the northern fringe of the basin, the Sveta Gora Formation is a unit of freshwater limestone interbedded with marly argillaceous beds (up to 100 m thick),

considered a lateral equivalent of the Buštranje Fm. The Novo Selo unit of coarse-grained conglomerates is present only in the southern margins of the basin. A coarse sandstone unit called Žbevac Formation is found in the southwestern part of the basin, and it is considered late Oligocene in age based on the fossil macroflora (Mihajlović, 1985). Numerous sedimentary structures within the basin indicate a paleotransport towards the southeast (Dimitrijević and Dimitrijević, 1981). Dimitrijević and Dimitrijević (1981, 1987) suggested that the Pčinja area was a part of a much larger Eocene-Oligocene basin, which

included the Tikveš and Ovče Pole basins in FYR Macedonia (for more information on these basins see Stojanova and Petrov, 2012). Based on their studies of the fossil macroflora from the middle to upper course of the river Pčinja (i.e., south to southeastern part of the basin), Milaković (1960) and Pantić (1966) estimated a Paleogene age of the sediments from the basin. Furthermore, fossil plants from the Buštranje Formation described by Mihajlović (1985) suggested a late Eocene age. More recently, Marković et al. (2013) sampled argillaceous sandstones from several sites on the northern fringe of the Pčinja basin (including Rusce), and collected remains of small mammals by wet-screening of fossiliferous sediment samples. Although samples from Rusce did not yield any faunal remains, an assemblage from the nearby site of Buštranje, located northwest of Rusce, showed a late Eocene age for the Vražja Crkva Fm. New data from the region of Buštranje confirm a late Eocene age for the Sveta Gora Fm as well (de Bruijn et al., 2018).

The village of Rusce lies on top of thick upper Eocene strata (Terzin et al., 1977) formed by underwater sliding, consisting of marls, claystones, and sandstones (i.e., Buštranje Fm, according to Marković et al., 2013); massive or bedded limestones (i.e., Sveta Gora Fm), and a mixed horizon of shallow water clastites and limestones (i.e., transitional facia, according to de Bruijn et al., 2018; Vražja Crkva Fm, according to Marković et al., 2013), found north of Rusce; a turbidite horizon, consisting of marls, siltstones, and sandstones (i.e., Buštranje Fm/Kukavica turbidites), found to the south. All these formations are late Eocene in age. The ruminant fossil from Rusce was originally embedded in the matrix described as “greenish-grey micaceous sandstone” (Laskarev, 1939), most likely belonging to the transitional facies between the late Eocene terrestrial formations of Vražja Crkva and Sveta Gora (marked as mixed unit on Figure 1).

MATERIAL AND METHODS

The ruminant specimen from Rusce was an accidental find by a local resident, who donated the fossil in 1937 to the collection of the former Geological-paleontological Institute (University of Belgrade). Along with the large part of this collection, the specimen was then transferred to the Paleontological Collection of the Faculty of Mining and Geology (University of Belgrade). However, the specimen was lost under unclear circumstances. We were not able to locate it in any of the known

collections, and we consider the fossil to be temporarily lost. We base our reassessment of the Rusce jaw fragment on the publication by Laskarev (1939). The original measurements have a precision of 0.5 to 1.0 mm. The dental nomenclature follows Bärmann and Rössner (2011).

Abbreviations. MN – Mediterranean Mammal Neogene-Zone; Mya – Million years ago; d – deciduous; p – lower premolar; m – lower molar; NMNHS – National Museum of Natural History, Sofia, Bulgaria.

SYSTEMATIC PALEONTOLOGY

Ruminantia Scopoli, 1777

Bachitheriidae Janis, 1987

Bachitherium Filhol, 1882

Bachitherium cf. *thraciensis* Mennecart et al., 2018

Figure 2

Type specimen. NMNHS FM3320, Right mandible with p2-m3.

Type locality and horizon. Basal breccia-conglomerate-sandstone Formation at Sladun (Bulgaria), latest Bartonian or earliest Priabonian.

Translated Original Description of the Rusce Specimen from Laskarev (1939)

“The specimen from Rusce village represents a right mandible, attached to a firm sandstone slab. The original appearance is shown on figure 1 on table 1 [Figure 2 in this article]. As the jaw is cracked, we were forced to limit our preparation only to the dentition and the outer face; the inner face of the jaw was cleaned earlier, partly by natural processes.

For genus and species attribution of the Rusce jaw, only dental morphology and jaw and teeth metrics can be used. Based on the dental morphology, the jaw belongs to a juvenile form of deer, which preserves deciduous dentition d2-d4 and molars m1-m3. The jaw and teeth metrics are given on figure 1 [Figure 2 in this article], within the text. Molar morphology is typical for a deer, with four lunate (selenodont) cusps, of which the outer ones are pronouncedly bent, while the interior ones are only very weakly bent. The last molar m3 has a talonid (t) [actually a posterior lobe surrounding the back fossa], an addition consisting of the third pair of selenodont cusps. The enamel surface is wrinkled on the upper border of the tooth. At the base of the last slope of the outer frontal selenodont cusps, there is a very characteristic transverse fold [i.e., external postprotocristid], with a weak pillar [i.e., ectostylid]. This is the so-called *Palaeomeryx* fold (*Palaeomeryx-Falte*), characteristic for the

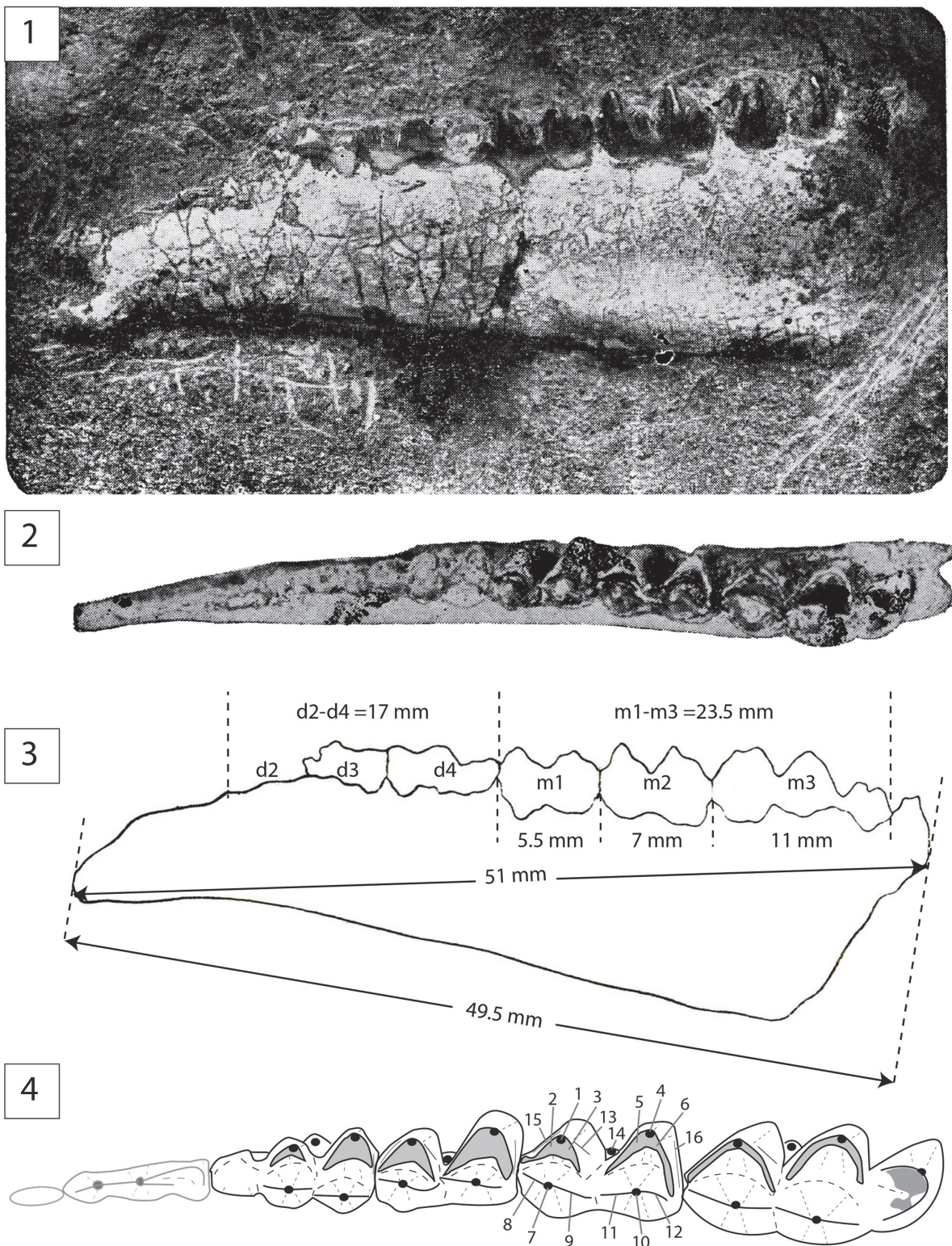


FIGURE 2. Original pictures and drawing of the Eocene ruminant from Rusce in lingual (1) and occlusal (2) views with associated measurements (3) (from Laskarev, 1939), and occlusal view interpretation (4). Dental nomenclature: 1, protoconid; 2, preprotocristid; 3, internal postprotocristid; 4, hypoconid; 5, prehypocristid; 6, posthypocristid; 7, metaconid; 8, premetacristid; 9, postmetacristid; 10, entonconid; 11, preentocristid; 12, postentocristid; 13, external postprotocristid; 14, ectostylid; 15, anterior cingulid; 16, posterior cingulid. The outline in grey (d2 and d3) is interpretative.

older members of *Cervulina* (*Amphitragulus*, *Palaeomeryx*, *Micromeryx*), and gradually lost in younger members (*Cervavus*, *Procervus*). The first molar m1 is only weakly worn. The m2 shows only slight wear on the first two selenodont cusps. The m3 is unworn, and the talonid is not fully erupted from the jaw. This shows that our form is still juvenile, which is in agreement with the state of premolars, which are still deciduous. Deciduous dentition is characterized by the premolar d4, which displays three pairs of weak lunate cusps, where the last pair is the widest one (See Hofmann, 3, taf. XII, fig. 16-17, *Dicrocerus*). The penultimate deciduous molar [in fact deciduous premolar] has a wider posterior part, with an inward-folded enamel, and with the formation of the so-called “coulisse”. In our specimen, the deciduous premolars are very worn (down to the root region), and soon to be replaced with permanent teeth. The d4 shows conspicuous enamel folding around the three pairs of cusps, typical for this tooth. The d3 morphology is obscured by wear. The d2 is completely broken. Aforementioned characteristics provide sufficient evidence to attribute our specimen to Cervulinae, the last of which survive on the Sunda Islands and in the Southeast Asia. According to Rüttimeyer “among all the living *Cervulina*, the most hypsodont and smallest, *Coassus rufinus* [= *Mazama americana*] (i.e., muntjac), is the most closely related to *Micromeryx*. [Actually, *Mazama americana* is not a Muntiacini but an Odocoileini; see in e.g., Mennecart et al., 2017; *Micromeryx* is not a Cervidae, but a Moschidae see in e.g., Sánchez and Morales, 2008; Sánchez et al., 2010; Sánchez et al., 2015; Aiglstorfer et al., 2017].

The metrics of the jaw and dentition allow us to attribute the specimen to *Micromeryx*, which is differentiated from other members of Cervulinae by its small size. Concerning the species attribution, our specimen is close to the widely distributed species *M. flourensianus* Lartet. According to Rüttimeyer (2, p. 92), *M. flourensianus* tooth row is 40 mm long (in our specimen it is $17 + 23.5 = 40.5$ mm), premolar tooth row is 15 to 18 mm (in our specimen it is 17 mm), molar tooth row is 22 mm (in our specimen it is 23.5 mm). According to Hofmann (3, p. 67), m1-m3 = 21.5 mm (23.5 mm in our specimen), m3 length = 9.4 mm, and m3 width = 4.6 mm (compared to 11 and 6 mm in our specimen, respectively). Therefore, dental metrics of the Rusce specimen fit with *M. flourensianus* metrics. Further, Rüttimeyer (2, p. 92) claims that Lartet himself noticed “säulenförmige” [meaning column-shaped] teeth in *M. flourensianus* and “auf-

falend stumpfe Zahnrelief” [meaning extraordinary acute tooth relief]. Hofmann notices that teeth crowns are positioned high above the jaw, higher than in other Cervulinae. These characteristics are also observed in our specimen.

Based on these observations, our specimen is close to *M. flourensianus* but also to *Palaeomeryx* sp. Unfortunately, I was not able to procure the papers by Depéret and Filhol, necessary for this topic. Lartet described his *M. flourensianus* from Sansan, from the early [actually middle] Miocene. In Switzerland, this species was discovered in La-Grive St. Alban [in France, actually], from middle to upper [in fact middle] Miocene deposits. The species was also found in Steinheim (Würtemb.) and Eppelsheim (upper Miocene). In Styria, this species is found with the fauna characteristic for the middle and partly for the late Miocene. It seems to me that our *Micromeryx flourensianus* specimen allows for the dating of the lacustrine sediments from the Vranje basin [=Pčinja basin] to the late Miocene; it is quite possible that there are also middle Miocene sediments in the series. Thus, the Vranje lacustrine sediments were formed during the same interval as the Skopje lacustrine sediments and the lower-*Congerina* beds of the Leskovac basin. After the finds of *Listriodon splendens*, *Hyotherium sömmeringi* etc., our specimen witnesses the expansion of the rich mammalian Styrian-coal-bed fauna far to the Southeast.”

Taxonomical Attribution of the Rusce Specimen

Some similarities do exist between the Rusce specimen and Moschidae (*Micromeryx* and *Hispantomeryx*), such as the small size of the mandible and the absence of p1 (Sánchez and Morales, 2008; Aiglstorfer et al., 2017). However, the Rusce specimen cannot be attributed to *Micromeryx* based on Laskarev’s (1939) description. Most of the mentioned characters are plesiomorphic while typical moschid characters are missing from the specimen. Bovoidea, which includes Moschidae and Bovidae, is characterized by “the distally closed lower molars so typical” (Sánchez et al., 2010). In the specimen from Rusce, there is a space between the postentocristid and the posthypocristid on m1, a feature, which excludes this specimen from this Bovoidea and thus from Moschidae. Moreover, several other characters support the exclusion of this specimen from this family. Members of Moschidae possess a double crescentic third basin of the m3 (Sánchez and Morales, 2008; Sánchez et al., 2010; Sánchez et

al., 2015; Aiglstorfer et al., 2017). Here we interpret this broken part to lack a well-developed entoconulid. In Moschidae, the molars are more laterally compressed with a relatively higher crown than in the Rusce mandible (Sánchez et al., 2010; Aiglstorfer et al., 2017). The ventral outline of the mandible is straight, which differs from Moschidae (Sánchez and Morales, 2008; Sánchez et al., 2010; Aiglstorfer et al., 2017). The lingual wall in the m3 is less flat than in moschids. The assertion that this specimen likely does not represent Moschidae is also supported by the age of the locality. The first estimation of the age of the Pčinja basin sediments was based entirely on the supposed presence of the “late Miocene” *Micromeryx flourensianus* (Laskarev, 1939). The Suoidea mentioned by Laskarev (1939) come from two other basins containing Miocene deposits - “*Listriodon splendens*” (= *Buno Listriodon lockharti* (Pomel) after Petronijević, 1967) from Kruševica near Aranđelovac (Central Serbia) and “*Hyotherium sömmeringi*” from Petrovac na Mlavi (Eastern Serbia) (Laskarev, 1936, 1937). However, the sediments in the area of Rusce have since been dated with certainty to the late Eocene (de Bruijn et al., 2018), and there are no trace of Neogene sediments in the basin. Furthermore, the latest phylogenetic analyses combining morphological and DNA characters, including fossil specimens, revealed that the clade Moschidae most likely originated during the early Miocene (Sánchez et al., 2015; Mennecart et al., 2017). The recently discovered MN4 *Micromeryx* (Alaburić and Radović, 2016) supports the hypothesis of the early Miocene moschid origin of Sánchez et al. (2015) and Mennecart et al. (2017). Thus, the Rusce specimen is necessarily much older than the probable first appearance of the Moschidae.

The specimen is a minute ruminant mandible, which preserves the tooth-row with d3-m3 in place and d/p2 tooth socket. The p1 (if present) is not directly juxtaposed to the p2. Lophiomerycidae, Gelocidae and the Asiatic *Gobiomeryx* and *Pseudomeryx* do possess a p2 directly following the p1 without diastema in between. However, this is not the case for the Bachitheriidae (p1 caniniform, Sudre, 1986, 1995; Geraads, 1987; Mennecart, 2012, 2015; Mennecart and Métais, 2015, Mennecart et al., 2011); *Mosaicomeryx* and *Prodremotherium* (p1 absent, Mennecart and Métais, 2015), and the Praetragulidae (p1 absent, Vislobokova, 1998, Vislobokova and Daxner-Höck, 2002, Métais and Vislobokova, 2007). Unfortunately, while the lingual view of the specimen embedded in matrix

shows the presence of the d3, this tooth is absent from the occlusal view (after the extraction from matrix). Nevertheless, the lingual view seems to show that two elongated cristids go towards the distal end of the d3 from the mesolabial conid, which is not observed in pecoran ruminants, in contrast to tragulines (Sudre, 1986; Mennecart, 2012, 2015). The molars possess anteriorly closed trigonids, confined by the anterior fusion of the premetacristid and the preprotocristid. This is different from the state seen in the molars of the Lophiomerycidae and stem Tragulidae (sensu Mennecart and Métais, 2015), which do not show a clearly developed and elongated premetacristid (Janis, 1987; Mennecart et al., 2011). The molars are laterally compressed and relatively high crowned in Asiatic Praetragulidae such as *Praetragulus* (Vislobokova, 1998; Vislobokova and Daxner-Höck, 2002); in contrast, they are more bunodont and low crowned in Bachitheriidae (Sudre, 1986; Mennecart, 2012, 2015; Mennecart et al., 2018). The mandible from Rusce possesses low crowned and relatively bunodont molars. The diastema anterior to the p2 is elongated, with strong dorso-ventral constriction just anterior to the p2. In Gelocidae (sensu Mennecart and Métais, 2015) and Paleogene Tragulidae the diastema is shortened (Mennecart et al., 2011). The constriction is not as marked in Praetragulidae (Vislobokova, 1998) as in Bachitheriidae (Sudre, 1986; Mennecart et al., 2011, 2012, 2018; Mennecart, 2015). The ventral outline of the mandible is straight, which differs from the Tragulidae, Lophiomerycidae, and Gelocidae, but is very similar to Bachitheriidae (Mennecart et al., 2011, 2012).

Based on this evidence, the specimen most probably belongs to the genus *Bachitherium* (the only genus of Bachitheriidae). Species-level distinctions within *Bachitherium* are based mainly on the inferred complexity of the lower permanent premolars, the tooth size, and limb bone proportions (Sudre, 1986, 1995; Mennecart et al., 2018). Unfortunately, lower permanent premolars and limb bone proportions are not known in the Rusce specimen. Nevertheless, its size is in agreement with those of the smallest Bachitheriidae, *Bachitherium viretti* Sudre, 1986, and *B. thraciensis*, which are the oldest bachitheriids known (the slight size differences in the measurements provided by Laskarev (1939) are most likely due to measurement error). The roughness of the enamel and the pronounced bunodont character of the cuspids are very similar to those observed in *B. thraciensis* (Mennecart et al., 2018). Currently this ruminant is

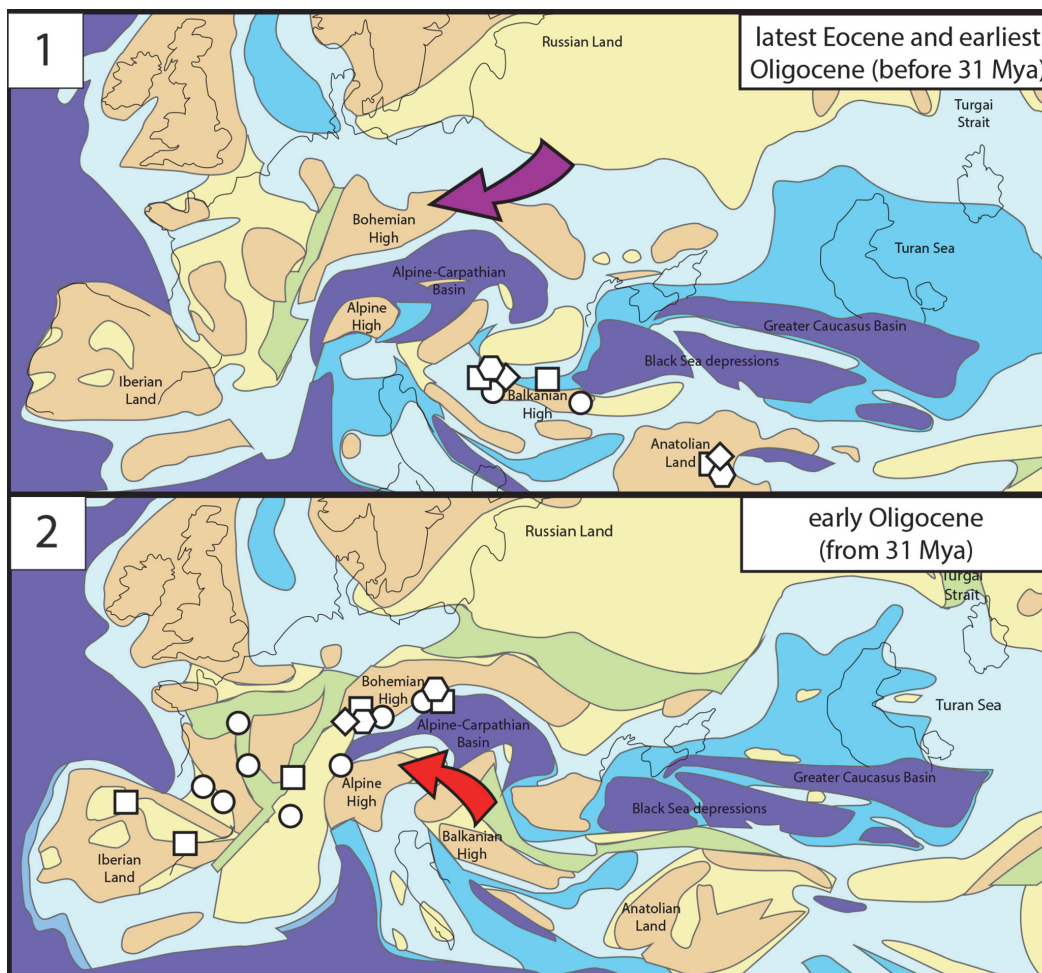


FIGURE 3. Paleobiogeography of the ruminant *Bachitherium* and associated Balkanic rodents absent from Western Europe during the late Eocene (mostly Priabonian) and earliest Oligocene (MP21-22) (**1**) and dispersing through Western Europe from ca. 31 Mya (MP23-24; **2**). The purple arrow represents the Grande-Coupure dispersal event (MP21). The red arrow represents the *Bachitherium* dispersal event (MP23). Circle, *Bachitherium* spp.; square, *Pseudocricetodon* spp.; hexagon, *Paracricetodon* spp.; diamond, Melissiodontinae. The map has been modified from Mennecart et al. (2018) based on Popov et al. (2004). Biogeographical and biostratigraphical data are from Alvarez Sierra et al. (1999), Baciu and Hartenberger (2001), Martín-González et al. (2014), and de Bruijn et al. (2018).

only known from the late Eocene of Sladun (late Bartonian or early Priabonian, Bulgaria), which is similar in age to the sediment of the Rusce area (late Eocene). However, since we did not have a direct access to the specimen, we preferred to use open nomenclature and keep the ascription of the Rusce ruminant as *Bachitherium* cf. *thraciensis*.

PALAEOBIOGEOGRAPHY OF THE LATE EOCENE AND OLIGOCENE MAMMALS FROM BALKANS

The late Eocene Balkanic fauna is very different from the Western European ones. The oldest known European ruminants (two records of *Bachitherium thraciensis*) come from the late

Eocene “Balkanian High” (Figure 3). While older ruminants are known in Asia, none are currently described from Western Europe before the Grande-Coupure (Mennecart, 2012; Mennecart and Métais, 2015). *Bachitherium* is only known in Western Europe from MP23 (ca. 31 Mya, Mennecart et al., 2018). Similarly, the Balkanic Perissodactyla and rodent fauna compositions are drastically different from the contemporaneous Western European ones (i.e., prior to the Grand-Coupure) (Heissig, 1979; de Bruijn et al., 2018; Mennecart et al., 2018; see Figure 3). The Perissodactyla and the ‘Anthracotheriidae’ *Bakalovia* present in the Balkans are typical Asiatic faunal elements (Böhme et al., 2013; Mennecart et al.,

2018). The Serbian Eocene rodent community is very diverse in Muridae (no less than 8 species, de Bruijn et al., 2018), similar to the situation observed in Anatolia (de Bruijn et al., 2003). This is the only rodent family currently described from the Eocene of Serbia (de Bruijn et al., 2018). This is in agreement with the rodent fauna observed in the Priabonian from Romania with the presence notably of the Muridae *Pseudocricetodon* sp. (Baciu and Hartenberger, 2001). Among the latest Eocene/earliest Oligocene Muridae from Anatolia, we may recognize *Pseudocricetodon* and *Paracricetodon*, which are more primitive than the younger Western European ones (de Bruijn et al., 2003). The composition of the late Eocene rodent fauna from Serbia is unique in Europe with the co-occurrence of Melissiodontinae and a Spalacinae in Zvonce and Melissiodontinae, Pappocricetodontinae, *Pseudocricetodon* and *Paracricetodon* in Buštranje (de Bruijn et al., 2018). It is noteworthy that the oldest Pappocricetodontinae have been identified in the middle Eocene of Mongolia (Baciu and Hartenberger, 2001).

De Bruijn et al. (2018) observed that *Eucricetodon*, the oldest post-Grande-Coupure Central and Western European cricetid, is completely absent from the Serbian Oligocene faunas and may also be absent from Anatolia as suggested by de Bruijn et al. (2003), the Anatolian *Eucricetodon* may be in fact an *Atavocricetodon*.

Except for the Perissodactyla that did not survive the early Oligocene (Mennecart et al., 2018), the Eocene Balkan mammals are first recorded in Western Europe ca. 31 Mya (Figure 3), after the Grande-Coupure dispersal event that occurred ca. 33 Mya. Similarly to Bachitheriidae and Tragulidae, the oldest occurrence of Melissiodontinae in Western Europe is during the early Oligocene, at MP23 (Wessels et al., 2018). *Pseudocricetodon* and *Paracricetodon* may appear at MP22 in Germany at Herrlingen I (Baciu and Hartenberger, 2001). However, Dawson, (2003) supports that the

Pseudocricetodontinae also arrived in Western Europe at MP23.

Therefore, two different and diachronous pathways for east-west dispersal event(s) may be observed during the early Oligocene. The Northern Route, at the Eocene-Oligocene transition (ca. 33 Mya), is marked by the typical Grande-Coupure migrants. This event has been very well-documented for more than a century (Stehlin, 1909) and is marked by the presence of the first Western European ruminants (Gelocidae and Lophiomerycidae), Rhinocerotidae, and the rodent *Eucricetodon*. The dispersion via the Balkan Route occurred a little later (ca. 31 Mya) and is responsible for the appearance of the ruminants Bachitheriidae and Tragulidae, and the rodents Melissiodontinae, *Pseudocricetodon* and *Paracricetodon* in Western Europe (Figure 3). During the Eocene, the Balkan region was isolated from Western Europe (Figure 3). The Paratethys Sea may have been a geographical barrier separating the Balkan area from Western Europe until the early Oligocene (Berger et al., 2005; Kocsis et al., 2014). The formation of a landbridge ca. 31 Mya allowed faunal exchanges between the Balkans and Western Europe known as *Bachitherium* dispersal event (Mennecart et al., 2018).

ACKNOWLEDGMENTS

K. Bradić-Milinović and L. Jović (Geological Survey of Serbia, Belgrade, Serbia) are thanked for their help with the geologic map, J. Lindal (Faculty of Medicine, University of Belgrade, Serbia) for proofreading the paper and his great help with English. B. Mennecart warmly thanks the Swiss National Science Foundation for granting the SNF Projects P300P2_161065 and P3P3P2_161066. I. Sánchez and M. Aiglstorfer are thanked for improving the manuscript through their review and the editors of *Palaeontologia Electronica* for the entire process.

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