



Discovery of the oldest European ruminant in the late Eocene of Bulgaria: Did tectonics influence the diachronic development of the Grande Coupure?

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Short title: Oldest European ruminant and *Bachitherium* Event

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Abstract

The Terminal Eocene global cooling Event created a substantial sea-level drop. This caused biological extinctions and allowed for large scale dispersal events (e.g. European Grande-Coupure, Mongolian Remodelling). Originating from Asia, the first western European ruminant appeared during this dispersal and climatic event, correlated with the Eocene-Oligocene boundary. A second wave composed by Bachitheriidae and Tragulidae arrived in Europe 2 Myr later. The origins of this diachronism have remained unknown until now. Here we describe the first ante-Grande-Coupure ruminant from Europe, found in the Late Eocene of Bulgaria (south-eastern Europe). We ascribe it to *Bachitherium patriarcha* nov. sp. which predates its western European relatives by at least 4.5 Myr; the specimen possesses the most primitive dental morphology known in the family. During the entire Eocene and until the early Oligocene (ca. 31 Ma), south-eastern Europe remained isolated from the rest of Europe by the Paratethys sea. Early Oligocene orogenic events restored dryland conditions and enabled the arrival of *Bachitherium* in Western Europe (herein named “*Bachitherium* event”). However, none of the abundant perissodactyl fauna from south-eastern Europe migrated to Western Europe during this time, because, like their relatives in Central Asia, they did not survive the Terminal Eocene cooling and aridity event.

Keywords

Bulgaria; *Bachitherium*; Ruminantia; Eocene-Oligocene boundary; Mammalian dispersal

1. Introduction

During the Cenozoic, the Earth experienced several episodes of global warming and cooling (Zachos et al., 2001; Vandenberghe et al., 2012). The most impressive cooling event, called “Terminal Eocene Event” (Zachos et al., 2001) occurred at the Eocene-Oligocene Boundary: a 4°C decrease of the deep-sea temperature is observed in Northern Atlantic benthic fauna (Zachos et al., 2001; Liu et al., 2009) and a ca. 5°C decrease in Central Europe (Mosbrugger et al., 2005, Uhl et al., 2007). The changes in the ocean circulation due to the opening of the southern Ocean gateways created the first Antarctic glaciations forced by a decrease in atmospheric CO₂ and a minimum solar insolation (Zachos et al., 2001; Liu et al., 2009). This caused a global sea level drop of 30 to 90 meters depending on the region of the world (Coxall and Pearson, 2007). This tectonic and climatic event led to the main worldwide extinction phase of the entire Cenozoic (Raup and Sepkoski, 1984). In Asia, the Eocene

perissodactyl-dominant fauna was abruptly replaced by the Oligocene rodent/lagomorph-dominant fauna, with a contemporaneous extreme change in the floral composition: the Mongolian Remodelling (Meng and McKenna, 1998; Kratz and Geisler, 2010; Sun et al., 2014,). These faunal turnovers were probably correlated with climatic and environmental changes from a warm and humid to a cooler and drier world (Legendre, 1987; Hartenberger, 1998; Meng and McKenna, 1998). Until the beginning of the Oligocene, Europe was almost isolated from Asia, notably by the Turgai Strait in Asia (Prothero, 1994). Stehlin (1909) described an extinction/origination event at the Eocene-Oligocene boundary that he named Grande-Coupure. This faunal turnover sees new Asiatic immigrants, including ruminants, replacing most of the endemic Eocene European genera (Prothero, 1994; Hartenberger, 1998). Around 60% of the mammal fauna disappears during the Grande-Coupure faunal turnover (Prothero, 1994). Nevertheless, the issue of the synchronism of the Grande-Coupure immigration event throughout Europe remains debated (Legendre, 1987; Baciú and Hartenberger, 2001).

Here we describe the first Eocene (early? Priabonian) ruminant from Europe. It presents the twofold interest of being the first Paleogene ruminant known in Eastern Europe (Sladun, south-eastern Bulgaria, Fig. 1) and the earliest one outside Asia and Northern America. A complement to the scenario of the Grande-Coupure dispersals is proposed, correlating local tectonic event with later dispersals.

2. Geological setting

The Thrace Basin (known also as East Thrace depression, Lower Thrace depression, Basin of Thrace and Ergene) is situated almost entirely within European Turkey but extends westwards of the Tundzha and Maritsa (Evros/Meriç) rivers in Bulgaria and Greece (Kozhoukharov et al., 1993; Kozhoukharov et al., 1995; Elmas, 2011; see Fig. 1A). This basin developed over a heterogeneous basement including metamorphics and granites dating from Late Precambrian to Mesozoic. The basin is filled by Paleogene sedimentary and volcanic formations, and by Neogene sediments with a total thickness of more than 7000 m. The development of the Paleogene Thrace Basin has been thoroughly studied and related to the gradual activation of a number of normal WNW-ESE trending faults (Elmas, 2011; and references therein). The sedimentation began in the Southern Thrace Basin in the early to middle Eocene and reached the Northern Thrace Basin during the Late Eocene. Our study is restricted to the Bulgarian part of the Northern Thrace Basin (South Sakar Depression),

around the villages Shtit, Sladun and Matochina (Fig. 1B). In this area the Paleogene sediments are covered by the Neogene Ahmatovo Formation.

Three Paleogene formations have been distinguished there during the extensive geological mapping accompanied by drilling (Kozhoukharov et al., 1995; Boyanov and Goranov, 2001): the basal breccia-conglomerate-sandstone formation (from 300 to 500 m; formed within an alluvial plain); the transgressive terrigenous-limestone-marl formation (100 – 600 m; formed in lagoonal to shelf environments); the pyroclastic-marl-limestone formation (50 – 100 m; formed in shelf environment with reefs and pyroclastic material transported from the Rhodope volcanoes). A Late Eocene age (Priabonian) has been determined thanks to an abundant marine fauna found in the two upper formations (Kozhoukharov et al., 1995; determinations by P. Dikova and V. Sapundzhieva), namely, the co-occurrence of *Nummulites fabianii* Prever, *N. chavannesi* de la Harpe (A, B), *N. incrassatus* de la Harpe (A, B), *N. cf. garnieri* Boussac. A similar fauna has been cited in the Upper Eocene limestones from the northernmost parts of the Northern Thrace Basin in Turkish territory (Less et al. 2011). The exact determination of the age of the basal breccia-conglomerate-sandstone formation is not possible (terrestrial character, lack of guide fossils). Nevertheless, this terrestrial formation is overlain by the two previous marine Priabonian formations and it most likely should be referred to the early? Priabonian.

The fossil material reported here was found in the Sladun Borehole (Fig. 1B) at a depth of 176 m. It is included in a brownish siltstone with dispersed fine psammitic quartz grains. The rock is compacted, finely laminated, and belongs to the upper part of the basal breccia-conglomerate-sandstone formation. No pollen had been found in the sediment. However, the sediments are characteristic for a marshy alluvial plain that existed before the gradual transgression of the Paratethys Sea in the Thrace basin.

3 Material and method

The fossil is stored at the National Museum of Natural History, Sofia (NMNHS). The material used for comparison belongs to the Muséum National d'Histoire Naturelle, Paris (MNHN); the Université of Montpellier (UM); the University Claude Bernard; Lyon (UCBL).

The biostratigraphic framework follows the recent synthesis of Vanderberghe *et al.* (2012). Measurements are in millimetres. The dental terminology follows Figure 2, based on the work of Mennecart and Métais (2015).

4. Systematic palaeontology

Ruminantia Scopoli, 1777

Tragulina Flower, 1883

Bachitheriidae Janis, 1987

Bachitherium Filhol, 1882

Bachitherium patriarcha nov. sp.

Figure 2

4.1. Holotype and only specimen

Right mandible with p2-m3, NMNHS FM3320 of the coll. of the National Museum of Natural History, Sofia. Measurements: length of the diastema p1-p2 >14.0 mm; p2-p4 = 18.0; p2 = 5.1 x 2.2; p3 = 5.4 x 2.6; p4 = 5.7 x 3.3; m1 = 6.3 x 5.3; m2 = 8.2 x 6.1.

4.2. Species etymology

Patriarcha is attributed in Jewish mythology (Old Testament) to someone with numerous and successful descendants, which is the case of *Bachitherium* during the Oligocene in Western Europe.

4.3. Type locality and horizon

The specimen has been found South of Sladun near the border between Bulgaria and Turkey in a borehole at a depth of 176 meters, in sandy siltstone of the basal breccia-conglomerate-sandstone formation (early? Priabonian; Late Eocene).

4.4. Diagnosis

Very small *Bachitherium* differing from *Bachitherium vireti*, *B. curtum*, *B. guirounetensis*, *B. lavocati*, and *B. insigne* in having the structure of p3 similar to that of the p2. Only one posterior cristid descends from the mesiolabial conid on the p2 and p3. In *B. vireti*, *B. curtum*, *B. guirounetensis*, *B. lavocati*, and *B. insigne*, the structure of the p3 is similar to those of the p4 in having the transverse cristid and the posterolabial cristid

155 descending from the mesiolabial conid on p3. The lower molars lack a labial postprotocristid
156 present in the other species. The mandible is more massive in *B. patriarcha* than in the
157 younger species.

159 4.5. Description

161 The type and only specimen is a right mandible bearing p2-m2; m3 and the posterior
162 part of the mandible are missing. The mandible ventral border is straight. The anterior part is
163 missing, including the p1 tooth socket. Nevertheless, the incomplete diastema between p1 and
164 p2 is very long, being comparable to the p2-p4 row length. The ramus is strongly dorso-
165 ventrally constricted just in front of p2. The symphysis is very long.

166 The premolars are very long, slender, and simple in their structure. They increase in
167 size from p2 to p4. The p2 and p3 are similar in shape. The oblique anterior conid becomes
168 larger from p2 to p4; it lacks an additional cristid. The anterolabial cristid is straight and
169 anterior. The mesolabial conid is the highest premolar conid. It is central and become larger
170 from p2 to p4. None of the premolars possess a mesolingual conid, and p2 and p3 do lack an
171 elongated posterolabial cristid. However, on p4, this cristid is elongated, reaching the
172 posterolabial edge of the tooth. The transverse cristid extends posteriorly. On p2 and p3, it is
173 slightly curved and in the posterior quarter of the tooth it splits into two cristids that reach the
174 posterolingual edge and the posterolabial corner of the tooth respectively. On p4, the
175 transverse cristid is straight and reaches the posterolingual edge of the tooth. The
176 posterolabial conid becomes larger and less salient from p2 to p4. No posterior stylid is
177 present on these premolars, so that the posterior valley is open posteriorly. The anterior
178 cingulid is well-marked.

179 The lower molars m1 and m2 are well-worn. The talonid is wider than the trigonid.
180 The preprotocristid is short and straight on m1. It fuses anteriorly with the curved
181 premetacristid on m1 and remains isolated on m2. The internal postprotocristid is straight and
182 slightly tilted backward. It fuses with the short and straight internal postmetacristid. Neither
183 the external postmetacristid nor the external postprotocristid (probably absent) can be
184 observed. The straight and anteriorly oriented preentocristid reaches the posterior part of the
185 postmetacristid and the internal postprotocristid. The oblique and straight prehypocristid ends
186 between the preentocristid and the external postprotocristid without reaching them. The
187 posthypocristid is straight and transverse. It ends without reaching the curved postentocristid
188 leaving a very small gap between these cristids. All lingual cristids are weak, slightly

laterally compressed, and roughly aligned. The ectostylid is large and possesses an additional posterior spur. The anterior and posterior cingulids are well-marked. The enamel is a little wrinkled.

4.6. Taxonomic attribution

The shape of the lower premolars, lacking a mesolingual conid, is characteristic of the traguline ruminants Tragulidae and Bachitheriidae, and is relatively rare in the pecoran ruminants Gelocidae (Heissig, 1978; Geraads et al., 1987; Métais et al., 2001; Mennecart et al., 2011; Mennecart and Métais, 2015). The presence of an elongated postentocristid excludes an attribution to the Gelocidae and Tragulidae (Geraads et al., 1987; Mennecart et al., 2011; Mennecart and Métais, 2015; Métais and Vislobokova, 2007). Janis (1987) first defined the Bachitheriidae as Tragulina possessing a narrow and pinched hypoconulid on m3. Following Geraads et al. (1987), *Bachitherium* is characterized by the unique association of a hook-shaped upper canine, a caniniform p1, and a metatarsal with an almost circular proximal surface. None of these characters can be observed on the studied specimen. However, Geraads et al. (1987) also note the presence of a distally isolated posterolabial cristid (“anticrête”) on p3 and p4 and a strong “*Dorcatherium*” fold on the molars. A posterolabial cristid is present on p2 and p3 of NMNHS FM3320 (Fig. 2). Mennecart and Métais (2015) defined the Bachitheriidae by the following autapomorphies: a diastema between p1 and p2 longer than the premolar row p2-4; a shallow external postprotocristid, not linked to the prehypocristid; and the absence of lateral metacarpals. The Bulgarian specimen possesses a very long diastema between p1 and p2 (incomplete anteriorly), comparable to the premolar row p2-p4 (Fig. 2), but the external postprotocristid is absent. The mandible NMNHS FM3320 displays a straight ventral border and the corpus sharply decreases in depth just anterior to p2, which are characteristics of the Bachitheriidae (Janis, 1987; Mennecart et al., 2011). Thus the studied specimen belongs to the Bachitheriidae (Fig. 3), a monogeneric family hitherto known only from the Oligocene of Western Europe (Sudre, 1986; Métais and Vislobokova, 2007; Mennecart, 2012). *Bachitherium patriarcha* nov. sp. is the earliest and easternmost known Bachitheriidae.

The structure of the premolars clearly differs from that of other species of *Bachitherium*. The p2 is very similar to that of *B. vireti* (see Sudre, 1986; Fig. 3). The p3 of *B. patriarcha* is unique among the Bachitheriidae. It retains a primitive shape, similar to that of p2, having the posterolabial cristid isolated at its distal end, not connecting the posterolabial

conid (Fig. 2); all the other Bachitheriidae species display a p3 already possessing the derived morphology of the p4. There is little intra-specific variation in the lower premolars among the Bachitheriidae (Sudre, 1986; Mennecart, 2012, 2015) and such differences warrant specific distinction.

5. Discussion

5.1. Evolution of the Bachitheriidae

Five species of *Bachitherium* (*B. vireti*, *B. curtum*, *B. insigne*, *B. guirounetensis*, *B. lavocati*) have been described from Western Europe before the latest Oligocene environmental 'Microbunodon Event' (Métais and Vislobokova, 2007; Mennecart, 2015; Scherler et al., 2013; see Fig. 4). They generally differ in tooth size and proportions as well as in their postcranial features (Sudre, 1986; Mennecart, 2015; Mennecart and Métais, 2015; see Fig. 3). The smallest and earliest Western European species are *B. vireti* and *B. curtum*; according to Sudre (1986), they differ in the length of the diastema and tooth row, *B. vireti* being slightly smaller. *Bachitherium patriarcha* nov. sp. differs from these two species in the primitive aspect of its premolars: its p2 and p3 possess a different structure than p4 (Fig. 3). Later Bachitheriidae develop more complex premolars. Within the European Bachitheriidae two contemporaneous lineages can be recognized (Sudre, 1986). A first lineage composed of *B. vireti* and *B. insigne* retains the primitive pattern of p2, but the p3 of these species are more advanced than in *B. patriarcha* nov. sp. in being very similar to p4. In the second lineage, composed of *B. curtum*, *B. guirounetensis*, and *B. lavocati*, the p3 and p4 display a closed posterior valley, linked to the presence of a posterior stylid.

The oldest Bachitheriidae were reported from German localities ca. 32.5 Ma (MP22 European Reference Level; Heissig, 1978; Sudre, 1986). However, reassessment of this material by one of us (B.M., unpublished data) shows that most of these German fossils belong instead to the Gelocidae and that the earliest occurrences of Bachitheriidae in Western Europe are ca. 31 Ma (MP23). They went extinct by the latest Oligocene (ca. 24-24.5 Ma, MP28) during the *Microbunodon* Event (Scherler et al., 2013; Mennecart 2015).

5.2. Biogeographic affinities of the Balkan land megafauna during the Eocene

Known Paleogene mammals of Bulgaria are scarce (Bakalov and Nikolov, 1962; Nikolov, 1985, Nikolov and Heissig, 1985) and remain largely undescribed (Spasov, 1989). They show marked affinities with Asia and a high degree of isolation from Central and Western Europe (Nikolov and Heissig, 1985; Spasov and Popov, 2007). Eocene Asian faunal elements in the Balkans include the bothriodontin anthracothere *Bakalovia* Nikolov & Heissig, 1985, based upon two species from the latest Bartonian/earliest Priabonian of Chernomore quarry (Burgas region). The only other occurrence of the genus is from deposits of similar age in Vietnam (Böhme et al., 2013), suggesting that it might be of Asian origin. *Sivatitanops? rumelicus* (Toula, 1892) from middle/late Eocene deposits near Burgas in Bulgaria (Bakalov and Nikolov, 1962; Nikolov and Heissig, 1985) and *Brachydiastemarium transilvanicum* from the middle(?) Eocene of Romania (Nikolov and Heissig, 1985; Baciú and Hartenberger, 2001) are the only European brontotheres, and attest to the westernmost extension of this North American and Asian family. The occurrence of the Asian rhinocerotoid *Forstercooperia* is established (Tzankov et al., 2000) in the southeastern Bulgarian Priabonian (Kanchev, 1995). It was first described as *Prohyracodon* aff. *meridionale* and was mistakenly said to have come from Bobov Dol (Nikolov and Heissig, 1985) instead of the quarry from Borov Dol, near Sliven, as written on the original label (Sofia NMNHS collections). The scarce *Prohyracodon* remains from Europe (Mera in northwestern Romania, and Moettig in Slovenia) are only known from the southern/southwestern periphery of the Paleogene Paratethys Sea (Heissig, 1989; Codrea, 2000; Baciú and Hartenberger, 2001). The Central Asian amynodontid *Cadurcodon* (*C. ardynense*, according to Spasov and Popov (2007), was reported from the Bartonian/Priabonian deposits of Kameno (Burgas region) and Nikolaevo (North of Nova Zagora) quarries of southeastern Bulgaria. The genus persisted in Central Romania till the ?early Oligocene (Codrea, 2000). An undescribed allaceropine rhinocerotoid is also known from the Burgas region (Debelt).

All these large mammals, together with *Bachitherium patriarcha* nov. sp. that probably originated in the middle Eocene from Asia (Métais and Vislobokova, 2007), demonstrate that the Balkan Peninsula was probably connected to Asia through the Caucasian-Anatolian as well as the Balkan-Transylvanian regions during the middle / late Eocene (Gabunia, 1964; Popov et al., 2004). Nevertheless, there is a strong endemism of the middle Eocene mammal faunas of Central Anatolia (e.g. Licht et al., 2017; Métais et al., 2017), which shows that the biogeographic affinities of the various islands forming the northern margin of the Neotethys and Asia were more complex than previously thought.

Almost none of the above mentioned perissodactyls survived the Eocene-Oligocene boundary.

5.3. Tectonism and polyphasic migrations during the Grande-Coupure

The Grande-Coupure is a well-documented major faunal event that greatly modified the European fauna (e. g. Stehlin, 1909; Prothero, 1994). This Asiatic immigration is supposed to have occurred at the base of the Oligocene when the Turgai Strait dried out, permitting colonisation of Western Eurasia (Prothero, 1994). However, some forerunners of this immigration can already be observed during the latest Eocene among reptiles and mammals (Franzen, 2003; Rage, 2013; Solé et al., 2014). In parallel to the Priabonian massive extinction of the Proviverrinae (Creodonta), the Asiatic Hyaenodontinae (Creodonta) and *Cynodictis* (Carnivora) immigrated into Western Europe (Solé et al., 2014). This massive faunal remodelling is named second Intra-Eocene mammalian turnover (Franzen, 2003). Similarly, numerous artiodactyls (e.g. *Elomeryx*, *Anoplotherium*, *Diplobune*, and *Oxacron*) are found for the first time in that area in latest Eocene deposits (Franzen, 2003; Erfurt & Métais, 2007). The origin of these latest Eocene migrants could be Scandinavia (Franzen, 2003; see Fig. 4), but there is no strong evidence for this. Most of these new migrants do not survive the Eocene-Oligocene transition (Baciu and Hartenberger, 2001).

The early Oligocene Western European immigration of ruminants occurred in two distinct waves. The first immigrants are the Lophiomerycidae and Gelocidae, which belong to the Asiatic cortege of the Grande-Coupure immigrants, marking the base of the Oligocene ca. 34-33 Ma (MP21; Mennecart, 2012; see Fig. 4). To reach western Europe from Asia, they probably benefited from the sea level drop that dried out the Turgai Strait (Prothero, 1994). Western European Bachitheriidae and Tragulidae only arrived 2 Myr later (Mennecart, 2012; Mennecart and Métais, 2015). During the entire Eocene, Paratethysian deep waters filled with flysch deposits connected the Northern Alpine depression to the Carpathian Basin and the Greater Caucasus Basin (Popov et al., 2004; Berger et al., 2005) forming a long water barrier, more than 50 km wide in the Alpine sea and 200-500 km in the Carpathian one, which isolated south-eastern Europe from western Europe (Baciu and Hartenberger, 2001; see Fig. 4). Due to this barrier, the Bulgarian *Bachitherium* was unable to make it to western Europe at that time.

Becker (2009) suggested that southern Europe was a likely route for Asiatic dispersal during the Grande-Coupure. However, this hypothesis is only supported by dating of the

Monteviale locality (Italy) to MP21 and the occurrence of *Epiaceratherium*. However, an age of MP21 to MP23 has recently been suggested for this locality (Pandolfi et al. 2017), and we favour a MP23 age. Only from ca. 31 Ma (MP23), Paratethys Sea environments turned into shallow water and then into continental deposits diachronically from West to East (MP23; Mennecart et al., 2011; Berger et al., 2005). Synchronously, isotopic signal of the $\delta^{18}\text{O}$ changed drastically (Héran et al., 2010) indicating different air trajectories with different moisture sources (Atlantic versus Paratethys) induced by the regression and by the Alpine-Dinaridic orogenic system uplift that reached an estimated altitude of 1200 m (Kocsis et al., 2014). The creation of this terrestrial land bridge between Western Europe and south-eastern Europe (Berger et al., 2005) allowed the migration of the Bachitheriidae into Western Europe (Fig. 4). We propose to name this faunal event, linking Western to south-eastern Europe fauna by tectonics, the “*Bachitherium* event”. The Tragulidae were also involved in this dispersal, because *Iberomeryx*, which was already known in Georgia during the earliest Oligocene (Métais and Vislobokova, 2007), appears in Europe simultaneously. Moreover, we observe that the Eocene south-eastern European perissodactyls disappeared in a similar fashion to their relatives in Asia during the Mongolian Remodelling (Meng and McKenna, 1998; Kratz and Geisler, 2010). The transition from warm and humid conditions towards cooler and dryer environments may have caused the extinction of south-eastern European and many Asian perissodactyls at the Eocene-Oligocene Boundary (Meng and McKenna, 1998) may have boosted rodent and ruminant diversification (Meng and McKenna, 1998). Ruminants became dominant in the Oligocene faunas of Eurasia (Blondel, 2001; Métais and Vislobokova, 2007).

6. Conclusions

The description of the oldest European ruminant in Bulgaria leads to a better understanding of the early Oligocene polyphasic Asiatic dispersal events. *Bachitherium patriarcha* nov. sp. predates its Western European relatives by at least 4.5 Myr; the specimen possesses the most primitive dental morphology known in the family. During the entire Eocene and until the early Oligocene (ca. 31 Ma), south-eastern Europe remained isolated from the rest of Europe by the Paratethys sea. Early Oligocene orogenic events restored dryland conditions (herein named “*Bachitherium* event”) and enabled the arrival of *Bachitherium* in Western Europe. Thus, we highlight that a second and later Asiatic migration occurred from the South of Europe ca. 31 Ma, while the migration pathway may have been Northern at the Eocene-Oligocene transition (33.9 Ma). However, none of the abundant

perissodactyl fauna from south-eastern Europe migrated to Western Europe during this time, because, like their relatives in Central Asia, they did not survive to the Terminal Eocene cooling and aridity Event.

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Author contributions

B.M. led the writing of the paper. I.Z. conducted the field work and prepared the geological and chronological setting. B.M. and D.G. developed the taxonomical part and described the specimen. N.S. prepared the biogeographic part. The dispersion concept is developed by B.M. B.M., D.G., N.S., and I.Z. co-wrote the paper.

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Figure legends

528

529 Figure 1. Location and geological context of the Sladun fossiliferous locality (Bulgaria). **A**
530 Geographical and simplified geological setting of the Thrace basin (Bornovas and
531 Rondogianni-Tsiambaou, 1983; Cheshitev and Kanchev, 1989; Elmas, 2011; Less et al.,
532 2011). Fossil fauna sites: B – Borov dol, Byala coal basin; S – Sladun (white circle). **B**
533 Geological map of the northern edge of the South Sakar Depression and the mammal locality
534 of Sladun (late Eocene, Bulgaria; Kozhoukharov et al., 1993). [1.5 column]

535

536

537 Figure 2. *Bachitherium patriarcha* nov. sp. NMNHS FM3320 (Holotype). **A** labial view, **B**
538 lingual view, **C** stereoscopic view of the occusal surface (scale bare is 2cm). Dental
539 nomenclature **D** molar: 1 metaconid, 2 premetacristid, 3, internal postmetacristid, 4
540 protoconid, 5 preprotocristid, 6 internal postprotocristid, 7 entonconid, 8 preentocristid, 9
541 postentocristid, 10 hypoconid, 11 prehypocristid, 12 posthypocristid, 13 anterior basin, 14
542 posterior basin, 15 ectostylid, 16 anterior cingulid, 17 posterior cingulid; **e** premolar: 1
543 anterior stylid, 2 mesolabial conid, 3 transverse cristid, 4 posterior valley, 5 posterolabial
544 conid, 6 posterolabial cristid, 7 anterolabial cristid, 8 anterior cingulid. [2 columns]

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546

547 Figure 3. *Bachitherium* species metric data, basic information, and pictures of type specimen.
548 **A** *B. patriarcha* nov. sp. (NMNHS FM3320); **B** *B. vireti* (UCBL FSL9672); **C** *B. insigne*
549 (MNHN QU4258); **D** *B. curtum* (MNHN Qu3917); **E** *B. guirounetensis* (UM GAR441); **F** *B.*
550 *lavocati* (UM PDS1330). Diast. is length of the diastema. Measurements are in millimetres. [2
551 column]

552

553

554 Figure 4. Palinspastic map of Europe (based on Popov et al., 2004) with migration ways from
555 the late Eocene to the early Oligocene with biogeography of the Bachitheriidae during the
556 Priabonian and the Rupelian. **A** ca. 35 Ma, 1: second intra-Eocene mammalian turnover (after
557 the hypothesis of Franzen, 2003); **B** ca. 34-33 Ma, 2: Grande-Coupure event; **C** ca. 31 Ma, 3:
558 “*Bachitherium* event”. Dots: red *B. patriarcha* nov. sp.; blue *B. vireti*; green *B. insigne*;
559 yellow *B. curtum*; purple *B. guirounetensis*. [1.5 column]