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4

5 Short title: Oldest European ruminant and *Bachitherium* Event
6

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19 Abstract

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

36

37 *Keywords*

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

39

40 **1. Introduction**

41

42 During the Cenozoic, the Earth experienced several episodes of global warming and
43 cooling (Zachos et al., 2001; Vandenberghe et al., 2012). The most impressive cooling event,
44 called “Terminal Eocene Event” (Zachos et al., 2001) occurred at the Eocene-Oligocene
45 Boundary: a 4°C decrease of the deep-sea temperature is observed in Northern Atlantic
46 benthic fauna (Zachos et al., 2001; Liu et al., 2009) and a ca. 5°C decrease in Central Europe
47 (Mosbrugger et al., 2005, Uhl et al., 2007). The changes in the ocean circulation due to the
48 opening of the southern Ocean gateways created the first Antarctic glaciations forced by a
49 decrease in atmospheric CO₂ and a minimum solar insolation (Zachos et al., 2001; Liu et al.,
50 2009). This caused a global sea level drop of 30 to 90 meters depending on the region of the
51 world (Coxall and Pearson, 2007). This tectonic and climatic event led to the main worldwide
52 extinction phase of the entire Cenozoic (Raup and Sepkoski, 1984). In Asia, the Eocene

53 perissodactyl-dominant fauna was abruptly replaced by the Oligocene rodent/lagomorph-
54 dominant fauna, with a contemporaneous extreme change in the floral composition: the
55 Mongolian Remodelling (Meng and McKenna, 1998; Kratz and Geisler, 2010; Sun et al.,
56 2014,). These faunal turnovers were probably correlated with climatic and environmental
57 changes from a warm and humid to a cooler and drier world (Legendre, 1987; Hartenberger,
58 1998; Meng and McKenna, 1998). Until the beginning of the Oligocene, Europe was almost
59 isolated from Asia, notably by the Turgai Strait in Asia (Prothero, 1994). Stehlin (1909)
60 described an extinction/origination event at the Eocene-Oligocene boundary that he named
61 Grande-Coupure. This faunal turnover sees new Asiatic immigrants, including ruminants,
62 replacing most of the endemic Eocene European genera (Prothero, 1994; Hartenberger, 1998).
63 Around 60% of the mammal fauna disappears during the Grande-Coupure faunal turnover
64 (Prothero, 1994). Nevertheless, the issue of the synchronism of the Grande-Coupure
65 immigration event throughout Europe remains debated (Legendre, 1987; Baciú and
66 Hartenberger, 2001).

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

72

73 **2. Geological setting**

74

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

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

89 Three Paleogene formations have been distinguished there during the extensive
90 geological mapping accompanied by drilling (Kozhoukharov et al., 1995; Boyanov and
91 Goranov, 2001): the basal breccia-conglomerate-sandstone formation (from 300 to 500 m;
92 formed within an alluvial plain); the transgressive terrigenous-limestone-marl formation (100
93 – 600 m; formed in lagoonal to shelf environments); the pyroclastic-marl-limestone formation
94 (50 – 100 m; formed in shelf environment with reefs and pyroclastic material transported
95 from the Rhodope volcanoes). A Late Eocene age (Priabonian) has been determined thanks to
96 an abundant marine fauna found in the two upper formations (Kozhoukharov et al., 1995;
97 determinations by P. Dikova and V. Sapundzhieva), namely, the co-occurrence of *Nummulites*
98 *fabianii* Prever, *N. chavannesi* de la Harpe (A, B), *N. incrassatus* de la Harpe (A, B), *N. cf.*
99 *garnieri* Boussac. A similar fauna has been cited in the Upper Eocene limestones from the
100 northernmost parts of the Northern Thrace Basin in Turkish territory (Less et al. 2011). The
101 exact determination of the age of the basal breccia-conglomerate-sandstone formation is not
102 possible (terrestrial character, lack of guide fossils). Nevertheless, this terrestrial formation is
103 overlain by the two previous marine Priabonian formations and it most likely should be
104 referred to the early? Priabonian.

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

111

112 **3 Material and method**

113

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

117 The biostratigraphic framework follows the recent synthesis of Vanderberghe *et al.*
118 (2012). Measurements are in millimetres. The dental terminology follows Figure 2, based on
119 the work of Menecart and Métais (2015).

120

121 **4. Systematic palaeontology**

122

123 Ruminantia Scopoli, 1777

124 Tragulina Flower, 1883

125 Bachitheriidae Janis, 1987

126 *Bachitherium* Filhol, 1882

127 *Bachitherium patriarcha* nov. sp.

128 Figure 2

129

130 *4.1. Holotype and only specimen*

131

132 Right mandible with p2-m3, NMNHS FM3320 of the coll. of the National Museum of
133 Natural History, Sofia. Measurements: length of the diastema p1-p2 >14.0 mm; p2-p4 = 18.0;
134 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.

135

136 *4.2. Species etymology*

137

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

141

142 *4.3. Type locality and horizon*

143

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

147

148 *4.4. Diagnosis*

149

150 Very small *Bachitherium* differing from *Bachitherium vireti*, *B. curtum*, *B.*
151 *guirounetensis*, *B. lavocati*, and *B. insigne* in having the structure of p3 similar to that of the
152 p2. Only one posterior cristid descends from the mesiolabial conid on the p2 and p3. In *B.*
153 *vireti*, *B. curtum*, *B. guirounetensis*, *B. lavocati*, and *B. insigne*, the structure of the p3 is
154 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.

158

159 4.5. Description

160

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 styloid 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

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

192

193 4.6. Taxonomic attribution

194

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

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

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

227

228 **5. Discussion**

229

230 *5.1. Evolution of the Bachitheriidae*

231

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

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

253

254 *5.2. Biogeographic affinities of the Balkan land megafauna during the Eocene*

255

256 Known Paleogene mammals of Bulgaria are scarce (Bakalov and Nikolov, 1962;
257 Nikolov, 1985, Nikolov and Heissig, 1985) and remain largely undescribed (Spassov, 1989).
258 They show marked affinities with Asia and a high degree of isolation from Central and
259 Western Europe (Nikolov and Heissig, 1985; Spassov and Popov, 2007). Eocene Asian faunal
260 elements in the Balkans include the bothriodontin anthracothere *Bakalovia* Nikolov &
261 Heissig, 1985, based upon two species from the latest Bartonian/earliest Priabonian of Cherno
262 More quarry (Burgas region). The only other occurrence of the genus is from deposits of
263 similar age in Vietnam (Böhme et al., 2013), suggesting that it might be of Asian origin.
264 *Sivatitanops? rumelicus* (Toula, 1892) from middle/late Eocene deposits near Burgas in
265 Bulgaria (Bakalov and Nikolov, 1962; Nikolov and Heissig, 1985) and *Brachydiastematerium*
266 *transilvanicum* from the middle(?) Eocene of Romania (Nikolov and Heissig, 1985; Baci
267 and Hartenberger, 2001) are the only European brontotheres, and attest to the westernmost
268 extension of this North American and Asian family. The occurrence of the Asian
269 rhinocerotoid *Forstercooperia* is established (Tzankov et al., 2000) in the southeastern
270 Bulgarian Priabonian (Kanchev, 1995). It was first described as *Prohyracodon* aff.
271 *meridionale* and was mistakenly said to have come from Bobov Dol (Nikolov and Heissig,
272 1985) instead of the quarry from Borov Dol, near Sliven, as written on the original label
273 (Sofia NMNHS collections). The scarce *Prohyracodon* remains from Europe (Mera in
274 northwestern Romania, and Moettig in Slovenia) are only known from the
275 southern/southwestern periphery of the Paleogene Paratethys Sea (Heissig, 1989; Codrea,
276 2000; Baci and Hartenberger, 2001). The Central Asian amynodontid *Cadurcodon* (*C.*
277 *ardynense*, according to Spassov and Popov (2007), was reported from the
278 Bartonian/Priabonian deposits of Kameno (Burgas region) and Nikolaevo (North of Nova
279 Zagora) quarries of southeastern Bulgaria. The genus persisted in Central Romania till the
280 ?early Oligocene (Codrea, 2000). An undescribed allaceropine rhinocerotoid is also known
281 from the Burgas region (Debelt).

282 All these large mammals, together with *Bachitherium patriarcha* nov. sp. that
283 probably originated in the middle Eocene from Asia (Métais and Vislobokova, 2007),
284 demonstrate that the Balkan Peninsula was probably connected to Asia through the
285 Caucasian-Anatolian as well as the Balkan-Transylvanian regions during the middle / late
286 Eocene (Gabunia, 1964; Popov et al., 2004). Nevertheless, there is a strong endemism of the
287 middle Eocene mammal faunas of Central Anatolia (e.g. Licht et al., 2017; Métais et al.,
288 2017), which shows that the biogeographic affinities of the various islands forming the
289 northern margin of the Neotethys and Asia were more complex than previously thought.

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

292

293 5.3. Tectonism and polyphasic migrations during the Grande-Coupure

294

295 The Grande-Coupure is a well-documented major faunal event that greatly modified
296 the European fauna (e. g. Stehlin, 1909; Prothero, 1994). This Asiatic immigration is
297 supposed to have occurred at the base of the Oligocene when the Turgai Strait dried out,
298 permitting colonisation of Western Eurasia (Prothero, 1994). However, some forerunners of
299 this immigration can already be observed during the latest Eocene among reptiles and
300 mammals (Franzen, 2003; Rage, 2013; Solé et al., 2014). In parallel to the Priabonian massive
301 extinction of the Proviverrinae (Creodonta), the Asiatic Hyaenodontinae (Creodonta) and
302 *Cynodontis* (Carnivora) immigrated into Western Europe (Solé et al., 2014). This massive
303 faunal remodelling is named second Intra-Eocene mammalian turnover (Franzen, 2003).
304 Similarly, numerous artiodactyls (e.g. *Elomeryx*, *Anoplotherium*, *Diplobune*, and *Oxacron*)
305 are found for the first time in that area in latest Eocene deposits (Franzen, 2003; Erfurt &
306 Métais, 2007). The origin of these latest Eocene migrants could be Scandinavia (Franzen,
307 2003; see Fig. 4), but there is no strong evidence for this. Most of these new migrants do not
308 survive the Eocene-Oligocene transition (Baciu and Hartenberger, 2001).

309 The early Oligocene Western European immigration of ruminants occurred in two
310 distinct waves. The first immigrants are the Lophiomerycidae and Gelocidae, which belong to
311 the Asiatic cortege of the Grande-Coupure immigrants, marking the base of the Oligocene ca.
312 34-33 Ma (MP21; Mennecart, 2012; see Fig. 4). To reach western Europe from Asia, they
313 probably benefited from the sea level drop that dried out the Turgai Strait (Prothero, 1994).
314 Western European Bachitheriidae and Tragulidae only arrived 2 Myr later (Mennecart, 2012;
315 Mennecart and Métais, 2015). During the entire Eocene, Paratethysian deep waters filled with
316 flysch deposits connected the Northern Alpine depression to the Carpathian Basin and the
317 Greater Caucasus Basin (Popov et al., 2004; Berger et al., 2005) forming a long water barrier,
318 more than 50 km wide in the Alpine sea and 200-500 km in the Carpathian one, which
319 isolated south-eastern Europe from western Europe (Baciu and Hartenberger, 2001; see Fig.
320 4). Due to this barrier, the Bulgarian *Bachitherium* was unable to make it to western Europe at
321 that time.

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

324 Monteviale locality (Italy) to MP21 and the occurrence of *Epiaceratherium*. However, an age
325 of MP21 to MP23 has recently been suggested for this locality (Pandolfi et al. 2017), and we
326 favour a MP23 age. Only from ca. 31 Ma (MP23), Paratethys Sea environments turned into
327 shallow water and then into continental deposits diachronically from West to East (MP23;
328 Menecart et al., 2011; Berger et al., 2005). Synchronously, isotopic signal of the $\delta^{18}\text{O}$
329 changed drastically (Héran et al., 2010) indicating different air trajectories with different
330 moisture sources (Atlantic versus Paratethys) induced by the regression and by the Alpine-
331 Dinaridic orogenic system uplift that reached an estimated altitude of 1200 m (Kocsis et al.,
332 2014). The creation of this terrestrial land bridge between Western Europe and south-eastern
333 Europe (Berger et al., 2005) allowed the migration of the Bachitheriidae into Western Europe
334 (Fig. 4). We propose to name this faunal event, linking Western to south-eastern Europe fauna
335 by tectonics, the “*Bachitherium* event”. The Tragulidae were also involved in this dispersal,
336 because *Iberomeryx*, which was already known in Georgia during the earliest Oligocene
337 (Métais and Vislobokova, 2007), appears in Europe simultaneously. Moreover, we observe
338 that the Eocene south-eastern European perissodactyls disappeared in a similar fashion to
339 their relatives in Asia during the Mongolian Remodelling (Meng and McKenna, 1998; Kratz
340 and Geisler, 2010). The transition from warm and humid conditions towards cooler and dryer
341 environments may have caused the extinction of south-eastern European and many Asian
342 perissodactyls at the Eocene-Oligocene Boundary (Meng and McKenna, 1998) may have
343 boosted rodent and ruminant diversification (Meng and McKenna, 1998). Ruminants became
344 dominant in the Oligocene faunas of Eurasia (Blondel, 2001; Métais and Vislobokova, 2007).

345

346 **6. Conclusions**

347

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

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

361

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363

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375

376 **Author contributions**

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

381

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525

526 **Figure legends**

527

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]

545

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]