



**HAL**  
open science

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

Bastien Mennecart, Denis Geraads, Nikolai Spassov, Ivan Zagorchev

## ► To cite this version:

Bastien Mennecart, Denis Geraads, Nikolai Spassov, Ivan Zagorchev. Discovery of the oldest European ruminant in the late Eocene of Bulgaria: Did tectonics influence the diachronic development of the Grande Coupure?. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2018, 498, pp.1-8. 10.1016/j.palaeo.2018.01.011 . hal-02470733

**HAL Id: hal-02470733**

<https://hal.sorbonne-universite.fr/hal-02470733v1>

Submitted on 7 Feb 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 MENNECART B, GERAADS D, SPASSOV, N. 2018. Discovery of the oldest European ruminant in  
2 the late Eocene of Bulgaria: Did tectonics influence the diachronic development of the  
3 Grande Coupure ? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 498: 1-8.  
4

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

7 Bastien Mennecart<sup>1,2,3,\*</sup>, Denis Geraads<sup>2</sup>, Nikolai Spassov<sup>4</sup>, Ivan Zagorchev<sup>5</sup>  
8

9 <sup>1</sup>Naturhistorisches Museum Basel, Augustinergasse 2, 4001 Basel, Switzerland.

10 <sup>2</sup>CR2P, Paléobiodiversité et Paléoenvironnements, UMR 7207 (CNRS, MNHN, UPMC),  
11 Muséum National d'Histoire Naturelle, 8 rue Buffon, CP 38, F-75231 Paris Cedex 05, France.

12 <sup>3</sup>Naturhistorisches Museum Wien, Burgring 7, 1010 Vienna, Austria

13 <sup>4</sup>National Museum of Natural History, Bulgarian Academy of Sciences, Boulevard Tzar  
14 Osvoboditel 1, 1000 Sofia, Bulgaria.

15 <sup>5</sup>Geological Institute, Bulgarian Academy of Sciences, 1113 Sofia, Bulgaria  
16  
17

18 \*Corresponding author: [mennecartbastien@gmail.com](mailto:mennecartbastien@gmail.com)

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 CO<sub>2</sub> 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; Baciu 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; Baciu  
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; Baciu 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 *Cynodictis* (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

## 362 **Acknowledgments**

363

364 The authors gratefully acknowledge N. Gospodinov for discovering the fossil in 1987,  
365 L. Stoev for the information about the drilling locality, D. Dachev for donating the fossil to  
366 the NMNHS, C. Bouillet (MNHN) for preparing the material, L. Caze (MNHN) for taking the  
367 photos, G. Métais (MNHN) for helpful discussions, B. L. Beatty and an anonymous reviewer  
368 for improving a previous version of the manuscript, C. Baudouin (pollens & Cores) for  
369 searching pollens, as well as E. Robert (UCBL), C. Argot and G. Billet (MNHN), and  
370 L. Costeur (NMB). Special thanks go to T. Fairbanks-Freund (NMB) for improving the  
371 English text. We would like to acknowledge G. Métais, an anonymous reviewer, and the  
372 editor Falcon-Lang, for their most helpful remarks on the manuscript. The Swiss National  
373 Foundation is warmly thanked (BM) for granting the SNF Projects 200021\_159854 / 1,  
374 P300P2\_161065 & P3P3P2\_161066.

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

## 382 **References**

383

384 Baciu, C., Hartenberger, J.-L., 2001. Un exemple de corrélation marin–continental dans le  
385 Priabonien de Roumanie. Remarques sur la Grande Coupure. C. R. Acad. Sci. Paris  
386 333, 441–446.

387 Bakalov, P., Nikolov, I., 1962. Les Fossiles de Bulgarie. X. Mammifères Tertiaires. Académie  
388 des Sciences de Bulgarie, Sofia.

389 Becker, D., 2009. Earliest record of rhinocerotoids (Mammalia: Perissodactyla) from  
390 Switzerland: systematics and biostratigraphy. Swiss J. Geosci. 102, 489–504.

391 Berger, J.-P., Reichenbacher, B., Becker, D., Grimm, M., Grimm, K., Picot, L., Storni, A.,

392 Pirkenseer, C., Derer, C., Schaefer, A., 2005. Paleogeography of the Upper Rhine  
393 Graben (URG) and the Swiss Molasse Basin (SMB) from Eocene to Pliocene. *Int. J.*  
394 *Earth Sci.* 94, 697–710.

395 Blondel, C., 2001. The Eocene-Oligocene ungulates from Western Europe and their  
396 environment. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 168, 125–139.

397 Böhme, M., Aiglstorfer, M., Antoine, P.-O., Appel, E., Havlik, P., Métais, G., The Phuc, L.,  
398 Schneider, S., Setzer, F., Tappert, R., Ngoc Tran, D., Uhl, D., Prieto, J., 2013. Na  
399 Duong (northern Vietnam) – an exceptional window into Eocene ecosystems from  
400 Southeast Asia. *Zitteliana* 53, 120–167.

401 Bornovas, J., Rondogianni-Tsiambaou, T., 1983. Geological map of Greece 1:500 000.  
402 IGME, Athens.

403 Boyanov, I., Goranov, A., 2001. Late Alpine (Paleogene) superimposed depressions in parts  
404 of Southeast Bulgaria. *Geo. Balcanica* 31(3–4), 3–36.

405 Cheshitev, G., Kanchev, I., 1989. Geological map of P. R. Bulgaria 1:500 000. Committee of  
406 Geology, Sofia.

407 Codrea, V., 2000. Rinoceri și tapiri Terțiari din România. Presa universitări Clujeană, Cluj.

408 Coxall, H.K., Pearson, P.N., 2007. The Eocene-Oligocene Transition, in: Williams, M.,  
409 Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds), *Deep time perspectives on*  
410 *climate change marrying the signal from computer models and biological proxies.*  
411 *Geological Society, London*, pp. 351–388.

412 Elmas, A., 2011. The Thrace Basin: stratigraphic and tectonic palaeogeographic evolution of  
413 the Palaeogene formations of northwest Turkey. *Int. Geol. Rev.* 54(12), 1419–1442.

414 Erfurt, J., Métais, G., 2007. Endemic European Paleogene artiodactyls, in: Prothero, D.R.,  
415 Foss, S.E. (Eds), *The evolution of artiodactyls.* The Johns Hopkins University Press,  
416 Baltimore, pp. 59–84.

417 Franzen, J.L., 2003. Mammalian faunal turnover in the Eocene of central Europe. *Geol. Soc.*  
418 *Am. special paper* 369, 455–461.

419 Gabunia, L., 1964. The Oligocene Benara fauna of land vertebrates. Metzniereba Publisher  
420 House, Tbilisi.

421 Geraads, D., Bouvrain, G., Sudre, J., 1987. Relations phylétiques de *Bachitherium* Filhol,  
422 ruminant de l'Oligocène d'Europe occidentale. *Palaeovertebrata* 17, 43–73.

423 Hartenberger, J.-L., 1998. An Asia Grande Coupure. *Nature* 394, 321.

424 Heissig, K., 1978. Fossilführende Spaltenfüllungen Süddeutschlands und die Ökologie ihrer  
425 oligozänen Huftiere. *Mitt. Bayer. Staatssaml. Paläont. Hist. Geol.* 18, 237–288.

426 Heissig, K., 1989. The Allaceropine hyracodonts, in: Prothero, D.R., Schoch, R.M. (Eds) The  
427 evolution of Perissodactyls. Oxford University Press, New York, pp. 355–357.

428 Héran, M.A., Lécuyer, C., Legendre, S., 2010. Cenozoic long-term terrestrial climatic  
429 evolution in Germany tracked by  $\delta^{18}\text{O}$  of rodent tooth phosphate. *Palaeogeogr.*  
430 *Palaeoclimatol. Palaeoecol.* 285(3-4), 331–342

431 Janis, C.M., 1987. Grades and Clades in Hornless Ruminants Evolution: the Reality of the  
432 Gelocidae and the Systematic Position of *Lophiomeryx* and *Bachitherium*. *J. Vertebr.*  
433 *Paleontol.* 7, 200–216.

434 Kanchev, I., 1995. Geological map of Bulgaria 1:100000. Map sheet Sliven. Explanatory  
435 note. Committee of Geology and Mineral Resources, “Geology and Geophysics” Ltd.

436 Kocsis, L., Ozsvárt, P., Becker, D., Ziegler, R., Scherler, L., Codrea, V., 2014. Orogeny  
437 forced terrestrial climate variation during the late Eocene– early Oligocene in Europe.  
438 *Geology* 42(8), 727–730.

439 Kozhoukharov, D., Boyanov, I., Shilyafov, G., Kozhoukharova, E., Goranov, A.. 1993.  
440 Geological map of RP Bulgaria 1:100 000, Sheet Svilengrad. VTS, Troyan.

441 Kozhoukharov, D., Boyanov, I., Kozhoukharova, E., Goranov, A., Savov, S., Shilyafov, G.,  
442 1995. Explanatory Note to the Geological map of RP Bulgaria 1:100 000, Sheet  
443 Svilengrad. “Avers”, Sofia.

444 Kratz, B.P., Geisler, J.H. 2010. Eocene–Oligocene transition in Central Asia and its effects on  
445 mammalian evolution. *Geology* 38(2), 111–114.

446 Legendre, S., 1987. Les communautés de mammifères et leur milieu en Europe occidentale de  
447 l'Eocène supérieur et Oligocène. *Rev. Paléobiol.* 6, 183–188.

448 Less, G., Özcan, E., Okay, A., 2011, Stratigraphy and Larger Foraminifera of the Middle  
449 Eocene to Lower Oligocene Shallow-Marine Units in the Northern and Eastern Parts  
450 of the Thrace Basin, NW Turkey. *Turkish J. Earth Sci.* 20, 793–845.

451 Licht et al., 2017

452 Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S.R., Leckie,  
453 M.R., Pearson, A., 2009. Global cooling during the Eocene-Oligocene Climate  
454 transition. *Science* 323, 1187–1190.

455 Meng, J., McKenna, M.C., 1998. Faunal turnover of Palaeogene mammals from the  
456 Mongolian Plateau. *Nature* 394, 364–367.

457 Menecart, B., 2012. The Ruminantia (Mammalia, Cetartiodactyla) from the Oligocene to the  
458 Early Miocene of Western Europe: systematics, palaeoecology and  
459 palaeobiogeography. *GeoFocus* 32, 1–263.

- 460 Mennecart, B., 2015. The European ruminants during the "*Microbunodon* Event" (MP28,  
461 latest Oligocene): Impact of climate changes and faunal event on the ruminant  
462 evolution. PlosOne 10(2), e0116830.
- 463 Mennecart, B., Métais, G., 2015. *Mosaicomeryx* gen. nov., a ruminant mammal from the  
464 Oligocene of Europe, and the significance of "gelocids". J. Syst. Palaeont. 13(7), 581–  
465 600.
- 466 Mennecart, B., Becker, D., Berger, J.-P., 2011. *Iberomeryx minor* (Mammalia, Artiodactyla)  
467 from the Early Oligocene of Soulce (Canton Jura, NW Switzerland): systematics and  
468 palaeodiet. Swiss J. Geosci. 104(suppl 1), S115–S132.
- 469 Métais, G., Vislobokova, I., 2007. Basal ruminants, in: Prothero, D.R., Foss, S.E. (Eds), The  
470 evolution of artiodactyls. The Johns Hopkins University Press, Baltimore, pp. 189–  
471 212.
- 472 ; Métais et al., 2017
- 473 Métais et al., 2001
- 474 Mosbrugger, V., Utescher, T., Dilcher, D.L. 2005. Cenozoic continental climatic evolution of  
475 Central Europe. Proc. Natl. Acad. Sci. U.S.A. 102(42), 14964–14969.
- 476 Nikolov, I., 1985. Catalogue of the localities of tertiary Mammals in Bulgaria. Paleont.  
477 Stratigr. Lithol. 21, 43–62.
- 478 Nikolov, I., Heissig, K., 1985. Fossile Säugetiere aus dem Obereozän und Unteroligozän  
479 Bulgariens und ihre Bedeutung für die Paläogeographie. Mitt. Bayer. Staatssaml.  
480 Paläont. Hist. Geol. 25, 61–79.
- 481 Pandolfi, L., Carnevale, G., Costeur, L., Del Favero, L., Fornasiero, M., Ghezzi, E.,  
482 Maiorino, L., Mietto, P., Piras, P., Rook, L., Sansalone, G., Kotsakis, T., 2016.  
483 Reassessing the earliest Oligocene vertebrate assemblage of Monteviale (Vicenza,  
484 Italy). J. Syst. Palaeontol. 15(2), 83–127.
- 485 Popov, S.V., Rogl, F., Rozanov, A.Y., Steininger, F.F., Shcherba, I.G., Kovac, M., 2004.  
486 Lithological-Paleogeographic maps of Paratethys 10 Maps Late Eocene to Pliocene.  
487 Cour. Forschungsinst. Senckenb. 250, 1–46.
- 488 Prothero, D.R., 1994. The Eocene-Oligocene transition: paradise lost. Columbia University  
489 Press, New York.
- 490 Rage, J.-C., 2013. La "Grande Coupure" Eocène/Oligocène et les herpétofaunes (Amphibiens  
491 et Reptiles); problèmes du synchronisme des évènements paleobiogéographiques.  
492 Bull. Soc. Géol. France S7-XXVI(6), 1251–1257.
- 493 Raup, D.M., Sepkoski, J. Jr., 1984. Periodicity of extinctions in the geological past. Proc.



- 494 Nati. Acad. Sci. U.S.A. 81, 801–805.
- 495 Scherler, L., Menecart, B., Hiard, F., Becker, D., 2013. Evolution of terrestrial hoofed-  
496 mammals during the Oligocene-Miocene transition in Europe. *Swiss J. Geosci.* 106,  
497 349–369.
- 498 Spassov, N., 1989. On the taxonomic status of *Indricotherium Borissiak* and the giant  
499 Rhinocerotoids - *Indricotheres* (Perissodactylia). *C. R. Acad. Bulg. Sci.* 42(3), 61–64.
- 500 Spassov, N., Popov, V., 2007. History of the formation of the Bulgarian mammal fauna, in:  
501 Miteva, S., Mihova, B., Georgiev, K., Petrov, B., Vansink, D. (Eds), *The mammals,*  
502 *important for conservation in Bulgaria*, Dutch Mammal Society VZZ, Arnhem, pp.  
503 31–46.
- 504 Solé, F., Falconet, J., Laurent, Y., 2014. New Proviverrines (Hyaenodontida) from the Early  
505 Eocene of Europe; Phylogeny and Ecological Evolution of the Proviverrinae. *Zool. J.*  
506 *Linn. Soc.* 171, 878–917.
- 507 Stehlin, H.G., 1909. Remarques sur les faunules de mammifères des couches éocènes et  
508 oligocènes du Bassin de Paris. *Bull. Soc. Géol. France* 9, 488–520.
- 509 Sudre, J., 1986. Le genre *Bachitherium* Filhol 1882 (Mammalia, Artiodactyla): diversité  
510 spécifique, phylogénie, extension chronologique. *C. R. Acad. Sci. Paris* 303(8), 749–  
511 754.
- 512 Sun, J, Ni, X., Bi, S., Wu, W., Ye, J., Meng, J., Windley, B.F., 2014. Synchronous turnover of  
513 flora, fauna, and climate at the Eocene–Oligocene Boundary in Asia. *Sci. Rep.* 4, 1–6.
- 514 Tzankov, T., Spassov, N., Nikolov, G., 2000. On the character of Late Paleogene and  
515 Neogene relief and landscape building in South West Bulgaria. *Rep. Geod.* 4(49),  
516 137–144.
- 517 Uhl, D., Klotz, S., Traiser, C., Thiel, C., Utescher, T., Kowalski, E., Dilcher, D.L., 2007.  
518 Cenozoic paleotemperatures and leaf physiognomy – a European perspective.  
519 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 248, 24–31.
- 520 Vandenberghe, N., Speijer, R., Hilgen, F.J., 2012. The Paleogene period, in: Gradstein, F.M.,  
521 Ogg, J.G., Shmitz, M., Ogg, G. (Eds), *A geological time scale*. Elsevier, Amsterdam  
522 pp. 855–922.
- 523 Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and  
524 aberrations in global climate 65 Ma to present. *Science* 292, 686–693.

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]