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1 **First detailed description of *Cricetodon albanensis* from La Grive-**
2 **Saint Alban (France)**

3
4 Raquel López-Antoñanzas^{1,2} and Pablo Peláez-Campomanes²

5
6 ¹Laboratoire de Paléontologie, Institut des Sciences de l'Évolution (ISE-M, UMR 5554,
7 CNRS/UM/IRD/EPHE), Université de Montpellier, Montpellier, France

8 ²Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, Madrid,
9 Spain.

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12 The material of *Cricetodon albanensis* (Rodentia, Cricetodontinae) from La Grive-Saint
13 Alban (carrière Milliat, fissure M) is described in detail for the first time. This species is a
14 large sized Cricetodontinae that is characterized by having incomplete ectolophs and
15 indistinct or very short mesolophs on the upper molars and by the presence of double
16 metalophids and the absence of mesolophids on the lower molars. The acquisition of a
17 dominant anterior metalophulid on the m1 has been developed independently in different
18 lineages over time and could be related to a change in dietary habits towards more abrasive
19 food, which may be linked to the cooling event Mi3 (circa 13.8 Ma). However, the
20 development of this character does not seem to have been enough to prevent these Middle
21 Miocene European cricetodontines to become extinct, while their more evolved European
22 competitors (*Hispanomys*) flourished.

23 Keywords: *Cricetodon albanensis*, Rodentia, Cricetodontinae, Miocene, France,
24 Systematics

25

26 **Introduction**

27 La Grive-Saint-Alban is the name used to refer to various Upper Aragonian pits located on
28 the territory of the municipality of Saint-Alban-de-Roche (Isère, France) (Mein and
29 Ginsburg, 2002). All pits have yielded micromammals, but remains of *Cricetodon albanensis*
30 have only been found in La Grive L (pit Lechartier) and M (pit Milliat) (Maridet, 2003). As
31 related in López-Antoñanzas and Mein (2009, 2011), in 1887, Depéret revealed the presence
32 of two taxa of *Cricetodon* in La Grive Saint-Alban: *C. medium* and *C. rhodanicum* (Depéret
33 1887a, 1887b). In 1925, Schaub revised the myomorph cricetine rodents and he included all
34 the large-sized *Cricetodon* species from the Upper Aragonian (Sansan, La Grive Saint-Alban,
35 swiss Molasa, Ries) in the species *Cricetodon sansaniensis* Lartet, 1851. In this work he
36 synonimized *C. rhodanicus* with *C. sansaniensis* because the former taxon could be
37 differentiated neither by the morphology nor by the size with the latter one (Schaub, 1925:9).
38 Moreover, during the revision of the material of *C. sansaniensis* housed in the Museum of
39 Lyon, he identified the presence of two morphotypes for *Cricetodon sansaniensis* from La
40 Grive Saint-Alban: the first one, slightly larger and with less developed ectolophs
41 (*Cricetodon sansaniensis*) and the smaller one, with better developed ectolophs (*Cricetodon*
42 *sansaniense* var. *decedens*) (Schaub, 1925:13). In 1963, Freudenthal pointed out that
43 *Cricetodon sansaniensis* from La Grive Saint-Alban should be reallocated to *C. rhodanicus*.
44 After that, Mein and Freudenthal (1971b) erected the new species *Cricetodon albanensis* on
45 the basis of a right mandible with m1-m3 (65484) from La Grive M (pit Milliat). The large
46 sized *Cricetodon* material from La Grive Saint-Alban (pit M and pit L7) has been considered

47 as belonging to this species. No additional material of this taxon has been recovered up to
48 date.

49 Mein and Freudenthal's (1971b) work dealt with a whole revision and a new classification
50 of the European tertiary cricetid record. Thus nor description neither comparisons nor
51 photographs of the material of *Cricetodon albanensis* could be provided but merely a brief
52 diagnosis. Therefore, the aim of the present work is to offer a detailed description, an
53 extended and differential diagnosis of this taxon.

54 **Material and Methods**

55 The systematic study presented below is based on the examination of original specimens
56 listed in Tab. 1. The material described here comes from La Grive Saint-Alban and it is
57 housed in the Naturkunde Museum of Berlin. It includes a number of osseous (from the
58 cranial and postcranial skeleton) and dental remains (Figs 1-2). The present work focuses on
59 the latter. They are:

60 MB. Ma. 27835: 3 maxillae with M1-M3 (specimen labelled as *Cricetodon minus*); MB. Ma.
61 27827: left hemi-mandible with m1-m3 (specimen labelled as *Cricetodon rhodanicus*); MB.
62 Ma. 27829: 2 hemi-mandibles with m1-m3; 1 hemi-mandible with m2-m3 and a maxillary
63 fragment with M2-M3, MB. Ma. 27828: 1 hemi-mandible with m1-m3 and 1 hemi-mandible
64 with m1-m2, MB. Ma. 27831: 2 maxillary fragments with M2; 1 maxillary fragment with
65 M1-M2; 1 maxillary fragment with M1; 1 maxillary fragment without teeth and 3 isolated
66 teeth (1M1 and 2M2) (specimens labelled as *Cricetodon sansaniensis*); MB. Ma. 27848: 2
67 isolated m1, MB. Ma. 27850: 8 isolated teeth (a broken M1, 1 M3, 1m1, 2m2 and 3m3, MB.
68 Ma. 27849: 6 isolated M1 (specimens labelled as *Cricetidae* indet).

69 The measurements of the occlusal surface of the teeth (maximum length and maximum
70 width) have been taken following van de Weerd (1976) for all dental elements except for the

71 second upper molars, for which the maximum length has been taken parallel to the labial side
72 of the tooth. Measurements have been obtained with a Nikon digital counter CM-6S
73 measuring device and descriptive statistics were calculated using Microsoft Excel 2016 (Tab.
74 2).

75 First, second, and third lower molars are designed as m1, m2, and m3 respectively
76 whereas first, second, and third upper molars as M1, M2, and M3. The terminology used in
77 the tooth descriptions follows the rodent dental terminology of López-Antoñanzas et al.
78 (2010).

79 **Systematics**

80 Family Cricetidae Fischer, 1817

81 Tribu Cricetodontini Simpson, 1945

82 Genus *Cricetodon* Lartet, 1851

83 *Cricetodon albanensis* Mein and Freudenthal 1971b (Figs. 1 and 2)

84 **Diagnosis:** Size similar to *C. sansaniensis* but with ectolophs slightly more developed;
85 mandible slightly more oblique than the latter species so that the mental foramen is hidden in
86 vertical view; diastema slightly concave; mesolophid absent; metalophulid always anterior;
87 M1 four-rooted (translated from Mein and Freudenthal, 1971b).

88 **Emended diagnosis:** *Cricetodon* species of large size, brachyodont cheek teeth with thick
89 and crenulated enamel and third lower and upper molars not reduced in size; upper molars
90 with low cingula surrounding the labial valleys, incomplete ectolophs and very short or
91 indistinct mesolophs; lower molars with complete metalophulid I and usually incomplete
92 metalophulid II and without mesolophid.

93 **Differential diagnosis:** *Cricetodon albanensis* differs from all the Middle Miocene species of
94 *Cricetodon* in having an indistinct posteroloph on the M3 and from all but *C. sansaniensis*, *C.*
95 *jumaensis* and *C. engesseri* in its larger size (Fig. 3). *Cricetodon albanensis* differs from *C.*
96 *meini* and *C. aureus* in lacking the ectomesolophid and having double metalophulid on the
97 lower molars, in having the M1 with weak or absent lingual anteroloph and mesoloph, with
98 more developed anterior ectoloph and forward paracone spur and in the presence of a
99 vestigial lingual posteroloph. It differs from *C. orientalis* in having shorter backward
100 paracone spur and weaker (even absent) mesolophs on the upper molars, in having the lingual
101 anteroloph less developed, a protostyle and a vestigial lingual posteroloph on the M1, in
102 having the M2 more elongated, in lacking the posteroloph on the M3, and in having the m1
103 with a well-developed labial anterolophid and without a metaconid ridge. *Cricetodon*
104 *albanensis* differs from *C. soriae* in having the M1 with a weak or absent lingual anteroloph,
105 more developed anterior ectoloph and backward paracone spur, with a protostyle and a
106 vestigial lingual posteroloph, the M2 more elongated than in *C. soriae*, no mesoloph on the
107 M3 and in having the labial anterolophid on the m1. *Cricetodon albanensis* differs from *C.*
108 *jotae* in the presence of a protostyle on the M1, in showing no mesoloph on the M3, and in
109 lacking a ridge on the metaconid and having the labial anterolophid well developed on the
110 m1. *Cricetodon albanensis* is distinct from *C. sansaniensis* in having the anterior ectoloph
111 and backward paracone spur better developed and in the presence of a protostyle on the M1,
112 in having the M2 more elongated than *C. sansaniensis*, and in the absence of a mesoloph on
113 the M3. *Cricetodon albanensis* is distinct from *C. bolliegeri* in having a weak or absent
114 lingual anteroloph, in lacking the enterostyle on the M1, in having a shorter backward
115 paracone spur on the M2 and M3, and in the absence of an ectostylid and ectomesolophid on
116 the m1. *Cricetodon albanensis* differs from *C. jumaensis* in having a weak or absent lingual
117 anteroloph on the M1, a weaker backward paracone spur on the M2 and M3, in lacking the

118 mesoloph and the posteroloph on the M3, in having a well-developed labial anterolophid, and
119 lacking the entomesolophid on the m1. It differs from *C. nievei* and *C. engesseri* in having
120 weak or absent lingual anteroloph on the M1, in the presence of a protostyle on the M1, in
121 having the M2 more elongated and the backward paracone spur and the mesoloph shorter.

122 ***Description of the material housed in the Naturkunde Museum of Berlin***

123 *M1*: The M1 of *Cricetodon albanensis* show a shallow and narrow groove between the two
124 sub-equal lobes of the anterocone. The labial anterocone bears an anterior ectoloph (remains
125 of the labial anteroloph). The lingual anterocone connects to the protocone by the
126 anterolophule. The lingual spur of the anterolophule is either present (e.g., MB. Ma. 27835-1,
127 MB. Ma. 27831-3, Fig.1D) or absent (MB. Ma. 27835-2, Fig.1A). These teeth have low
128 cingula surrounding the labial valleys. The protosinus is partially closed by a protostyle. The
129 anterior ectoloph is short, high as the anterocone and does not reach the anterior wall of the
130 paracone. The forward paracone spur is absent. The protolophule is anterolabially directed.
131 The backward paracone spur is short but distinct and the posterior ectoloph is absent. The
132 mesoloph is very short or indistinct (as in MB. Ma.27849-2 and MB. Ma. 27849-4, Figs II,
133 K). The sinus is nearly transverse and partially closed by a ridge originating from the
134 hypocone. The labial posteroloph is very short and disappears with wear. The lingual one is
135 indistinct in all but one specimen (MB.Ma.27835-3, Fig. 1C), in which it is very short. These
136 teeth have four roots.

137 *M2*: In occlusal view, the outline of these teeth is sub-rectangular, longer than wide, with the
138 posterior part somewhat narrower than the anterior one. They have quite developed lingual
139 anteroloph and a narrow but distinct protosinus in the anterior margin. The anterosinus is
140 usually open due to the absence of anterior ectoloph. The forward paracone spur is short but
141 distinct in all specimens. The posterior ectoloph is absent. A true mesoloph is indistinct and

142 merely a slight inflation at the beginning of the anterior arm of the hypocone is observed. The
143 protolophule is slightly anterolabially oblique. The anteriorly directed sinus is partially or
144 completely closed by a ridge originating from the hypocone. The labial posteroloph is very
145 short and disappears with wear. The lingual posteroloph is usually indistinct, except for a few
146 specimens (e.g. MB. Ma. 27835-1, MB. Ma. 27831-5, Figs 1B and P). These teeth have four
147 roots.

148 *M3*: The outline of these teeth in occlusal view is rounded, longer than wide, with its
149 posterior part much narrower than the anterior one. The labial anteroloph is long and the
150 lingual one absent. Both the anterior ectoloph and the forward paracone spur are lacking. The
151 backward paracone spur is short and the posterior ectoloph is absent, so the mesosinus
152 remains open. The protolophule is slightly anterolabially directed. These teeth lack the
153 posteroloph, but a small posterosinus is observed. The sinus is nearly transverse. These teeth
154 have three roots. The M3 of *C. albanensis* are not very reduced, as shown by the low value of
155 the ratio mean LM1/mean LM3 (Tab. 3).

156 *m1*: The occlusal outline of these teeth is sub-rectangular, longer than wide, with the anterior
157 part somewhat rounded and narrower than the posterior one. The lingual anterolophid is
158 absent, whereas the labial one is well developed, but does not reach the anterior side of the
159 protoconid. All specimens show a double metalophulid. The metalophulid I is directed
160 anterolabially and it connects the metaconid with the anteroconid. The metalophulid II is
161 usually incomplete and does not reach the posterior side of the metaconid except for
162 specimen MB. Ma. 27829-2 (Fig. 2D). None of the specimens show a mesolophid. The
163 sinusid is directed anterolingually. There is a small and semi-circular sinusid on the posterior
164 wall of the hypoconid. The posterolophid does not reach the posterior side of the entoconid.
165 These teeth are two-rooted.

166 *m2*: These teeth are rectangular in shape, although they are anteriorly and posteriorly
167 rounded. They show a strong labial anterolophid that reaches the anterolabial side of the
168 protoconid. The metalophulid and the hypolophulid are anterolabially directed. A low ridge
169 closes the mesosinusid. As for the *m1*, all the specimens show a double metalophulid with the
170 metalophulid II more developed than in the *m1* but still short. The mesolophid is absent. The
171 posterolophid is long, but does not reach the posterior side of the entoconid. They are two or
172 three rooted.

173 *m3*: The occlusal outline of these teeth is trapezoidal, longer than wide, with the posterior
174 part rounded and narrower than the anterior one. The labial anterolophid is well developed
175 and connected to the anterior wall of the protoconid, closing the protosinusid. All the
176 specimens show a double metalophulid with the metalophulid II longer than in the *m1* and
177 the *m2*. The mesolophid is absent. A low ridge usually closes the nearly transverse sinusid.
178 The posterolophid is short and the labial sinusid, situated on the posterior wall of the
179 hypoconid, is very weak or lacking. These teeth are two-rooted.

180 **Discussion**

181 *Cricetodon albanensis* is one of the western European Middle Miocene species that are
182 characterized by having brachyodont cheek teeth with short or absent ectolophs. This species
183 together with *C. meini*, *C. aureus*, *C. jotae*, *C. sansaniensis*, *C. soriae*, *C. bolligeri*, *C.*
184 *jumaensis*, and *C. engesseri*, was included by Prieto et al. (2010) inside a single group, which
185 they called “group 5”. The topology of the tree obtained via the tip-dating Bayesian analysis
186 that includes most of the species of *Cricetodon* (López-Antoñanzas and Peláez-Campomanes,
187 2021) shows a clade that comprises all the above-mentioned species of *Cricetodon* and two
188 additional ones: *Cricetodon nievei* and *Cricetodon orientalis*. These two species should be
189 added in “group 5” (*sensu* Prieto et al., 2010). However, preliminary results of a larger

190 phylogenetic analysis (López-Antoñanzas et al. in prep.) provide evidence that *C. meini* and
191 *C. aureus* should be excluded from this group as they may in fact belong to a more basal
192 clade, which includes a set of plesiomorphic species of *Cricetodon* from China.

193 The sample of *Cricetodon albanensis* (Rodentia, Cricetodontinae) from La Grive-Saint
194 Alban housed in the Museum für Naturkunde in Berlin (Germany) shows a low degree of
195 morphological variability in this taxon, a characteristic common in Upper Aragonian
196 populations of *Cricetodon*. *Cricetodon albanensis* shows some progressive characters when
197 compared with the remaining Miocene congeneric species, such as a more pronounced
198 anterior ectoloph and backward paracone spur on the upper molars and the presence of a
199 strong anterior metalophulid and the absence of mesolophids on the lower molars (Figs 1 and
200 2). However, this taxon also retains primitive characters, such as the presence of a posterior
201 (though incomplete) metalophulid on the lower molars, the existence of a protostyle and a
202 lingual spur of the anteroloph on the first upper molar, the loss of mesolophs, and the
203 presence of labial cingula surrounding the valleys on the upper molars (Figs 1 and 2).

204 The results of the phylogenetic analyses carried out by López-Antoñanzas and Peláez-
205 Campomanes (2021) provide evidence that the clade to which *C. albanensis* belongs
206 originated in the Early Miocene of Turkey. This clade includes most of the western Middle
207 Miocene species of *Cricetodon* and it has an independent origin from the more derived
208 European cricetodontines (*Hispanomys* and *Ruscinomys*).

209 *Cricetodon albanensis* has been considered to originate from *C. sansaniensis* (Mein and
210 Freudenthal 1971b), which is in agreement with the results obtained by López-Antoñanzas
211 and Peláez-Campomanes (2021). However, some differences are obvious between the
212 morphology of the cheek teeth of *C. albanensis* with *C. sansaniensis*. The first one concerns
213 the absence of a well-developed mesoloph in the upper molars of *C. albanensis*. Whereas this

214 structure is usually indistinct in *C. albanensis*, it is well-developed in *C. sansaniensis*. This is
215 particularly remarkable in the case of the M3. The second difference regards the degree of
216 development and position of the metalophulids. Whereas *C. albanensis* shows a double
217 metalophulid on the m1, with the anterior one complete and stronger than the posterior
218 (which is incomplete), *C. sansaniensis* has a strong posterior metalophulid (when it is double
219 the posterior metalophulid is stronger than the anterior one). It is interesting that the presence
220 of a dominant anterior metalophulid on the m1 is a trait that has been acquired independently
221 in different lineages through time. According to the topology of the tree of López-Antoñanzas
222 and Peláez-Campomanes (2021), inside the clade to which *C. albanensis* belongs (“group
223 5”), this trait would have appeared three times homoplastically at approximately 14 Ma: in
224 (*C. engesseri*+*C. nievei*), (*C. bolligeri*+*C. jumaensis*) and in *C. albanensis*. Taking into
225 account that circa 13.8 Ma an event of cooling has been evidenced (Miller et al. 2020), the
226 so-called Mi3 event, it is plausible that the presence of a strong anterior metalophulid on the
227 m1 could be related to a change in dietary habits toward food that includes more abrasive and
228 fibrous plants. Moreover, according to López-Antoñanzas and Peláez-Campomanes (2021),
229 the evolutionary radiation of another European clade of independent origin such as
230 *Hispanomys* took place during the Mi3 event. Not only have these cricetodontines acquired
231 the trait of having a strong anterior metalophulid but they also have reduced the length of the
232 third molars and developed complete backward paracone spurs. These characters may have
233 improved their diet specialization and made them more successful in those increasingly open
234 environments compared to the Middle Miocene cricetodontines, which were driven to
235 extinction.

236 It is uneasy to elucidate what *Cricetodon albanensis* gave rise to. Mein and Freudenthal
237 (1971b) already rejected the idea that *Hispanomys* evolved from *Cricetodon albanensis* due
238 to the lack of mesolophids on the lower molars (a derived character), which are present in

239 early species of *Hispanomys*. This hypothesis is reinforced by the results of López-
240 Antoñanzas and Peláez-Campomanes (2021), according to which *Cricetodon albanensis*
241 would be a dead-end offshoot inside the Cricetodontinae.

242

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- 327

Taxon	Locality	Institution	Temporal range	References
<i>Cricetodon aureus</i>	Vieux Collonges (France)	UL, MHNL, NBC	15.2-14	Mein & Freudenthal, 1971a
<i>Cricetodon meini</i>	Vieux Collonges (France)	UL, MHNL, NBC	15.2-14	Mein & Freudenthal, 1971a
<i>Cricetodon orientalis</i>	Tieersihabahe (China)	IVPP	15-13.4	Bi, 2005
<i>Cricetodon soriae</i>	Somosaguas , Las Planas 4A y 4B, Las Umbrias 11, 16, 19, 20 (Spain)	UCM, MNCN	14.3-13.9	López Guerrero et al, 2013
<i>Cricetodon jotae</i>	Manchones (Spain)	NBC, UU	13.6-12.6	Mein & Freudenthal, 1971b; López Guerrero et al., 2014
<i>Cricetodon sansaniensis</i>	Sansan (France)	MNHN, NMB	14.2-13.6	Baudelot, 1972; Maridet & Sen, 2012
<i>Cricetodon bolliegeri</i>	Petersbuch 10 (Germany)	BSPG, PIMUZ	13.9-13.8	Rummel, 1995
<i>Cricetodon albanensis</i>	La Grive-St. Alban M (France)	MB, UL, NBC	13-11.1	Mein & Freudenthal, 1971b
<i>Cricetodon jumaensis</i>	Petersbuch 18 , Schmidrüti (Germany)	SMF	13.9-13.8	Rummel, 2001
<i>Cricetodon engesseri</i>	Chäzerentobel 505m Schauenberg-Langriet 690m (Switzerland)	NMB	14-13.9	Rummel & Kälin, 2003
<i>Cricetodon nievei</i>	Toril 3A Las Planas 5H, Toril 2 y 3B (Spain)	MNCN	12.6-12.4	López Guerrero et al., 2014

328

329 **Abbreviations**

330 BSPG- Bayerische Staatssammlung für Paläontologie und Geologie

331 IVPP- Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of

332 Sciences in Beijing

333 MB-Naturkunde Museum of Berlin

334 MHNL- Natural History Museum of Lyon

335 MNCN- National Museum of Natural Sciences (CSIC)

336 NBC- Naturalis Biodiversity Center

337 NMB- Naturhistorisches Museum Basel

338 PIMUZ- Paläontologisches Institut und Museum - Universität Zürich

339 SMF- Forschungsinstitut Senckenberg Frankfurt am Main

340 UCM- Department of Paleontology, Complutense University

341 UL- Faculty of Sciences, Lyon University

342 UU-Faculty of Earth Sciences, Utecht University

343

344 **Table 1.** Material used for comparisons in this study. In bold are highlighted the type
345 localities.

346

	Length					Width				
	N	min.	mean	max.	s.d.	N	min.	mean	max.	s.d.
m1	8	2,60	2,86	2,99	0,136	8	1,73	1,81	1,97	0,090
m2	8	2,58	2,72	2,80	0,088	8	2,58	2,72	2,80	0,088
m3	8	2,55	2,66	2,95	0,130	8	1,83	1,97	2,12	0,102
M1	12	3,28	3,41	3,62	0,088	12	2,07	2,20	2,30	0,075
M2	8	2,49	2,64	2,83	0,130	9	1,95	2,09	2,20	0,093
M3	5	2,04	2,10	2,17	0,054	5	1,86	1,94	2,01	0,054

347

348

349 **Table 2.** Descriptive statistics of Length and Width for different dental elements of
350 *Cricetodon albanensis* material from La Grive Saint Alban deposited in the Naturkunde
351 Museum of Berlin. N= number of specimens; min.= minimum; max.=maximum; s.d.=
352 standard deviation.

353

Taxa	Locality	Age	Lm1/Lm3	LM1/LM3	reference
<i>C. aureus</i>	Vieux-Collonges	MN4/5	1.10	1.59	López Guerrero et al., 2013
<i>C. meini</i>	Vieux-Collonges	MN4/5	1.06	1.60	Freudenthal & Martín Suarez, 2015
<i>C. meini</i>	Mühlbach	MN5	1.07	1.41	Daxner-Höck, 2003
<i>C. soriae</i>	Las Umbrias 11	MN5	0.99	1.47	López Guerrero et al., 2013
<i>C. soriae</i>	Las Umbrias 19	MN5		1.56	López Guerrero et al., 2013
<i>C. soriae</i>	Las Umbrias 20	MN5	0.99		López Guerrero et al., 2013
<i>C. soriae</i>	Somosaguas	MN5	1.02		Hernández Fernández et al., 2006
<i>C. jumaensis</i>	Petersbuch 18	MN5	1.03	1.52	Rummel, 2001
<i>C. jumaensis</i>	Petersbuch 35	MN6	1.11	1.63	Rummel, 2001
<i>C. sansaniensis</i>	Sansan	MN6	1.08	1.62	Maridet & Sen, 2012
<i>C. jotae</i>	Manchones	MN6	1.12	1.69	Freudenthal & Martín Suarez, 2015
<i>C. bolligeri</i>	Petersbuch 10	MN6	1.10	1.63	Rummel, 1995
<i>C. engesseri</i>	Chräzerentobel 505m	MN6	1.34	1.33	Rummel & Kälin, 2003
<i>C. engesseri</i>	Schauenberg-Langriet 690m	MN6	1.16	1.79	Rummel & Kälin, 2003
<i>C. orientalis</i>	Tieersihabahe Loc. 9018	MN6	1.08	1.59	Bi, 2005
<i>C. nievei</i>	Toril 3A	MN7/8	1.13	1.70	López Guerrero et al., 2014
<i>C. albanensis</i>	La Grive M	MN7/8	1.13	1.75	Rummel, 2001
<i>C. albanensis</i>	La Grive (MB collection)	MN7/8	1.08	1.62	This study

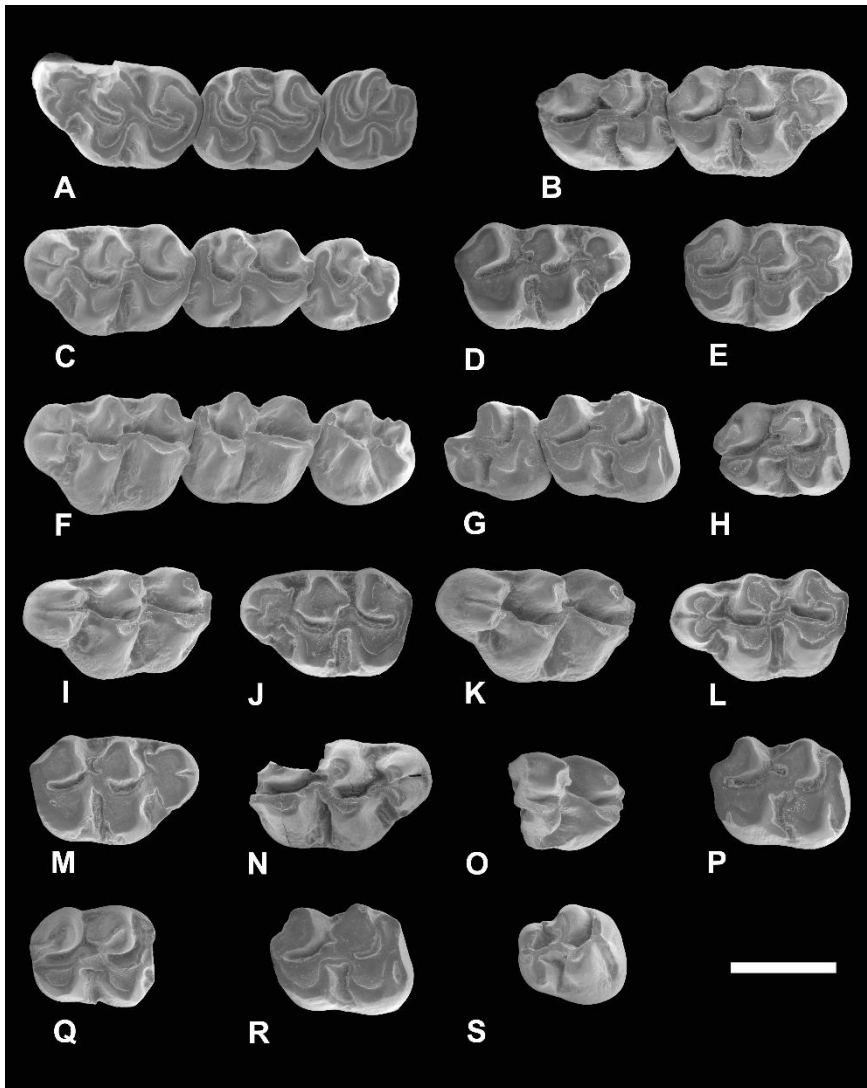
354

355 **Table 3.-** First/third molar length ratio for species of *Cricetodon* from various localities used for
356 morphological comparison. MN chronology according to Van der Meulen et al., 2011.

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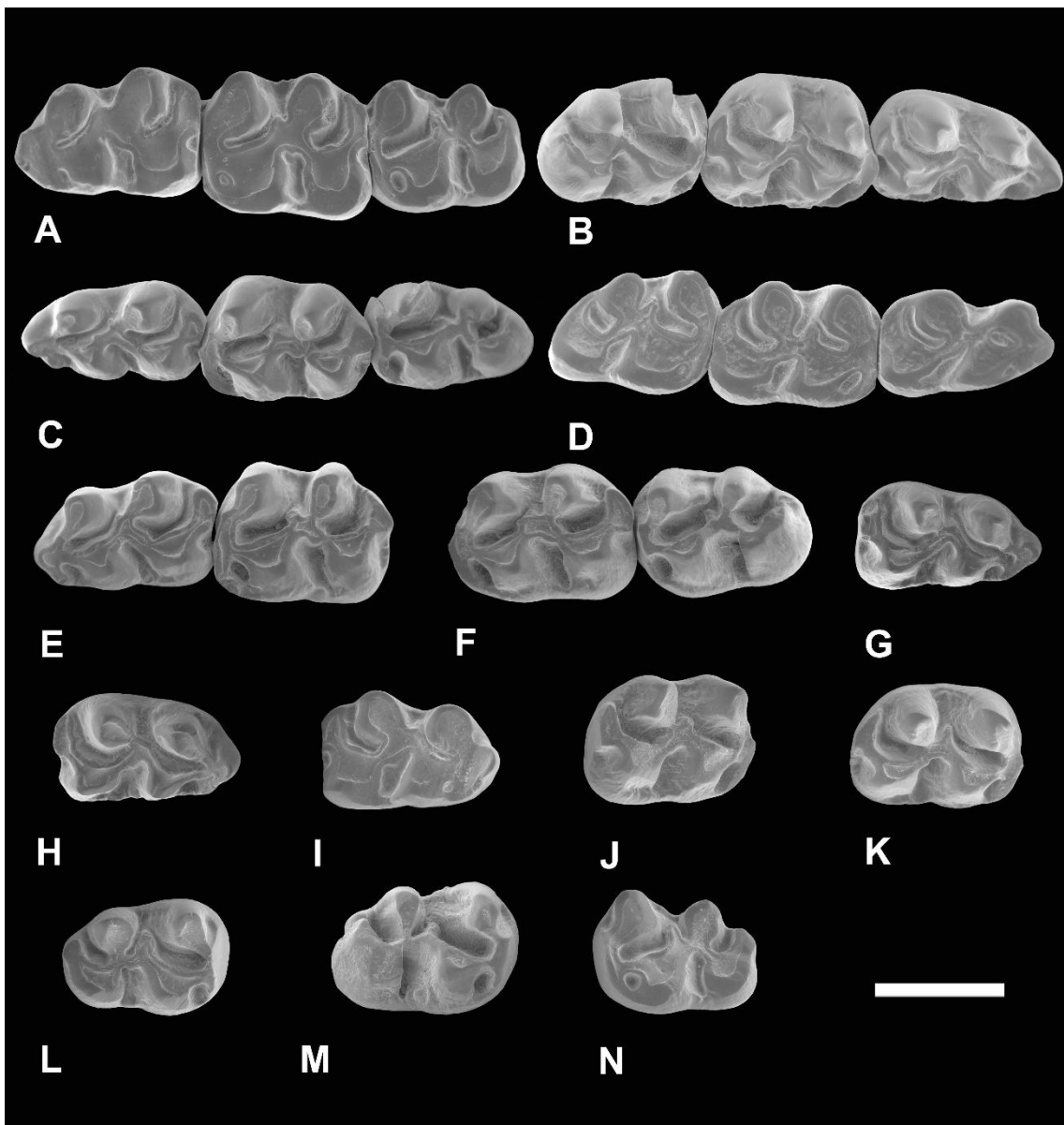
358 **Figure captions**

359 Fig. 1. Upper molars of *Cricetodon albanensis*. **A.** Left maxilla with M1-M3 (MB. Ma.
 360 27835-2). **B.** Right maxilla with M1-M2 (MB. Ma. 27831-1). **C.** Left maxilla with M1-M3
 361 (MB. Ma. 27835-1). **D.** Right M1 (MB. Ma. 27831-3). **E.** Right M1 (MB. Ma. 27831-6). **F.**
 362 Left maxilla with M1-M3 (MB. Ma. 27835-3). **G.** Right maxilla with M1-M2 (MB. Ma.
 363 27829-3). **H.** Right M2 (MB. Ma. 27831-4). **I.** Left M1 (MB. Ma. 27849-2). **J.** Left M1 (MB.
 364 Ma. 27849-5). **K.** Left M1 (MB. Ma. 27849-4). **L.** Left M1 (MB. Ma. 27849-3). **M.** Right
 365 M1 (MB. Ma. 27849-6). **N.** Right M1 (MB. Ma. 27849-1). **O.** Left M1 (MB. Ma. 27850-8).
 366 **P.** Right M2 (MB. Ma. 27831-5). **Q.** Right M2 (MB. Ma. 27831-7). **R.** Right M2 (MB. Ma.
 367 27831-2). **S.** Right M3 (MB. Ma. 27850-4). Scale bar represents 2mm.



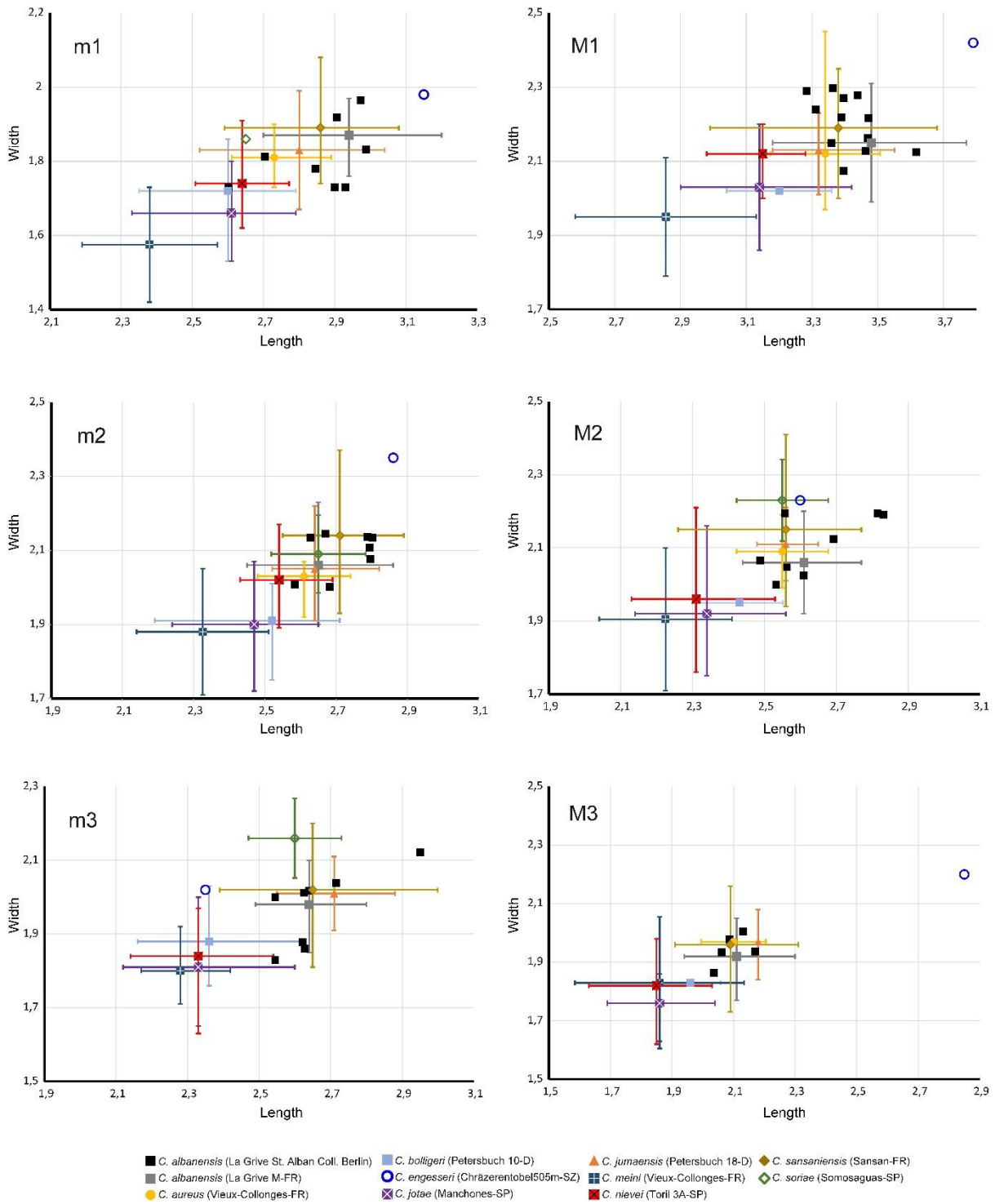
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369 Fig. 2. Lower molars of *Cricetodon albanensis*. **A.** Left mandible with m1-m3 (MB. Ma.
 370 27827). **B.** Right mandible with m1-m3 (MB. Ma. 27828-2). **C.** Left mandible with m1-m3
 371 (MB. Ma. 27829-1). **D.** Right mandible with m1-m3 (MB. Ma. 27829-2). **E.** Left mandibular
 372 fragment with m1-m2 (MB. Ma. 27828-1). **F.** Left mandible with m2-m3 (MB. Ma. 27829-
 373 4). **G.** Right m1 (MB. Ma. 27848-2). **H.** Right m1 (MB. Ma. 27848-1). **I.** Right m1 (MB. Ma.
 374 27850-1). **J.** Right m2 (MB. Ma. 27850-5). **K.** Right m2 (MB. Ma. 27850-3). **L.** Right m3
 375 (MB. Ma. 27850-7) **M.** Right m3 (MB. Ma. 27850-6). **N.** Left m3 (MB. Ma. 27850-2). Scale
 376 bar represents 2mm.



377

378 Fig. 3. Length/width scatter diagrams of the upper and lower molars of *Cricetodon*
 379 *albanensis* from La Grive-Saint Alban (France) housed in the Naturkunde Museum of Berlin.



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