



HAL
open science

Primates and Plesiadapiformes from Cos (Eocene; Quercy, France)

Marc Godinot, Cécile Blondel, Gilles Escarguel, Carine Lézin, Thierry
Pélissié, Rodolphe Tabuce, Dominique Vidalenc

► **To cite this version:**

Marc Godinot, Cécile Blondel, Gilles Escarguel, Carine Lézin, Thierry Pélissié, et al.. Primates and Plesiadapiformes from Cos (Eocene; Quercy, France). *Geobios*, 2021, 66-67, pp.153-176. 10.1016/j.geobios.2021.03.004 . hal-03432957

HAL Id: hal-03432957

<https://hal.umontpellier.fr/hal-03432957>

Submitted on 23 Nov 2021

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 **Primates and Plesiadapiformes from Cos (Eocene, Quercy, France)**

2

3

4

5 Marc Godinot¹, Cécile Blondel², Gilles Escarguel³, Carine Lézin⁴, Thierry Pélissié⁵, Rodolphe
6 Tabuce⁶, Dominique Vidalenc⁷

7

8

9 ¹ Ecole Pratique des Hautes Etudes, PSL, UMR 7207, 8 rue Buffon, 75005 Paris, France

10 ² Université de Poitiers, Laboratoire Paléontologie Évolution Paléoécosystèmes

11 Paléoprimatologie: UMR 7262, Bât. B35 TSA 51106, 6 rue M. Brunet, 86073 Poitiers Cedex

12 9, France

13 ³ Université Lyon 1, UMR 5023, Bd du 11 Novembre 1918, 69622 Villeurbanne, France

14 ⁴ Geosciences Environnement Toulouse, Université de Toulouse, CNES, CNRS, IRD, UPS ;

15 14 av. Edouard Belin, 31400 Toulouse, France

16 ⁵ Réserve naturelle nationale du Lot et Géoparc mondial UNESCO Causses du Quercy, 11 rue

17 traversière, 46240 Labastide-Murat, France

18 ⁶ ISEM, Université de Montpellier, CNRS, IRD, EPHE, Cc 064, Place Eugène Bataillon,

19 34095 Montpellier Cedex 5, France

20 ⁷ 103 Avenue François Mitterand, 31800 Saint-Gaudens, France

21 Corresponding author : Marc Godinot (marc.godinot@mnhn.fr)

22

23 Abstract

24 A new fauna has been collected from a fissure filling named Cos in the Quercy region, South-
25 West France. It includes four primate species and a plesiadapiform. The cercamoniine
26 adapiform *Protoadapis andrei* Godinot and Vidalenc nov. sp. is represented by a material
27 which completes our knowledge of the genus *Protoadapis* for upper canine, upper molar and
28 other details of morphology. It appears more primitive than *P. brachyrhynchus* from the Old
29 Quercy Collections. The other cercamoniine *Pronycticebus cosensis* Godinot and Vidalenc
30 nov. sp. completes our knowledge of the genus, including data on intraspecific variations.
31 Both species suggest a bushy evolution within these genera. Two teeth document the presence
32 of a third cercamoniine, *Anchomomys* sp. indet. The new microchoerid *Quercyloris eloisae*
33 Godinot and Vidalenc nov. gen. nov. sp. has very primitive characters and seems to document
34 a primitive member of the *Pseudoloris* clade. A poorly documented paromomyid
35 plesiadapiform is distinct enough to be named *Arcius moniquae* nov. sp.. It represents the first
36 discovery of a plesiadapiform in the Quercy fossil record and makes a link with paromomyids
37 surviving until the Lutetian MP 13 level. The primates indicate a broad age interval between
38 MP 10 and MP 12. The identification of the same species of *Pronycticebus* and of the new
39 genus in the Vielase fauna suggests more precisely the MP 10 – MP 11 interval.

40

41 Keywords: Adapiformes, Microchoeridae, Paromomyidae, Lutetian, Europe

42

43

44 1. Introduction

45 Fossil primates were found very soon after the beginning of the industrial exploitation
46 of phosphatic deposits known as Phosphorites du Quercy. Quercy is a limestone plateau
47 south-west of the French Central Mountain. Its name refers to abundant oak forests (*Quercus*)
48 which covered the region in historical time. At the end of the XIXth Century, fissure-fillings

49 rich in phosphatic deposits were exploited, and during industrial exploitation remains of
50 fossil vertebrates were discovered and soon made the region famous for them. Fossils
51 primates found at that time played a role in science. A cranium found in Beduer revealed that
52 the enigmatic mammal described by Cuvier (1822) as *Adapis* indeed was a primate,
53 something that had not been realized before (Delfortrie, 1873). Further fossil primates were
54 described by Filhol (e.g. 1874), among others by Grandidier (1904), Schlosser (1907), and a
55 major contribution was given in two steps by Stehlin (1912, 1916). Fossil primates found in
56 the XIXth or early XXth Centuries had sometimes no precise provenance, sometimes were
57 located with a village name. However, most of these village names are useless because a
58 number of fissures were exploited in their vicinity. A few exceptions are large fissures which
59 were given a name, e.g. Mémerlein, Prajoux. All the early finds are labelled Old Quercy
60 Collections.

61 A large number of the fissures were emptied by industrial exploitation. However, a
62 systematic search for fossil remains was started in the 1960s by paleontologists from
63 Montpellier, Poitiers and Paris. It was discovered that mounds of clay residues were
64 sometimes left at close proximity of the exploited fissures, which in a few cases allowed the
65 collecting of a small vertebrate fauna coming from that fissure. More importantly, there are
66 still remnants of pockets, sometimes deep in underground galleries, sometimes closer to the
67 surface. Some of them still contain filling without phosphatic deposit and often without fossils
68 (pure red clay). However, others yielded vertebrate fossils, collected by washing and
69 screening. A few entirely new untouched pockets were even found. The number of fossil
70 localities progressively increased, allowing the building of a new vertebrate record, known as
71 New Quercy Collections. Steps in the building and study of this record can be found in
72 paleontological syntheses (Crochet et al., 1981; Rémy et al., 1987; Mourer-Chauviré, 2006;
73 Rage, 2006; Sigé and Crochet, 2006; Sigé & Huguéney, 2006). Field work in the Quercy

74 continues, in large part in the context of a geological reserve in the Lot Department, where the
75 fossiliferous deposits now are protected.

76 Paleontological studies also continue in many groups, including plants, insects, lower
77 vertebrates, birds and mammals. Concerning primates, some well-dated material was
78 published (Godinot, 1984a, 1985, 1988, 2003), some postcranials were published (Dagosto,
79 1983, Godinot and Dagosto, 1983; Godinot, 1992; Bacon and Godinot, 1998). The
80 systematics of large adapines was revised (Godinot and Couette, 2008) and adapine
81 locomotion continues to be discussed (Boyer et al., 2013; Marigo et al., 2019). Until now,
82 some of the primates found in the XIXth Century had never been found again, e.g.
83 *Necrolemur zittelli*, *Pronycticebus gaudryi*, *Protoadapis (Cercamonius) brachyrhynchus*, *P.*
84 *angustidens*, etc... In this context, the new fauna of Cos provides crucial new evidence which
85 at the same time completes earlier finds and yields entirely unsuspected forms. The whole
86 underlines that our knowledge of Quercy primates still is far from complete. It is worth noting
87 that the Cos fissure was the very first to be discovered by Jean André Poumarède in 1865.
88 This eclectic scholar observed that wheat was exceptionally vigorous in the area, and
89 discovered that the soil was rich in nodules containing a high proportion of tricalcic
90 phosphate. He then started the first exploitation, for fertilizer, of what soon became famous as
91 Phosphorites du Quercy (Pulou, 1980).

92

93

94 2. Geological setting

95 The fissure, with its fossiliferous content, lies within marine limestones of the Cajarc
96 Formation, dated late Bajocian/Bathonian. It is a large excavation, almost empty, of around 80
97 x 50 m, elongated in a N110°E direction, which is one of the major directions of fracturation
98 for the Quercy plateaux. The bottom of the excavation is filled by a water body known as the

99 Lac de Cos. At its South-East are remnants of exploitation, which make a mound of ~65 x 60
100 m. The rims of the fissure are covered by vegetation, except in the small area cleaned by one
101 of us (D.V.) for quarrying in search of fossils (Fig. 1), during several decades.
102 The sedimentary unit, with the fossiliferous remains, is composed by small beds of granular
103 and porous limestones punctually alternating with red clays sometimes rich in small pisoliths.
104 The limestones are stratified, folded, probably affected by gliding (Fig. 1), and their relations
105 with the red clays remains unclear. There are fossils scattered all through the section, not
106 abundant, however concentrations of bird shells were found toward the top, and
107 micromammals were found in one bed. Toward the bottom is a 20 cm bed with complete bird
108 bones. This filling is unlike those found in other remnant pockets in the Quercy region, and a
109 more elaborated sedimentological study has been undertaken, which will be published
110 elsewhere.

111

112 3. Material and methods

113 All the fossils described here were excavated, prepared and catalogued by one of us (D.V.).
114 They are housed in the collections of Montpellier University. One exception is an M3/ from
115 an amateur collection, of which a cast is deposited in the University collection. Geological
116 observations were done on the site by the crew, especially the geologists (C.L. and T.P.).
117 Measurements were done with a digital caliper for the larger specimens (more than 1 cm), and
118 with a Nikon Measuring Microscope MM – 400/SL with electronic lecture on a Heidenhain
119 screen for smaller specimens, i.e. almost all teeth. When there is no special indication, two
120 successive measurements related by an x mean Length x Width; they are given in mm.
121 Photographs of specimens were taken with a digital camera with computer control (Canon
122 EOS 5D, Mark III camera and EOS Utility software). Most comparisons of the fossils were
123 done under a binocular using high quality epoxy casts for the comparative material of middle

124 sized species, and sometimes original fossils when they were available (e.g. for *Europolemur*
125 *mancyi* from the Paris basin). One exception is *Protadapis weigelti*, for which only the
126 description and figures in Thalmann (1994) could be used. For the very small microchoerid, a
127 cast of the type specimen of *P. isabena* was available, and the first author was able to take
128 excellent macro photographs of *P. saalae* during a visit in Halle. For the paromomyid, casts
129 were available for *Arcius rougieri* and *A. ilerdensis*, and excellent illustrations of the other
130 species are provided in Aumont (2003). Dental nomenclature follows usual terms for primate
131 dentitions (see Szalay and Delson, 1979), with the addition of two terms: for upper molars,
132 centrocrista is used for postparacrista + premetacrista; for lower molars and p/4, postvallid is
133 used for the valley situated between protoconid and hypoconid.

134

135 4. Systematic Paleontology

136 Class Mammalia Linnaeus, 1758

137 Order Primates Linnaeus, 1758

138 Suborder Strepsirrhini Geoffroy Saint-Hilaire, 1812

139 Infraorder Adapiformes Hoffstetter, 1977

140 Family Notharctidae Trouessart, 1879

141 Subfamily Cercamoniinae Gingerich, 1975

142 Genus *Protoadapis* Lemoine, 1880

143

144 4.1. *Protoadapis andrei* Godinot and Vidalenc nov. sp.

145 Figures 2 and 3

146 Derivation of the name: dedicated to Mr André Boutié, in recognition of his continuous
147 support of field work to one of us (D. V.).

148 Holotype: the right mandible Cos 253 bearing p/3 to m/3 (Montpellier University collection)

149 Referred material: a left jaw bearing the p/3 Cos 254; isolated teeth, m/3 Cos 246, upper
150 canine Cos 753, P4/ Cos 77, M2/ Cos 247, M3/ Cos 248; two lower incisors are referred with
151 less confidence, i/1 Cos 252 and i/2 Cos 249.

152 Type locality: Cos, fissure-filling in the Quercy region (South West France);

153 Occurrence: type locality only;

154 Measurements: type mandible Cos 253: p/3, 5.76 x 3.48; p/4, 5.55 x 3.87; m/1, 5.82 x 4.10;
155 m/2, 6.03 x 4.47; m/3, 7.14 x 3.98; p/3 Cos 254, 5.51 x 3.66; m/3 Cos 246, 6.98 x 4.14; P4/
156 Cos 77, 4.59 x 5.75; M2/ Cos 247, 5.83 x 7.47; M3/ Cos 248, 4.66 x \geq 5.94. Canine Cos
157 753, length at the cervix measured in profile, 6.30; perpendicular width, 4.71; height in the
158 middle, 11.80 on the labial side, 11.65 on the lingual side; i/2 Cos 249, 2.23 (mesio-distal) x
159 2.38 (labio-lingual); i/1 Cos 252, 1.94 x 1.90. Measurements of mandibles are given in the
160 descriptions.

161 Diagnosis: Large *Protoadapis* species, which differs from *P. weigelti* by its very high p/3,
162 posteriorly broader p/4, and m/1 with a broader trigonid, a paraconid and a lingually open
163 trigonid basin. Differs from *P. angustidens* by its much broader p/4, especially in its posterior
164 part, and by an m/2 which is not much broader than m/1 and m/3. Differs from *P.*
165 (*Cercamoni*) *brachyrhynchus* by the presence of a p/1 and a double-rooted p/2 instead of
166 only a single-rooted p/2 in the latter; by a p/4, which has a larger and higher placed
167 metaconid, and is posteriorly broader, having a broader talonid basin and a larger hypoconid;
168 by a slightly longer paralophid on m/1 and m/2.

169

170 4.1.1. Description

171 Description of mandibles.

172 The right mandible Cos 253, which is the type-specimen, is incomplete and somewhat
173 deformed (Fig. 2A-B). The corpus of the mandible is broken in several regions. Below and

174 posteriorly to m/3, and at the anterior extremity, fissures and small displacements are due to
175 taphonomic processes. In the middle of the corpus, a large fissure starting between m/1 and
176 m/2 and running anteroventrally, which was accentuated or produced when the specimen was
177 found, is repaired with plaster. In its present state, the mandible gives the impression of an
178 increase in height of the corpus from m/2 onward, however the height below p/4 is
179 exaggerated by the plaster reconstruction. Parts of the corpus are intact enough below the
180 anterior root of p/3 and below the posterior root of m/2 to permit measurement of corpus
181 height in these two places. Measurements give, below p/3, 14.6 mm in labial view and 15.8 in
182 lingual view; and below m/2 13.5 in labial view and 14.6 in lingual view. These
183 measurements show that there was a slight anterior increase in height between m/2 and p/3.
184 The maximum thickness of the corpus is 7.75 below p/3 and 7.0 below m/2.
185 The posterior part of the mandible is well preserved from its ventral rim to the level of the
186 articular condyle. The coronoid process is broken away. The condyle is well preserved on its
187 labial side, and slightly deformed on its lingual side by erosion of the dorsal surface and
188 breakage and repair of a small piece of bone. Continuity of the ventral and lingual surfaces
189 shows the deformation to be small. In dorsal view, the condyle is salient lingually. Its total
190 labiolingual extension is 9.6 mm. The dorsal articular surface seems to have been slightly
191 convex anteroposteriorly and almost flat mediolaterally. Judging from the posterior part of the
192 mandible as seen in lingual view, it seems that the condyle was relatively low, close to the
193 level of m/2-3. The angular process is preceded anteriorly by a marked dorsal concavity. It is
194 ventrally convex, hook-like with its extremity directed slightly dorsoposteriorly, and its whole
195 body is deflected posterolingually (Fig. 2B). Anteriorly, the symphyseal surface of Cos 253
196 starts below the posterior border of the posterior alveolus for p/2. Its limit is not sharply
197 defined, due to some erosion. The anterior part of the mandible is very well preserved on the
198 next specimen.

199 Cos 254, a left lower mandible bearing p/3, is not at all deformed (Fig. 2C-E). The p/3
200 of this specimen is very similar in size and morphology to the preceding one, however there
201 are differences in the size of the mare anterior premolars and diastemae. On Cos 253, the
202 alveoli for p/2 are large, the posterior being of similar size to the anterior alveolus of p/3.
203 They are separated from p/3 by a substantial diastema, as long as the posterior alveolus of p/2.
204 The crown of p/2 must have been as broad as the anterior part of p/3 but much shorter than the
205 latter, and slightly offset posterolingually. A small diastema separates p/2 from the alveolus
206 for p/1, which is again large (almost the size of the anterior root of p/2). The p/1 alveolus is
207 close to the posterior border of the large canine alveolus. On Cos 254, the alveoli for p/2 are
208 smaller than those of Cos 253 and the posterior one is appressed against the anterior border of
209 p/3, without any diastema. The alveolus for p/1 is also smaller than on Cos 253, separated
210 from the alveoli for p/2 by a longer diastema, and from the canine alveolus also by a slightly
211 longer and ventroposteriorly inclined diastema. The canine alveolus is large. In dorsal view, it
212 has an almost anteroposteriorly straight lingual rim. The labial rim is convex and shows an
213 oval and elongated outline in dorsal view, however in labial view it appears ventrally curved
214 (with a height slightly exaggerated by breakage of a small chip of the ventral border). This
215 suggests that a relatively large canine was anteriorly and labially inclined (the posterior
216 inclination of the canine root can be seen on Cos 253 through the posteroventral inclination of
217 the posterior border of its canine alveolus). On Cos 254, the curvature of the anteroventral
218 border of the jaw, anterodorsally inclined, suggests that little bone is missing. What remains of
219 the incisor alveoli shows that there was a small i/1 (root close in size to the root of p/1 but
220 more compressed) and a large i/2 (compressed, root length close to p/2 alveoli length, root
221 breadth similar to p/1 root breadth).

222 The mandibular corpus of Cos 254 shows a broad ventral convexity from below m/2 to the
223 anterior part. The symphyseal region is very well delineated by a salient dorsal rim starting

224 below the p/2-p/3 limit and a ventral rim more extended posteriorly (below p/3). The
225 symphyseal surface is long and high, only slightly anterodorsally inclined (angle difficult to
226 estimate because the alveolar rim is not preserved on enough length, the ventral border is
227 curved – possibly around 30°). The salient posterior extremity of the ventral symphyseal rim
228 underlines the presence, just behind, of a pit for the insertion of the geniohyoid muscles.

229

230 Description of lower teeth.

231 On Cos 253, the p/3 is a simple and high tooth (Fig. 3F,H). It is clearly higher than p/4. In
232 profile view, the preprotocrista is slightly curved, convex anteriorly; the postprotocrista is
233 straight in its first quarter below the summit, and after a point of inflexion it becomes slightly
234 more abrupt and very slightly concave posteriorly. Its base is lowered by wear. The lingual
235 cingulum is thin, continuous with a low dorsal convexity in its middle. The labial cingulum is
236 thinner, interrupted on a short length in its middle. On its posterior part, a large wear facet
237 with the dentine covered by black manganese cuts the base of the postprotocrista and a part of
238 the posterior cingulum. Thin wear surfaces are preserved along the enamel rims, ascending
239 until midheight of the protoctristid. The p/3 of Cos 254 is very similar in its global shape, its
240 height and its slightly convex anterior profile (Fig. 3G). It is in fact slightly shorter. Its cingula
241 are less differentiated, clear only at the anterolingual extremity. On the upper part of the
242 protoconid, there is no slope change visible in lingual view, however on the posterior face, at
243 a similar level, a posterolingual crest is starting, which descends until the base of the
244 protoconid and curves into a brief posterolingual cingulum, which isolates a vertical lingual
245 groove. From the same high point on the protoconid, a median postprotocristid was probably
246 starting, however it is affected by a long wear facet, fine at its departure and progressively
247 broadening downward and hollowing out the base of the crown (presumably having worn out
248 a small cingular talonid point).

249 The p/4 of Cos 253 is partly dorsally offset from the tooth row, and an unusual sheet of bone
250 around the anterior root prevents to put it back in a normal place (Fig 3.F,H). The tooth might
251 have been accidentally displaced during the life of the animal? In occlusal view, the crown of
252 p/4 is clearly broader posteriorly than anteriorly. Its protoconid is much lower than that of p/3.
253 A posterolingual protocristid joins its summit with a well formed metaconid. In dorsal view,
254 the protocristid is only slightly curved around the anterolingual groove which separates the
255 metaconid body from the protoconid. There is no corresponding groove on the posterior side
256 of the protoconid. Despite wear of the summit of the metaconid, in anterior or posterior view
257 one can see that the protocristid made only a shallow groove between the two cusps. A short
258 anterolingual cingulum is ascending along the base of the protoconid, its summit making a
259 cuspule, a small paraconid situated well above the base of the lingual cingulum. On the labial
260 side, the anterior cingulum vanishes at the base of the small paraconid. The labial cingulum is
261 continuous, thick at the level of an incipient postvallid. This cingulum was presumably
262 reducing along the base of the hypoconid, because tiny grooves behind the hypoconid suggest
263 an incipient posterior cingulum. However, the exact morphology is lost due to a relatively
264 large wear facet which affects the summit and the labial slope of the hypoconid. In occlusal
265 view, the summit of the hypoconid is situated labially. The main postprotocristid starts below
266 the summit of the protoconid, descends and curves slightly labially toward the hypoconid
267 until the groove which separates the latter. A secondary crest branches off the
268 postprotocristid, descending posterolabially, thickening ventrally, making a prominent relief
269 on the labial side between the protoconid and hypoconid walls. The lingual crest starting from
270 the hypoconid summit forms a long curve until a low summit, a crestiform entoconid, and
271 then curves anteriorly and ventrally until it ascends dorsally along the base of the metaconid.
272 The relatively vast talonid basin, mainly oriented labiolingually and slightly sloping
273 ventrolingually, is lingually closed by the latter crest.

274 The three lower molars are quite similar to each other (Fig. 3F,H). In occlusal view they have
275 a massive outline and a slight ectoflexus on m/1 and m/2 (barely on m/3). In labial view, they
276 have protoconids of similar height and volume from m/1 to m/3 (very slightly more
277 voluminous on m/2), and hypoconids slightly lower than the protoconids. The cristid obliqua
278 seems more abrupt on m/1, however this is due to the wear affecting the back of its trigonid.
279 On m/3, the cristid obliqua joins the posterior wall of the trigonid between the notch of the
280 protocristid and the protoconid summit in dosal view, and clearly below the level of this notch
281 in posterior view. On m/2, the cristid obliqua curves along the trigonid wall until a point
282 closer to the protoconid notch. On m/1, this junction is unclear due to wear, however the worn
283 zone clearly shows that the cristid was directed toward the protocristid notch, and not toward
284 the metaconid summit as occurs on some genera. In posterior view, the metaconid appears as
285 broad and lower than the protoconid on m/1, quite similar to the protoconid on m/2, and
286 narrower and as high as the protoconid on m/3. On the three molars, the notch of the
287 protocristid is deep in posterior view, close to a V on m/3 (it is shallower in many species). The
288 entoconid is low and small on m/3, well formed on m/2 and m/1. The pre-entocristid and the
289 postmetacristid are continuous on m/1 and m/2, closing the talonid basin. On m/3, the base of
290 the postmetacristid is more abrupt, making a deep notch which almost opens the talonid basin
291 lingually. On m/2 and m/3, the preprotocristid descends, curves into a subhorizontal and
292 transverse paralophid, which at its lingual end diminishes, curves dorsally in merging into the
293 base of the metaconid. On m/1, a cuspidated paraconid is well isolated from the base of the
294 metaconid by a groove. The labial part of the paralophid is inclined, slightly inflated, and
295 isolated from the protoconid base by a lingual groove. The labial cingulum is well formed on
296 the anterior half of the molars, faint on their posterior part, even on m/3 (it is highly placed on
297 the hypoconid of m/1). The third lobe of m/3 is moderate in size, simple, lingually placed,

298 limited in dorsal view by a very shallow lingual concavity, a deep labial concavity, and there
299 is no deep groove in these regions.

300 The isolated m/3 Cos 246 is broadly similar to that of Cos 253, however it also differs in a
301 series of characters (Fig. 3E). Its trigonid is relatively smaller, slightly anteroposteriorly
302 shorter, with a protoconid slightly shifted lingually in occlusal view and markedly lower in
303 labial view, and in anterior view a protoconid much smaller than on Cos 253, which is
304 accentuated by wear of its summit and of its preprotocristid, and a slightly lower metaconid. It
305 has a shorter paralophid, better isolated from the metaconid base lingually, less separated in
306 its lingual part due to the lack of groove. In occlusal view, the outline presents a less
307 quadrangular anterolabial corner. The third lobe is smaller, more triangular, less rounded
308 posteriorly and limited by a lesser labial concavity. In lingual view, the hypoconulid summit
309 is slightly lower, and the entoconid is almost no more distinguishable (minuscule swelling).
310 The labial cingulum is present around the hypoconid and continues below the anterior part of
311 the hypoconulid, instead of ascending between the two cusps.

312 Description of upper teeth.

313 A large upper canine, Cos 753, is interpreted as a left one, having one face more bulging and
314 more deeply grooved which is identified as its lingual face (Fig. 3A1-2). Crown and root
315 present a slight global anterior curvature. Its enamel is slightly wrinkled. Two salient crests
316 link the pointed summit to the base, joining the anterolingual cingulum anteriorly, and the two
317 cingula posteriorly. On the lingual face, there are two vertical and shallow grooves, one close
318 to the anterior crest and the second, deeper, slightly more distant from the posterior crest. The
319 lingual cingulum is almost continuous, ascending toward the tip at the level of the posterior
320 groove, and ascending at both extremities toward the anterior and the posterior crests. The
321 labial face is more flattened, showing only a very shallow posterior groove and only a
322 posterior basal cingulum, ascending at its extremity toward the posterior crest.

323 The P4/ Cos 77 is a robust and simple primate P4/, with a lingual part narrower than the labial
324 part (Fig. 3B). From the tip of the paracone, a preparacrista and a postparacrista, straight in
325 occlusal view, join the preprotocrista and the posterior cingulum, respectively. Parastyle and
326 metastyle can be recognized but are not cuspidated. The postparacrista is continuous with the
327 labial cingulum, and a metastyle is detectable only in labial view, isolated by a very shallow
328 groove. The preparacrista joins but does not merge into the continuous crest formed by the
329 extremity of the preprotocrista and the labial cingulum. The parastyle is made only by a
330 thickening of the curving cingulum, labially to the junction. The protocone is massive and
331 high, having at least three quarters of the paracone height in anterior or posterior views. Its
332 lingual slope is abrupt. The preprotocrista is salient, straight in occlusal view, strongly
333 deepening and curving again upward toward its junction with the labial cingulum in anterior
334 view. A postprotocrista is present, directed posteriorly, abrupt, not salient and interrupted
335 before the groove limiting the posterior cingulum. The posterior cingulum is well formed and
336 long, reaching the lingual border lingually and the postparacrista labially. The faint anterior
337 cingulum is much shorter, reaching less far lingually, and interrupted labially well below the
338 preprotocrista.

339 The M2/ Cos 247 is very simple in its morphology, quadrangular with its lingual part slightly
340 narrower than its labial part (Fig. 3C). Its enamel is slightly wrinkled. The metacone is
341 slightly lingually shifted in comparison with the paracone. The posterior part of the tooth also
342 is narrower than its anterior part. The protocone, almost central, is in fact slightly anteriorly
343 placed. The preprotocrista is continuous until the labial border; it bears a small paraconule. A
344 swelling similar to a tiny postparaconule-crista joins the base of an hypoparacrista; the latter
345 is not salient, however well formed as the edge between two faces having different
346 orientations. The postprotocrista takes a posterior direction before curving toward the
347 metacone; this way, it surrounds a vast trigon basin, anteroposteriorly broad. There is no

348 metaconule (a minuscule remnant can be detected at high magnification). The postprotocrista
349 ascends along the metacone wall and stops, continued through an edge issued from the
350 summit (almost an hypometacrasta). The link between protocone and metacone is
351 subcontinuous. The labial cingulum is continuous, well-formed and limited by a groove in its
352 median part, thinner on both sides. No style is present (a minuscule cuspule at the place of a
353 metastyle can be detected at high magnification). The anterior cingulum is interrupted labially
354 below the paraconule; lingually it is continuous with the lingual cingulum, which is
355 subcontinuous: interrupted only by three tiny grooves at the lingual base of the protocone. In
356 occlusal or in lingual view, the impression is that the lingual cingulum is almost continuous.
357 There is a small crestiform hypocone, barely visible in occlusal view, forming a low summit
358 in lingual or in posterior view. The posterior cingulum is thick, continuous, interrupted only
359 just at the junction with the base of the postmetacrasta.

360 The M3/ Cos 248 is incomplete in its basal part, however its triangular outline is exact (Fig.
361 3D). Small remnants of cingulum show that it must have possessed a continuous lingual
362 cingulum, a labial cingulum, and that the posterior cingulum is labially interrupted well before
363 reaching the postmetacrasta, which is labially curved. The metacone is moderately reduced.
364 The trigon basin is vast and the enamel is slightly wrinkled, as on the M2/. One difference
365 with the M2/ is that the protocone is lower. There is no paraconule, however the
366 preprotocrista is broad and thick until the groove surrounding the base of the paracone. The
367 postprotocrista is well formed and reaches until the base of the metacone. The lingual edge of
368 the metacone is blunt, nevertheless a continuity between protocone and metacone is visible in
369 anterior or posterior view. The M3/ is neither reduced nor transversally elongated as found in
370 many species.

371 A small tooth, Cos 252, has the right size to be an i/1 of this species. Its root is laterally
372 compressed and would fit in size with the remnant of alveolus on Cos 254. The crown is

373 heavily worn, no details can be seen. The outline in occlusal view is very circular, somewhat
374 flattened on the labial side, where the crown slope is abrupt. The outline is somewhat salient
375 lingually, with a more inclined surface making the usual broad lingual bulging of lower
376 canines. No cingulum is visible on the lingual part. The wear surfaces are inclined, one
377 mesially, the other distally, and they join in a very blunt labiolingual edge.

378 A larger incisor, Cos 249, has a compressed root compatible in size with the alveolus for i/2
379 of Cos 254. Its crown is better preserved, the labial outline is curved, the lingual side is more
380 expanded, without lingual cingulum. The tip of the crown is an elongated mesiodistal wear
381 facet, parallel to the labial face, thick in its mesial and median parts, narrowing in its curving
382 distal part, which continues as a slightly worn distal crest. A very shallow groove can be
383 followed from midheight at some distance of the mesial border, going upward, turning to
384 follow just along the wear facet, and turning downward and following the salient distal crest,
385 which is vertical.

386

387 4.1.2. Remarks

388 Comparisons

389 Comparisons are made only with fossils that have been described as large *Protoadapis*
390 species. *P. weigelti* differs from *P. andrei* through the loss of p/1 and the absence of diastema
391 between p/2 and the canine, p/3 strongly anterolabially implanted on the mandible, p/3 by far
392 not as pointed and as elevated, p/4 more elongated and narrower in its posterior part, m/1 with
393 a narrow trigonid, a short paralophid curving toward the metaconid, rendering the trigonid
394 basin “almost closed” according to Thalmann (1994), m/1 with a cristid obliqua directed
395 toward the metaconid and apparently reaching high on its posterior wall (fig. e on plate VIII
396 of Thalmann, 1994). All these differences show *P. weigelti* to be quite distinct from all other
397 Quercy *Protoadapis* species, including *P. andrei*. Its relatively low p/3 is a difference with all

398 species ascribed to *Protoadapis* until now, and the reduction of the trigonid of m/1 indicates a
399 derived stage of evolution.

400 Comparison with the type specimen of *P. angustidens* is made through the photographs
401 published by Teilhard de Chardin (1922). The latter shows an m/1 much smaller than the m/2,
402 whereas these teeth are close in size in *P. andrei* (such a size difference exists on *P.*
403 *brachyrhynchus*, however much less exaggerated). There might have been differences on the
404 trigonid of m/2 and m/3, possibly slightly reduced, narrower on *P. angustidens*, however this
405 is difficult to appreciate from the sole photograph. Conspicuous differences concerns p/4,
406 which is more elongated and narrower on *P. angustidens* than on *P. andrei* (and
407 *brachyrhynchus*), added in lingual view to a horizontal paraconid shelf (instead of ascending)
408 and a lower talonid. The p/3 of *P. angustidens* appears also very high. Several of these
409 characters could be explained by intraspecific variations, as has been found for the two m/3 of
410 *P. andrei*. However the differences on the p/4 clearly exceed the intraspecific variations found
411 in some cercamoniine assemblages (e.g. Godinot et al., 2018), and we consider *P. angustidens*
412 as probably representing a different *Protoadapis* species different from *P. andrei* and *P.*
413 *brachyrhynchus*.

414 The mandible PLV-35, referred by Gingerich (1977) to the same species as the type specimen
415 of *P. angustidens* (renamed by him *P. "filholi"*, a new name that cannot be accepted because
416 there is no synonymy among *Protoadapis* species), was figured in profile view by Gingerich
417 (1977) and its two molars are beautifully illustrated in Tattersall and Schwartz (1983). The
418 mandible is more gracile than those of *P. angustidens* and *P. andrei*. Its two molars are very
419 close in overall morphology to those of *P. andrei*. The third lobe is smaller than on Cos 243
420 but similar to Cos 246. Several details separate them: the extremity of the paralophid of m/2
421 and m/3 does not merge into the base of the metaconid but instead shows a slightly ventrally
422 oriented narrowing extremity; the paralophid bears a small paraconid medially situated on

423 m/2 and a tiny remnant cuspule on m/3; on m/3 the cristid obliqua is ascending further
424 dorsally, coming close to the protocristid notch, on m/3, whereas this crest meets the posterior
425 trigonid wall at a lower level on the two m/3 from Cos. The strongest difference on the molars
426 is the clearly stronger cingulum on PLV-35 molars, the latter being even continuous on the
427 labial side of the m/3. These differences on m/2 and m/3 could be significant or could be
428 accounted for by intraspecific variations. The anterior part of PLV-35 is well preserved, and
429 very similar to Cos 254. Alveoli for i/1, i/2 and the canine have similar shapes and
430 dimensions. However, there is a clear shortening around the anterior premolars. The alveoli
431 for its p/2 are quite large (around as large as on Cos 253, larger than on Cos 254). The p/2 was
432 just against p/3 as on Cos 254, however anteriorly a small alveolus shows that the p/1 was
433 small, markedly smaller than on Cos 254 (itself smaller than on Cos 253). This small p/1 sits
434 between two small diastemae, that with p/2 very small, that with p/1 slightly larger, however
435 still smaller than on Cos 254. If one compares, beyond differences in p/1, p/2 and diastemae,
436 the distance between the canine and the p/3, one can see that this distance is clearly shorter on
437 PLV-35 than on the two mandibles from Cos. For this shortening, PLV-35 is intermediate
438 between *P. andrei* and *P. brachyrhynchus*. Comparing the anterior part of PLV-35 with the
439 photograph of *P. angustidens*, it appears clearly that the latter has a much larger p/1 and a
440 longer diastema between p/1 and p/2, showing that it belongs with *P. andrei* to the group of
441 *Protoadapis* species having a large p/1 and long diastemae, very likely primitive.

442 The mandible of *P. (Cercamoniis) brachyrhynchus* is slightly higher and more robust than
443 those of *P. andrei*. Its preserved teeth, p/4 to m/2, are overall very similar to those of *P.*
444 *andrei*, however a few differences can be observed. Despite some wear on the summit of the
445 protoconid and the anterior slope of the trigonid, one can see that a paraconid is present,
446 slightly smaller than on *P. andrei*, and the paralophid is slightly curving posterolingually,
447 shifting the paraconid slightly closer to the metaconid. A slight degree of trigonid basin

448 closing has occurred on the m/1 of *P. brachyrhynchus*. On m/2 also, the paralophid appears
449 slightly shorter and meeting the metaconid wall at a higher level. On p/4, the protocristid
450 joining the summits of the protoconid and metaconid has the same length and orientation in
451 occlusal view. However in profile or posterior views, it appears that the metaconid is
452 markedly smaller, and more ventrally placed, in *P. brachyrhynchus*. Differences on the
453 paraconid shelf cannot be observed because the anterior part of the p/4 is eroded in *P.*
454 *brachyrhynchus*. Their p/4s markedly differ in their posterior part: the hypoconid is much
455 smaller on *P. brachyrhynchus*, associated with a much narrower talonid basin, and it did not
456 possess the supplementary labial fold described on *P. andrei*. Their p/4s therefore have a
457 different outline in occlusal view, posteriorly narrower in *P. brachyrhynchus*. In the anterior
458 part of the mandible, the two species differ markedly: there is only a single rooted p/2 on *P.*
459 *brachyrhynchus*, and no diastema on both sides of the tooth, showing a marked reduction in
460 anterior premolars and length of the anterior part of the jaw.

461 Discussion

462 This new species has p/4 to m/2 overall similar to the same teeth in *P. brachyrhynchus*,
463 differing only in details of the paralophid of m/1 and m/2 and differing more in their p/4s,
464 showing that the two species must be closely related. Strong differences occur in the anterior
465 part of the mandible, with only a single rooted p/2 and no diastema between p/3 and the
466 canine in *P. brachyrhynchus*. The surprise is to have *P. andrei* so primitive in its anterior
467 dentition, and so morphologically close to typical *Protoadapis* species by many characters,
468 particularly the high and pointed p/3. This confirms the interpretation of Stehlin (1916), who
469 described the specimen as a derived species of *Protoadapis*. The new material is important
470 because it completes our knowledge of large Quercy *Protoadapis* species, with for the first
471 time associated upper P4/ and molars, and an upper canine. Relatively unexpected is to find
472 an upper molar of such a large species with only an incipient crestiform hypocone. When we

473 extend the comparison to other large *Protoadapis* species, *P. weigelti* is the species which
474 appears the most divergent in its molar morphology. It was interpreted by Gingerich (1977) as
475 intermediate with *Caenopithecus*, something we doubt, however this proposition is consonant
476 with our interpretation of a diverging lineage for *P. weigelti*.

477 Among the large *Protoadapis* species found in the Quercy, we have seen that if details of
478 molar morphology and the gracility of PLV-35 could be accounted for by intraspecific
479 variabilities, the reduction of the anterior premolars and jaw would be the major evolutionary
480 trend, allowing the proposition of a *P. andrei* – PLV-35 – *P. brachyrhynchus* specific lineage.

481 One might even suspect *P. angustidens*, with its elongated p/4, to represent an even more
482 primitive evolutionary stage. If its p/4 and peculiar proportions of molars could be accounted
483 for by intraspecific variabilities, one could even suspect *P. andrei* to be a junior synonym of
484 *P. angustiens*, and the picture would be one lineage *P. angustidens* – PLV-35 – *P.*

485 *brachyrhynchus*. However, more information on intraspecific variations is needed to
486 strengthen such an interpretation. The material at hand seems to indicate a more bushy picture

487 of *Protoadapis* species: *P. angustidens* might be early specialized by its p/4, PLV-35 might
488 belong to a more gracile branch with slightly different molars, and *P. andrei* seems advanced
489 over *P. brachyrhynchus* in its p/4 morphology, which would imply two different specific
490 lineages or an unlikely reversal in p/ evolution. Clearly we do not have enough material, not

491 enough information about intraspecific variability, to favor one specific lineage over a more
492 complex history, which is suggested by the variety of p/4 morphologies. When comparing

493 with more distant *Protoadapis* species, it is striking that the early Eocene *P. curvicaudatus*,
494 the type species of the genus, has an already shortened anterior dentition, with a relatively
495 small and single-rooted p/2. Our Quercy species must be rooted in a more primitive stock. It

496 might be tempting to propose those species leading to *P. brachyrhynchus* as the *Cercamonius*
497 lineage, however we cannot identify significant characters which would separate its earlier

498 species from other *Protoadapis* species. As we have seen, the most divergent species of the
499 genus would be *P. weigelti*, and for this species as for earlier ones, upper teeth are unknown.
500 Our knowledge is still insufficient to allow a systematic reappraisal of all *Protoadapis*
501 species.

502

503 Genus *Pronycticebus* Grandidier, 1904

504

505 4.2. *Pronycticebus cosensis* Godinot and Vidalenc nov. sp.

506 Figures 4, 5 and 6

507 Derivation of the name: from the type locality, Cos;

508 Holotype: left mandible Cos 271 bearing i/2, C, broken p/1, p/2 to m/3, University of
509 Montpellier collection.

510 Referred material: right fragment of mandible bearing m/3, Cos 269; juvenile anterior part of
511 mandible with unerupted p/3, Cos 275; mandible fragment bearing p/4 and m/1, Cos 270;
512 maxillary fragment with P4/ and alveoli of P3/, P2/, and a more anterior part, Cos 265;
513 maxillary fragment with M1/ and M2/, Cos 258; and 26 isolated teeth (see Table 1).

514 Type Locality: Cos fissure-fill (Quercy region, South West France);

515 Occurrence: the type locality, possibly Vielase (Quercy);

516 Measurements: for all teeth, see Table 1 for Length and Width; complementary measurements
517 are: for the lower canine of Cos 271, length and height in labial view, 1.96 and 3.54 mm; for
518 the upper canines, height is 3.78 for Cos 863 and >3.45 for Cos 864. Measurements of the
519 type mandible Cos 271 are: total length of mandible without the incisor, 5.25 cm; length p/4-
520 m/3, 1.72 cm; height below p/2, 6.17 mm; height below m/2, 7.53 mm; width at the level of
521 m/2, 2.98 mm. Maxillary fragment Cos 265, length and height in labial view are 12.51 and
522 8.01 mm. Some complementary measurements are given with the descriptions.

523 Diagnosis: Species of *Pronycticebus* which differs from *P. gaudryi* by its smaller p/2, p/3s
524 having more complicated posterior creasing, a main posterolingual crest and varying
525 secondary crests often suggesting an incipient metaconid; p/4s with a larger and better
526 isolated metaconid; m/2 and m/3 with thinner paralophid, without bulge, and shorter m/3
527 paralophid; P3/ to M1/ have a smaller parastyle, and a less salient posterolabial corner
528 (straight postparacrista on P3-4/, less elongated and curved postmetacrista on M1/, no
529 metastylar expansion); P3/ has a more reduced protocone, M1/ is much less waisted, and M2/
530 has a continuous or subcontinuous lingual cingulum. Differs from *P. neglectus* by its smaller
531 size, presence of first premolar above and below, higher and more pointed entoconid on m/1,
532 continuous lingual cingulum on M2/. *P. neglectus* further differs from the two others by the
533 complete absence of metaconid on p/4, the thin paralophid joining the base of the metaconid
534 on m/1 and m/2 (long and posteriorly curved on m/1), and a smaller hypocone at least on M2/.

535

536 4.2.1. Description

537 Mandibles

538 The type specimen Cos 271 is a left mandible, very well preserved in its anterior half, partly
539 damaged in its part posterior to m/3 (Fig. 4A1-3). The corpus is relatively thin and elongated
540 anteriorly. Its ventral border is regularly convex. Some damage of its anterior extremity is
541 present on its labial side, probably causing a slight labial protrusion at the level of the canine
542 root. On the lingual side, the bone is intact, the symphyseal surface is very anteriorly inclined,
543 and extends posteriorly until below the space between p/2 and p/3 (Fig. 4A2). The corpus
544 shows a slight increase in height posteriorly until below m/3; posteriorly, the ventral border
545 makes a dorsal concavity followed by a ventral convexity. In labial view, the posterior
546 appears affected by two large cracks, one ventroposterior starting behind m/3, and a second
547 dorsoposteriorly oriented starting after the latter. Despite these large cracks and the dorsal

548 displacement of the m/3, one can see in lingual view that the ventral parts are almost joined;
549 their junction is masked by a calcite deposit, which shows that the breakages were natural,
550 due to taphonomical processes. The ventral border of the posterior convexity appears irregular
551 in labial view, due to some calcite still covering this side. However, in lingual view, that
552 border appears intact, and the whole outline of this mandible is almost not deformed when
553 seen in lingual view. Only at the posterior extremity is bone missing. The articular condyle is
554 not preserved, however the broadening of the bone just below the condyle is there, and in fact
555 the line below the condyle, which is very steep and slightly posteroventrally inclined, is intact.
556 It curves on the top of the angular process. Because the ventral line is curved, it seems that
557 very little of the angular process is missing, just its posterior border, which must have been
558 curved. The angular process must have resembled in smaller that of *Notharctus* (Gregory,
559 1920: Fig. 76). In ventral view, a slight displacement of the posterior part can be detected.
560 The mandibular fragment Cos 275, which bears a germ of p/3 in place (Fig. 4C1-2), appears
561 quite similar to Cos 271: p/2 of similar size, diastemae on both sides of p/1, the alveolus of
562 which is similar in size to that of Cos 271. Small differences between the two specimens are:
563 the height below p/2 is smaller on Cos 275, the symphyseal surface appears less grooved; in
564 labial view, a mental foramen is present below the anterior border of p/2, whereas on Cos 271
565 a small mental foramen is present below p/1 and a larger one below the anterior root of p/3.
566 Measurements of Cos 275 are: height of mandible below p/1 alveolus, 4.02 mm, height below
567 p/2, 4.72, width of mandible at p/1 alveolus, 2.81, and at the middle of p/2, 2.73 mm; length
568 of canine alveolus ~2.49 mm, alveolus for p/1, 1.35 x 1.11; roots of p/2, 1.70 x 1.19 mm.
569 A posterior part of mandible, Cos 269, bears its m/3. It is fragmented by taphonomical
570 processes. It gives some complementary information. A space is present between the m/3 and
571 the ascending ramus, which is steep. The ventral border appears less sinuous than on Cos 271.
572 At the posterodorsal extremity of the fragment, a part of the posterior rim is preserved, which

573 shows that the coronoid process was anteroposteriorly short. The base of this rim curves
574 posteriorly and becomes thicker, thus indicating the upper level of the articular condyle. The
575 latter appears to have been high, far above the tooth row.

576 Dentition of the type mandible Cos 271 (Fig 5A1-2, L-P).

577 The anterior extremity of the specimen is lacking only very little bone. The space for the i/1
578 alveolus cannot be directly observed because it is still covered with a sheet of calcite (and
579 some glue?), however it must have been very small, and i/1 was certainly very small. The i/2
580 is still in place, in front of the canine, partly out of its alveolus. Its root is close in size to the
581 root of p/1. Its crown is spatulate. Its anterodorsal rim is almost straight, linguolabially
582 oriented, showing only a slight irregularity of its middle (a very slight anterior groove). Its
583 lingual half is intact; its labial half is affected by a deep wear surface, a broad labial groove
584 having an anteroventral orientation.

585 The canine of Cos 271 is not large. It is only slightly higher than p/3 and p/4. In occlusal view
586 it appears oval, somewhat laterally compressed. Three main crests can be seen, however they
587 are blunt, not salient: 1, the anterior crest, arcuate, underlined by a slight lingual concavity; 2,
588 the posterior crest, very straight, affected by a moderate vertical wear facet in its dorsal half,
589 smooth in its ventral half; 3, a posterolabial ridge bordering an almost flat posterolabial face.

590 A faint basal cingulum can be seen only on both sides of the posterior crest. There is a sizable
591 diastema, as long as the canine length, between the p/1 and the canine. The small p/1 is
592 incomplete; the lingual part of its crown is broken away. Its labial part is still covered by a
593 thin layer of calcite. From what remains of this labial side, it appears difficult to predict its
594 crown height. However, its length in occlusal view is less than half the length of p/2, hence it
595 must have been quite small. p/2 is a small biradicated tooth, with a simple crown. The main
596 cusp is high, its anterior crest is arcuate; its posterior crest is straight, with an irregularity, a
597 slight bulge above its mid-height, visible in lingual view. A basal cingulum, not salient, is

598 present on its posterior face. It fades on both sides, on which it can be detected as very faint,
599 incipient.

600 The p/3 of Cos 271 is abnormal: its presents a labial expansion of its crown, above a third
601 labial root situated in the middle of the labial side. In lingual view, the tooth is slightly higher
602 than p/4, however this is due to the dorsally expanded anterior root. If the sole crowns are
603 compared, taking into account the fact that the tip of p/4 is worn, the crowns of p/3 and p/4
604 appear subequal in height. In lingual view, p/3 has a classic shape, with an anteriorly arcuate
605 preprotocristid; the lingual cingulum presents two concavities separated by a broad and high
606 dorsal convexity in its middle (Fig.). Two crests descend posteriorly from just below the tip of
607 the protoconid. In posterior view, the most salient of them descends and curves gently
608 lingually to join the lingual cingulum at a point just posterior to its rounded summit; in lingual
609 view, this crest shows a thickening below its midheight, which evokes a low placed incipient
610 metaconid. The second posterior crest issued from the the tip of the protoconid takes a more
611 labial course; it is blunt and continuous until it reaches the posterolabial cingulum; it seems to
612 correspond to the postprotocristid, labially displaced in relation with the abnormal labial
613 expansion of the crown. The continuous labial cingulum has its lowest point above the
614 supplementary root and is ascending on both sides, being more weakly expressed in its
615 anterior part. There is a talonid, well developed in lingual view, however not basined.

616 The p/4 of Cos 271 has a more usual aspect with its horizontal crown. The anterolingual
617 cingulum is thick, subhorizontal; posteriorly it vanishes in ascending at the base of the
618 metaconid. The metaconid is well formed, relatively acute in lingual view, isolated from the
619 protoconid by a deep groove; the protocristid makes a notch in posterior view despite the fact
620 that the tips of the protoconid and metaconid are partly worn out. A postmetacristid descends
621 lingually and curves into a lingual cingulum surrounding a small talonid basin. A
622 postprotocristid descends below the notch of the protocristid and at its posterior extremity

623 curves again dorsally, forming a low cingular hypoconid. A blunt posterolabial crest joins the
624 tip of the protoconid to the posterolabial cingulum. The labial cingulum appears nevertheless
625 subcontinuous, well-formed anteriorly, faint in the middle, thicker in its posterior part joining
626 the low hypoconid.

627 The three lower molars share an outline in occlusal view which is slightly narrower in the
628 anterior half than in the posterior one. Their trigonids are labiolingually narrower than their
629 talonids. They all have a relatively wide talonid basin. Some aspects of their proportions are
630 obscured by wear, which affects most strongly the protoconid of m/1, still strongly the
631 metaconid of m/1 and the protoconid and metaconid of m/2, and moderately the hypoconid
632 and entoconid of m/1 and the entoconid of m/2. Despite this inconveniency added to the fact
633 that the m/3 is no more aligned with the other teeth, it is recognizable in labial view that
634 protoconid volume and height decreased from m/1 to m/3; also, the hypoconid is clearly
635 higher on m/2 (and probably m/1) than on m/3. On the three molars, the paralophid is
636 relatively short, not reaching the lingual rim in occlusal view. On m/2 and m/3 it is
637 subrectilinear, with a slightly posterolingual orientation. On m/1, it is curved and more
638 anteriorly directed (the trigonid of m/1 is much more mesiodistally extended than those of
639 m/2 and m/3); it bears a bulging in its middle, which is a very small median paraconid. On all
640 molars, the lingual extremity of the paralophid tapers and is isolated from the base of the
641 metaconid by a groove (there is no premetacristid and no tendency toward a fusion of the
642 paralophid into the metaconid). The protocristid is not salient, very low, pushed under the
643 mesiodistal groove separating protoconid and metaconid. It is still recognizable on m/2 and
644 m/3, making the dorsal limit of the posterior wall of the trigonid (in posterior view, it makes a
645 very open V, almost a broad dorsal concavity, on m/3). It is present on m/1 as the edge
646 separating the mesiodistal trigonid groove from the postvallid extremity. The cristid obliqua is
647 low on m/3, curved, anteriorly and slightly lingually oriented, reaching the posterior trigonid

648 wall well below the protoconid summit. On m/2 it strongly lowers and curves more lingually,
649 reaching the posterior trigonid wall well below the protocristid notch. On m/1 the cristid
650 obliqua lowers less strongly than on m/2, it goes up again toward the mesiodistal groove of
651 the trigonid (very slightly lingually to it); it is not directed toward the metaconid summit,
652 however it joins the base of the wear facet labially descending from the latter's summit. The
653 crest joining the metaconid to the entoconid is continuous, little salient; it lingually closes the
654 talonid basin, at a level very slightly above the lowest point of the talonid. The entoconid is
655 slightly more anterior on m/2 than on m/1, and correlatively the postcristid is more posteriorly
656 arched on m/2. The entoconid was probably lower on m/3 than on the others, however this
657 cannot be precised because its summit is worn. The m/3 hypoconulid is broad. The crest
658 which links it to the entoconid is subcontinuous, whereas the crest which links it to the
659 hypoconid is interrupted by a deep groove, exaggerated on the specimen by a deep wear facet
660 hollowing the posthypocristid. The labial cingulum is well developed around the base of the
661 protoconid, lacking at the base of the hypoconid (slightly incipient there on m/1); in labial
662 view, it makes a broad dorsal convexity, subhorizontal on m/1; this convexity is more
663 accentuated and anterodorsally inclined on m/2, and even more on m/3; the latter seems to
664 have a deformed crown, with its base strongly ascending anteriorly.

665

666 Variations in the lower teeth

667 A small and simple tooth, Cos 278, is close in size to the P/1 of Cos 271 (Fig. 5B). It
668 has a robust root, and in occlusal view its outline is a broad oval, not far from circular. The
669 single cusp is very slightly procumbent. Its anterior side is a broad wear facet, pointed at its
670 summit (crest) and quickly broadening ventrally. It would well correspond to wear produced
671 by the upper canine. The posterior crest of the cusp is well formed. At its base, it is
672 continuous with a weak and blunt cingulum curving along the lingual side.

673 An unerupted right p/3 in its mandibular fragment Cos 275, is incomplete at its distal
674 extremity due to breakage. In lingual view its preprotocristid is markedly arcuate, its
675 anterolingual cingulum shows an anterior concavity shallower than on Cos 271, and this
676 cingulum is interrupted before joining the postprotocristid. In posterior view, the latter
677 descends with a slight lingual inclination; it makes below the midheight a lingual projection
678 more accentuated than on Cos 271 (better expressed incipient metaconid). Just labial to this
679 projection, a salient posterior crest descends toward the cingulum (broken); a salient
680 postmetacristid descends below the projection, and the posterior face appears broadly grooved
681 between these two crests (on Cos 271, only a very faint short crest can be detected below the
682 incipient metaconid). The right p/3 Cos 276 is slightly different (Fig. 5D1-2). In occlusal view
683 it appears narrower in its posterior part, with a slight labial concavity underlying this
684 narrowing. Its postprotocristid is very salient, descends posteriorly until a turn where it goes
685 ventrolingually and slightly anteriorly, continuing until it reaches the lingual cingulum. Close
686 to the turn point, slightly labially, a posterior crest continues descending, almost in
687 prolongation of the postprotocristid but less abrupt. In labial view the turn point appears as a
688 salient angle, again suggesting an incipient metaconid. Between the posterior crest and the
689 lingual cingulum, a small talonid basin is grooved. The p/3 Cos 277 is broad in its posterior
690 part (Fig. 5C1-2). It is the simplest of all p/3s. It has a posterolingual postprotocristid
691 continuous until it joins the posterolingual cingulum, without any projection evoking a
692 metaconid. Well below the midheight, a posterior crest starts at some distance of the
693 preceding crest; it joins the posterior cingulum, which is circular, without any summit: there is
694 no hypoconid, no talonid. The p/3 Cos 280, which is narrow in its posterior part, is again
695 different in its cresting. Its very salient postprotoconid is directed posterolingually in occlusal
696 view. It descends until a point where it divides in two branches: the most salient,
697 posterolabial, reaches the small posterior talonid point (salient, a true tiny hypoconid); the less

698 salient branch continues a posterolingual descent until the small talonid basin, without
699 interrupting it, without reaching the lingual cingulum. The lingual cingulum, very salient, has
700 a peculiar morphology. Its anterior half is made of two lines starting from a low ventral point;
701 the anterior ascending crest is thick (incipient paraconid shelf); the posterior crest is first
702 ascending, then subhorizontal until it divides in two parts: the main branch descends as a well
703 formed posterolingual cingulum, dorsally concave, and the minor branch ascends dorsally and
704 fades, disappearing into the lingual wall of the protoconid. On the labial side, the cingulum is
705 well formed in the posterior half of the tooth, then missing along the labial wall of the
706 protoconid, and again present only at its anterior extremity.

707 The mandible Cos 270 bears p/4 and m/1 (Fig. 5F). Its p/4 is very similar to that of Cos 271.
708 In occlusal view, its talonid basin is very slightly shorter. In posterior view, the metaconid
709 seems somewhat more distant from the protoconid, however the latter is worn, making this
710 difficult to appreciate. The posterior crest starts slightly labially to the protocristid notch (on
711 Cos 271 it starts just below). The lingual view confirms that the metaconid is slightly lower
712 on this p/4 than on Cos 271. In this view, the preprotocristid is less abrupt, slightly more
713 anteriorly directed; it joins an anterolingual cingulum which is more salient anterolingually
714 than on Cos 271; the latter cingulum is shorter than on Cos 271, but it ascends slightly
715 anterodorsally, it is thick and evokes an incipient paraconid. An isolated p/4 with two roots,
716 Cos 860, is anteriorly very short, and quite worn (Fig. 5E). It is very similar to the others, with
717 the same type of metaconid and simple posterior crests. Its talonid is more extended than on
718 Cos 270, and in occlusal view, it appears quite broad in its posterior part (broader than Cos
719 271). It is moderately worn in its posterior part: broad facet at the base of the postprotocristid,
720 with both anterior and posterior prolongations, hollowing of the posterolabial cingulum. It is
721 extremely worn in its anterior part, with a broad wear surface lowering the protoconid and
722 continuing through a long anterior vertical wear surface, descending until the base of the

723 crown; the anterior extremity of the crown is worn away. This is a very unusual type of wear.
724 Another p/4 bearing only one root, Cos 859, is quite similar to the others (Fig. 5G1-2). It
725 shows wear facets along the postprotocristid and on the posterior face of the metaconid. A
726 small wear facet hollows the cingulum at its posterolabial extremity. The enamel on the other
727 surfaces is less shiny than on the other teeth, suggesting some kind of chemical erosion. Its
728 notable character is a basal paraconid even better formed and developed than on Cos 270.
729 The m/1 of the Cos 270 mandible is very similar to that of Cos 271: same kind of paralophid
730 anteriorly salient, thickening of its labial part, the wear of which suggests the presence of a
731 small paraconid (Fig. 5F). It is less worn, so that one can well see the deep notch in V of the
732 protocristid; the cristid obliqua is directed toward this notch, but in posterior view it does not
733 reach it, being below and under its labial side; only a narrow wear facet joins this crest to a
734 broader wear facet descending from the tip of the metaconid. Two isolated lower molars are
735 important because they are unworn. They are interpreted as m/1 because they are narrow in
736 their anterior part and their cristid obliqua is directed as on the others or more lingually. The
737 first, Cos 272 (Fig. 5I), gives the impression that the protoconid and the metaconid are closer
738 than on Cos 271, and its trigonid slightly narrower (however the strong wear on Cos 271
739 might be misleading). The cristid obliqua has the same way than on Cos 271; as there is very
740 little wear, one can see the groove extending the hypoflexid, which reaches exactly the bottom
741 of the protocristid notch, and the cristid obliqua which ascends just next, lingually, and at its
742 extremity turns toward the tip of the metaconid, fusing into that part of the protocristid. The
743 paralophid is quite thick in occlusal view. Its extremity, which tapers abruptly, is much closer
744 to the lingual rim than on Cos 271. In anterior view, the preprotocristid is subvertical (slightly
745 curved), then it curves into the paralophid, which presents a summit (slightly labial to the
746 midline) and then descends ventrolingually, making again a small bump at its extremity. In
747 occlusal view, only two low bulges can be detected. Despite there is no well-formed cusp, one

748 can describe the paralophid as made of two successive bulges, a larger labial one (paraconid
749 equivalent) and a smaller lingual one. The other m/1, Cos 755 (Fig. 5H1-3), has the same kind
750 of paralophid, descending ventrolingually and well isolated from the base of the metaconid,
751 made of two bulges, a larger labial (paraconid) and a smaller lingual and more ventral. This
752 m/1 is striking through its cristid obliqua ascending directly toward the tip of the metaconid
753 (Fig. 5H1). The postvallid groove ascends and joins in continuity the mesiodistal groove
754 separating the metaconid from the protoconid. The protocristid has completely disappeared.
755 The m/2 Cos 273 is identified through its cristid obliqua, which at its anterior extremity
756 ascends below the summit of the protoconid, clearly more labially than on all m/1s (Fig. 5J).
757 Its anterolabial outline is rounded in occlusal view. Its paralophid is thick in its labial part,
758 narrower in its lingual part; it does not present the irregularities (bulges) present on the m/1s.
759 At its extremity, the paralophid is not isolated from the base of the metaconid by a groove; it
760 comes against, and the base of the metaconid presents there a blunt ridge, not salient, vertical
761 in anterior view; this makes an incipient link between paralophid and metaconid.
762 The m/3 still present on the mandibular fragment Cos 269 is very similar to that of Cos 271
763 (Fig. 5K). It differs from the latter through the lack of a labial groove separating hypoconid
764 and hypoconulid. Its paralophid is shorter, presenting a bulge along the base of the
765 protoconid. Lingually, a tiny low bulge unites the paralophid to the base of the metaconid, on
766 which a blunt ridge descends, becoming visible near the base through a small wear facet on its
767 surface. This weak ridge and the small bulge again makes an incipient continuity between
768 paralophid and metaconid, as on the m/2 Cos 273.

769 The DP/4 Cos 274 is much narrower and more elongated than the M/1s (Fig. 6R). As on Cos
770 755, the cristid obliqua is continuous from the hypoconid to the tip of the metaconid. It differs
771 from the latter by the strongly anteriorly shifted protoconid relative to the metaconid, and a
772 further anterior shifting of the paraconid, which is pointed, cuspidated but not inflated. There

773 is a wide space between the metaconid and the paraconid, each bordered by a vertical groove,
774 the two grooves (somewhat converging ventrally) being separated by the protoconid lingual
775 wall. The three anterior cusps are acute, and the pre- and the postprotocristid are salient. The
776 talonid is similar to that of the M/1s, being only smaller.

777

778 Maxilla and upper dentition

779 Maxillary fragment

780 A fragment of right maxilla, Cos 265, bears the P4/, posteriorly the alveolus for the
781 anterolabial root and half of the alveolus for the lingual root of M1/, and anteriorly it shows
782 three alveoli for P3/, two alveoli for P2/, one for P1/ and a part of the canine alveolus (Fig.
783 6A1-2). Breakage of the anterior part starts at the wall between the two alveoli of P2/, so that
784 the more anterior alveoli are seen only at a deeper level. The most anterior space, filled with
785 matrix (hard calcite), is probably a part of the canine alveolus, at a level relatively distant
786 from the palate surface. Compression of this space is congruent with the strong compression
787 of the two upper canines described below. No precise statement can be made concerning the
788 size of the canine root present in this fragment beyond the fact that it seems compatible with
789 the sizes of the roots of those canines. In occlusal view, the rim of the fragment curves
790 outward anteriorly. This curvature is exactly similar to the same region on the cranium of
791 *Pronycticebus gaudryi*, where it surrounds the base of the canine root. In lateral view, a large
792 infraorbital foramen is present just above the anterior root of the P4/, which is similar to that
793 seen on *P. gaudryi* (height of the foramen at its opening, 1.67 mm). Above, a short part of the
794 anterior orbital rim is present. In dorsal view, one can see a short part of the anterior orbital
795 floor; an anterior cavity seems to correspond to the opening of the infraorbital canal.

796

797 Upper canines

798 The upper canine Cos 863 is well-preserved (Fig. 6B1-2). Due to its slight curvature, its
799 anterior and posterior sides are easily recognizable. The posterior side presents a salient
800 vertical crest, whereas the anterior side is rounded and presents a shallow crest only at its
801 base, where it joins the lingual cingulum. If we identify the lingual side as the one presenting
802 the best developed cingulum, the tooth appears as a left canine. In occlusal view, the lingual
803 face is more extended than the labial. It bears a posterior vertical groove, deeply hollowed,
804 and an anterior part flattened (very slightly grooved in occlusal view). The labial side presents
805 only a flattening of its posterior part, with a very shallow groove visible in labial view. A thin
806 cingulum runs around the base of the crown, ascending in low summits under the crests and
807 making shallow concavities under the grooves; it completely disappears on the anterolabial
808 side. The second upper canine, Cos 864, is broken at its tip and eroded. It presents two deep
809 posterior grooves, one lingual and one labial. The crown outline is affected by a broad vertical
810 wear surface, which extends on the root; this surface is lateral to the blunt anterior crest,
811 which is recognizable through the faint ascending cingulum. Because the basal cingulum is
812 better developed on the other side, the latter would appear as lingual, and the wear surface
813 would be anterolabial. The tooth would thus also be a left canine, however the strange fact is
814 that in occlusal view its labial side is more extended than the lingual one (relative to the
815 anterior and posterior crests), which is the reverse of the other canine. The identification of
816 both canines as left is still unsecure.

817

818 Upper premolars

819 A small and simple tooth, Cos 279, is oval in outline in occlusal view, very slightly more
820 elongated than the (incomplete) presumed p/1 Cos 278. It is higher and more pointed than the
821 latter in lingual view; its posterior crest is more salient and slightly longer than the anterior
822 one. The labial side is entirely convex, whereas on the lingual side a slight flattening is

823 observed anteriorly, and a shallow grooving is present all along the posterior crest, which
824 gives to the tooth a premolar stamp (Fig. 6C). It is interpreted as a left P1/.

825 The premolar Cos 281 is interpreted as a left P2/ (Fig. 6D1-2). A part of its posterior root is
826 preserved, whereas the breakage of its anterior root cannot be seen. The presence of a space
827 between the two roots can be seen on the labial side. The crown is expanded above the roots.
828 These roots seem compatible in size with the two alveoli for a P2/ that are incompletely
829 preserved on Cos 265. In occlusal view, the crown has an oval outline, broader than that of
830 the lower P/3-4. The main cusp is high, pointed. Its anterior crest is very abrupt and blunt; its
831 posterior crest is very salient and slightly posteriorly extended (very slightly less abrupt than
832 the anterior one). Two vertical grooves are present, one on each side of the posterior crest, the
833 lingual being deeper than the labial one. A thick cingulum is present on the posterior part,
834 short on the labial side, making a small summit in front of the posterior crest (which does not
835 join it), longer on the lingual side, on which it ascends anteriorly along the posterior side of
836 the main cusp. It seems that there was a thin and short anterior cingulum, however it is very
837 difficult to distinguish from the breakage and glue of this zone. The line visible on the base of
838 the anterolingual side is a breakage, not a cingulum. This tooth is almost as high as the P3/
839 Cos 858, and these two teeth would well fit in the same tooth row. However, in this case P2/
840 appears unreduced, in contrast with the lower P/2, which is much smaller than P/3. Such a
841 discrepancy has been sometimes observed.

842 Two P3/, Cos 264 and Cos 858, have a main cusp (paracone) elevated and pointed, with a
843 lingual wall more expanded than the labial, a salient posterior crest and no anterior one
844 (rounded wall). Both have a protocone lobe, which is small, very short and broad on Cos 264,
845 more elongated, narrow and underlined by a deeper concavity of the posterior rim on Cos 858.
846 Cos 264 has a protocone very low, crestiform, integrated in the rounded cingulum (Fig. 6F1-
847 2). Cos 858 has a clearly higher protocone, whose summit and posterolingual slope are worn;

848 on the anterior side, the protocone shows a vertical crest which joins the irregular anterior
849 cingulum at right angle (Fig. 6E1-2). The notch which separates the protocone and the
850 paracone is deep and narrow, between a short crest at the base of the paracone and the vertical
851 anterior wall of the protocone. The anterior cingulum is continuous on both P3/s, without
852 summit or thickening (no parastyle). On Cos 264, the posterior cingulum, continuous,
853 broadens and ascends in a crestiform metastyle, very low. The labial cingulum is interrupted
854 in its middle. The posterolingual face of the paracone presents a broad and shallow groove,
855 which descends until the base, just above the cingulum, on Cos 264. On Cos 858, there is no
856 grooving of the posterolingual face of the paracone, neither a crest at the base of the paracone
857 on the lingual side; the labial cingulum is slightly more developed, however it is still incipient
858 in its central part, subcontinuous. On the posterior side, the outline of the crown is more
859 angulated in occlusal view, as if there were a more projected metastyle, however in posterior
860 view its cingulum summit is even less marked than on the other tooth, being low and rounded.
861 Three P4/s show the same basic and common plan, with a large paracone, a protocone with an
862 anterolabial preprotocrista joining the anterior cingulum near the parastyle, and a more abrupt
863 postprotocrista, posteriorly directed and joining the posterior cingulum close to the lingual
864 border, a continuous labial cingulum (Fig. 6G-I). However, they also show strong character
865 variations, including in the proportions of the main cusps. In occlusal outline, Cos 263 is
866 narrower anteroposteriorly, at the level of the paracone as well as at the level of the
867 protocone, than Cos 262. Their anterior and posterior rims have weak concavities in occlusal
868 view, more expressed on Cos 262 due to the more expanded stylar regions. The P4/ present on
869 the maxillary fragment Cos 265 contrasts with the two others through its strongly narrower
870 protocone relative to the paracone, resulting in an accentuated waisting of the crown
871 (exaggerated in occlusal view by a small broken fragment on its posterior side). In anterior
872 view, the protocone of Cos 262 is almost as high as its paracone (Fig. 6G2), whereas on Cos

873 265 the protocone is much lower than the paracone (Fig. 6I2); clearly Cos 265 has the
874 smallest protocone of the three P4/s. The lingual edge of the paracone becomes crested near
875 its base, limited by a groove, on Cos 262 and Cos 263, or it starts to build a continuity with a
876 blunt labial bulging of the protocone on Cos 265. There are a few variations of the styles. The
877 parastyle is round, crestiform and isolated by a groove in occlusal view on all; in anterior
878 view, it is low on Cos 262, and has a well formed summit on Cos 263 and Cos 265, which
879 have a cuspidated parastyle. There is no metastyle at all on Cos 265, and it is very weak,
880 incipient on the two others, with in labial view a cingulum ascending posteriorly on Cos 262,
881 but horizontal on Cos 263. On the latter, the postparacrista has a slight posterior orientation in
882 occlusal view, which is absent on the two others. On the anterior side, below the preparacrista,
883 a narrow cingulum is present on Cos 263, which is more extended lingually on Cos 262, on
884 which it turns around half of the protocone. This anterolingual cingulum is very faint, barely
885 incipient, on Cos 265.

886

887 Upper molars

888 A M1/ and a M2/ are present on the fragment of maxilla Cos 258 (Fig. 6M). The two molars
889 differ: M2/ is transversely more elongated, which gives more space between the paraconule
890 and the base of the paracone. The metacone is smaller than the paracone on M2/, something
891 conspicuous in posterior view. Its anterior cingulum is more extended lingually than on M1/.
892 Its hypocone is smaller, however its posterolingual hypocrista is much more extended than on
893 M1/, closing the hypocone groove, leaving only a short space on the lingual base of the
894 protocone without cingulum. In contrast, M1/ has no lingual cingulum. The two molars have a
895 slight entoflexus, that of M1/ being more accentuated in relation with its larger hypocone. On
896 M2/, the bottom of the large notch of the centrocrista is shifted labially, a character present
897 but less expressed on M1/. M1/ has a more accentuated concavity of its posterior side than

898 M2/, which gives it a more waisted outline. Both molars share many details, as a distinct
899 small parastyle, no metastyle, the postmetacrista directed posterolabially, a small thickening
900 of the labial cingulum in its middle, a relatively voluminous paraconule with an abrupt
901 preparaconule-crista, and no metaconule at all. There is a marked angle (in posterior view)
902 between the end of the postprotocrista and the blunt edge descending lingually from the tip of
903 the metacone (hypometacrista, not salient).

904 The smaller M1/ Cos 832 (Fig. 6L) differs from the preceding one by: an ectoflexus and a
905 posterior concavity more accentuated (more waisting of the crown), a slightly smaller
906 paraconule, a small metaconule which is only a small elevation of the postprotocrista, and
907 which is followed labially by an ascending crest on the metacone, making an increased
908 continuity between the postprotocrista and the tip of the metacone (not far from a continuous
909 crista obliqua). The hypocone seems not to be larger than on the preceding M1/, however it is
910 more lingually placed, which produces a posterolingual extension of the crown outline, absent
911 on the other. Its enamel is smooth and there is no parastyle. Another small M1/ with marked
912 waisting and smooth enamel is Cos 861 (Fig. 6J), which has a big hypocone, and
913 posterolingual extension of its outline, underlined by a small entoflexus. Its hypocone is larger
914 than that of Cos 832 and it is isolated by a groove which extends until the lingual rim. Its
915 posthypocrista is blunt, difficult to recognize. It has a parastyle and a well formed metaconule
916 (bulging on both sides of the postprotocrista). The M1/ Cos 257 (Fig. 6K1) is even smaller,
917 waisted; its enamel is slightly irregular, not smooth. It is transversally short and its labial
918 cusps appear very high and pointed (e.g. a very abrupt slope of the metacone in posterior
919 view, Fig. 6K2). Its hypocone appears small, especially because the groove which separates it
920 from the protocone is shallow and interrupted by the small posthypocrista, which is in a high
921 position; the groove has no lingual prolongation at all. However, the base of the hypocone is
922 voluminous, producing some posterolingual extension of the crown as on most M1/s. It bears

923 a small parastyle, close to the preparacrista, little salient in occlusal view but well formed;
924 there is also a thickening of the cingulum forming a metastyle. The posterior part of the labial
925 cingulum curves lingually in the middle of the labial rim, to reach the bottom of the notch of
926 the centrocrista (which is slightly labially shifted); on the point of curvature, a small summit
927 makes a true tiny mesostyle, underlined by a small groove separating it from the anterior half
928 of the ectocingulum. Cos 257 has no preparacone-crista. It has a tiny metacone visible
929 only in anterior or posterior view as a small summit; in occlusal view it has no bulging but
930 makes a slight turn of the postprotocrista, which further labially curves slightly posteriorly in
931 ascending toward the metacone tip. A labial half of tooth, Cos 862, probably represents an
932 M1/, because paracone and metacone have the same height; the paracone helps recognizing
933 the anterior side. There is a small parastyle not well separated from the preparacrista; the
934 postmetacrista is more labially directed than on the other teeth; it presents a marked
935 thickening, a metastyle. This fragmentary tooth is interesting because it presents the most
936 isolated and the most inflated metacone, well isolated lingually and labially by grooves,
937 posteriorly bulged into a thick ridge descending until the posterior cingulum, which is thin at
938 its level.

939 The M2/ Cos 255 is very close in size to the M2/ of Cos 258, however it is narrower in
940 its lingual part, which gives it a transversally more elongated appearance (Fig. 6N1). They are
941 close in overall shape, however in the details, Cos 255 differs through its metacone lingually
942 shifted, its slightly smaller hypocone; its anterior cingulum ends at its lingual extremity with a
943 bulging, a small pericone, which is separated only by a groove from the lingual cingulum
944 prolonging the posthypocrista; the lingual cingulum is subcontinuous. The paracone of Cos
945 255 is more deeply separated from the preprotocrista than on Cos 258. The lingual edge
946 issued from the tip of the paracone is salient, forming a conspicuous hypoparacrista (much
947 less expressed on Cos 258). There is a bulging metacone, which on its posterior side is

948 related to the posterior cingulum through a small crest, labially curving near the cingulum.
949 Labially to the metaconule, a small groove separates it from the sharp crest which ascends high
950 on the metacone edge, which is also sharp (well expressed hypometacrista). Except for the
951 small groove limiting the metaconule, the crista obliqua is continuous from protocone to
952 metacone (Fig. 6N2). In the middle of the labial cingulum, the thickening of the cingulum is
953 broader than on Cos 258 and it is accompanied by a small elevation: it is a very small
954 mesostyle. A very small parastyle is close in size to that of Cos 258, however it is closer to the
955 preparacrista, not isolated by a groove. The upper molar Cos 256 is interpreted as a M2/
956 because it is transversally elongated, with a large space between the paraconule and the
957 paracone, it has a metacone smaller than the paracone, and its lingual cingulum is continuous
958 (Fig. 6O). It has a big crestiform parastyle, an enormous paraconule deeply separated from the
959 protocone by grooves, no metaconule. The place of the metaconule can be localized through
960 the small groove interrupting the continuity of the postprotocrista, by a small crest ascending
961 from the posterior cingulum in its direction, and in occlusal view through a slight curvature of
962 the postprotocrista, however there is no bulging, no real metaconule. This tooth has strongly
963 crenulated enamel. It is remarkable by two characters: it is the upper molar showing the
964 maximum labial shift of the centrocrista, the bottom of its notch coming close to the
965 ectocingulum; and it presents an enormous hypocone with a base bulging far lingually; this
966 hypocone is isolated from the protocone by a deep groove, interrupted lingually by the
967 cingulum, which is continuous with the low posthypocrista. This hypocone produces such a
968 strong deformation of the crown outline that it seems anomalous, especially for an M2/,
969 knowing that the others have hypocones smaller than the M1/s.

970 The M3/s are known through a labial fragment (Cos 261) and casts of two M3/ present
971 in a private collection. The best preserved, the Cos 259 cast (Fig. 6P), is a triangular tooth,
972 transversely elongated, with a metacone much smaller than the paracone but well-formed and

973 distant. Its postprotocrista is cut in two parts by a groove, the first part issued from the
974 protocone is posterior and abrupt (incipient protocone fold?), the second part slightly shifted
975 labially, directed toward the metacone, borders a trigon basin as broad as on the other upper
976 molars. The lingual cingulum ascends along the protocone and forms a lingual cusp with a
977 low summit close to the cingular groove and the protocone wall, however with a broad
978 bulging base. Its location is almost lingual to the protocone (only slightly posterior). By
979 comparison with the M2/ Cos 256, which has a tiny pericone, it seems more appropriate to
980 call this cusp a hypocone (it being a pericone might be discussed).

981 The DP4/ Cos 266 differs from the M1/s in being transversally shorter, the protocone
982 base being much less lingually expanded (Fig. 6Q). It is narrower in its lingual part relative to
983 the labial, with an accentuated concavity of the posterior border, resulting in a more triangular
984 outline. The base of the hypocone is posterolingually salient as on several M1/s. The
985 protocone is anteriorly shifted, and the postprotocrista has a strong sloping which is posterior
986 instead of posterolabial in occlusal view. The two conules are more cuspidated and pointed
987 than on most other M1/s. The hypocone has a size similar to that of Cos 257, however it is
988 more deeply separated from the protocone base, and it appears less crestiform. There is a
989 small and well formed parastyle which, as the weak metastyle, enters the variations seen in
990 the upper molars. The labial cingulum is more irregular than on all upper molars, being
991 completely interrupted along the paracone posterolabial base; posterior to this interruption, a
992 marked swelling makes a real small mesostyle; further posteriorly, the labial cingulum is
993 faint, visible in occlusal view but not isolated by a groove.

994

995 4.2.2. Remarks

996 Variability, pathology and function

997 The differences existing between some teeth are so large that the question must be raised:
998 does all this material represents one or several species? First, two specimens show variations
999 that we consider pathological. The case is obvious for the p/3 present on the type mandible,
1000 with its three roots. It seems also the case for the M2/ Cos 256, with its enormous hypocone
1001 whereas other M2/s have a much smaller one; it looks as if a very large hypocone as that of
1002 some M1/ had developed on a M2/, making such a huge bulge lingually that the tooth seems
1003 deformed, its lingual extremity probably being excluded from any significant function against
1004 the lower molars. The question also was raised if the m/3 of the type mandible might be in
1005 part abnormal through its anterolingual crown excessive elevation. It is not common o have in
1006 such a limited sample two clear cases of pathology, and a possible third one. Apart from the
1007 latters, among the most striking differences are those seen among the four M1/s. If one places
1008 side to side under the binocular the M1/ of Cos 258 (associated with its M2/) and the smallest
1009 Cos 257, one would tend to place them in two distinct species, because there is a strong size
1010 difference added to a series of other differences. However, the other M1/s appear intermediate
1011 in size between them, and all the characters of the upper molars appear to vary independently,
1012 in a mosaic way: hypocone size, lingual bulging and posterior cresting, conules size, bulging
1013 and cresting, labial shifting of the centrocrista, presence of a mesostyle, enamel crenulation. It
1014 does not seem possible to separate two groups, or one specimen wich would be clearly outside
1015 the rest of the group. A similar situation exists, more simple, with the three P4/s: Cos 263 is
1016 narrower than Cos 262 and one could wonder if they can belong to the same species; however
1017 the third one, Cos 265, is lingually narrow and labially broad, being an intermediate which
1018 differs in its own way, having the smallest protocone. Separation in two groups appears
1019 difficult. With the P/3s, the variations are also strong. Most of them have crest sinuosities
1020 and/or bifurcations at the level of a presumptive metaconid, but one of them, Cos 277, which
1021 is the broadest, has none at all and has the simplest and shortest talonid. Should we place it

1022 apart? Considering the series, it does not seem necessary to distinguish it, to take it out of the
1023 sample, especially when considering the important variations existing between the others (e.g.
1024 narrow posterior part present or not, variable paraconid shelf, ...), and the fact that Cos 277
1025 still has two posterior crests; it is not a completely simple p/3, it has a first step in its posterior
1026 complication. Other notable variations were mentioned on the paralophid and cristid obliqua
1027 (with the protocristid which can be lost) of the m/1s, the size of the protocone on the P3/s and
1028 P4/s. In fact, all along our descriptions, notable variations occurred on all teeth for which we
1029 have several specimens. All this suggests that we are dealing with one dentally variable
1030 species.

1031 Several observations present in our descriptions deserve a functional comment. On the small
1032 i/2 preserved in front of the type specimen, the peculiar labial wear does not show a clear
1033 wear facet. Hence it was not caused by contact with a superior tooth, and probably is due to
1034 food pieces grasped between the anterior teeth during biting. A large and high wear facet was
1035 described on the p/4 Cos 860. The latter tooth is moderately worn on the back of the
1036 metaconid and on the talonid, and the vertical anterior wear, starting obliquely on the
1037 protoconid summit, which is lowered, and continuing until it affects the base of the crown,
1038 appears enigmatic. It hardly seems of taphonomical origin. Had the preceding p/3 been
1039 accidentally lost? Was an occluding upper premolar too high? Was some pathology present?
1040 Last, the tooth identified as a P2/, Cos 281, would be quite unreduced, as high as a P3/,
1041 whereas the p/2 of the mandible is a very reduced tooth (reduced in length and breadth,
1042 however still quite high). Is this congruent? Close examination of Cos 281 reveals that it
1043 presents a wear facet, not yet extensive, high on the labial side of its main cusp. And close
1044 examination of the p/2 of the type mandible also reveals a short zone of wear on its posterior
1045 crest, at around two thirds of its height. It is not a vertical wear facet as would produce the
1046 wear facet of the upper P2/, however this p/2 is extremely fresh, unworn at first glance, and

1047 the small facet indicates that contact with the occluding tooth did exist; therefore, there is no
1048 objection from occlusion to the identification of the P2/.

1049

1050 Comparisons

1051 Comparison of the lower teeth and jaws from Cos with the mandible of *Pronycticebus*
1052 *gaudryi* shows that the latter was slightly larger. From the base of the crown, it appears that its
1053 p/2 was less reduced. *P. gaudryi* had a very simple p/3, bearing only a median postprotocristid
1054 reaching the tiny talonid in its middle. In contrast, all the p/3s from Cos have some
1055 complication of the posterior crests, the simplest of them, Cos 277, having its main posterior
1056 crest clearly posterolingual in occlusal view, and a second crest starting from the latter at a
1057 high level (level of a presumptive metaconid) and joining the middle of the posterior rim of
1058 the tooth. The four p/4s from Cos have a metaconid larger and better isolated from the
1059 protoconid than the p/4 of *P. gaudryi*. None of the p/4 from Cos has a paraconid shelf as
1060 transversally extended as it is on *P. gaudryi*, and none has a small paraconid as cuspidated as
1061 it is on *P. gaudryi*. On the available m/2s and m/3s from Cos, the paralophid is more
1062 attenuated than on *P. gaudryi*, none of them having the labial bulge present on the m/2 and
1063 m/3 of *P. gaudryi*, and the two m/3s having a paralophid shorter than on the m/3 of *P.*
1064 *gaudryi*. No clear difference occurs on m/1, as Cos 755 has a paralophid extremely similar to
1065 that of *P. gaudryi*. Concerning the upper dentition, the two P3/s from Cos have a
1066 postparacrista straight, posteriorly directed, simple; on the cranium of *P. gaudryi*, this crest
1067 has a slight labial inclination and its base joins the cingulum which goes labially around a
1068 “metastylar lobe” which is completely absent on the P3/s of Cos. The protocone of P3/ is
1069 smaller on the right P3/ than on the left on *P. gaudryi*. However, even the P3/ from Cos which
1070 has the largest protocone, Cos 858, has one which is even narrower and lower; and the second

1071 p3/ has almost no more protocone, only an elevation of its lingual cingulum. There is clearly a
1072 reduction of the protocone of P3/ in *P. cosensis* in comparison with *P. gaudryi*.

1073 On the P4/s also, there is a difference in the postparacrista, which on the three P4/s of Cos is
1074 never as labially curved as on *P. gaudryi*, and is never associated with a labial stylar
1075 expansion. On P3/ and P4/ of *P. gaudryi* there is a large salient paratsyle, never present on
1076 these teeth at Cos.

1077 On the M1/s, we have seen variations in the degree of waisting of the crown. However, even
1078 the small Cos 257, which has the highest waisting at Cos, is less waisted than the M1/ of *P.*
1079 *gaudryi*. The latter has a long labial part, with an extended postmetacrista within a somewhat
1080 triangular posterolabial corner, whereas this part is more squared on the M1/s from Cos,
1081 which have a less extended postmetacrista. The M1/s of *P. gaudryi* also seem to have a more
1082 developed parastyle than on those from Cos. All this results in a triangular aspect more
1083 expressed in *P. gaudryi* than on all the M1/s from Cos. It is possible that the M1/s of *P.*
1084 *gaudryi* would have had a hypocone smaller than on *P. cosensis*, however the strong degree of
1085 wear of the specimen makes this very unsecure (there is no groove of the lingual border in *P.*
1086 *gaudryi*), and the variations in hypocone size are quite strong in *P. cosensis*.

1087 The three M2/s from Cos have a lingual cingulum which is continuous or subcontinuous,
1088 whereas it is really absent on the M2/s of *P. gaudryi*.

1089 All these differences taken together show that the species from Cos is distinct from *P. gaudryi*
1090 and deserves a new species name. The most significant differences are summarized in the
1091 diagnosis of the new species. If we try to place these differences in a phylogenetic context, it
1092 appears that these species seem to belong to two divergent lineages. In *P. cosensis*, the
1093 reduction of P/2, the complication of the posterior part of p/3, the development of the lingual
1094 cingulum on M2/, are certainly apomorph characters in comparison with cercamoniines in
1095 general. Likewise, the development of the posterolabial corner of P3/, P4/ and the M1/s, with

1096 long curved postparacrista or postmetacrista, are apomorph in *P. gaudryi*, so that even without
1097 any precise statement concerning more ambiguous characters (as the size of the metaconid on
1098 P/4, or the size of the protocone of P3/), these two species show divergent specializations, and
1099 thus cannot be placed in one hypothetical specific lineage. It is very possible that the larger
1100 p/4 metaconid, the reduction of the P3/ protocone (also starting on P4/) and a larger hypocone
1101 would be further advanced traits in *P. cosensis*, however more assemblages of *Pronycticebus*
1102 are needed to further elaborate likely character polarities.

1103 Comparison with *P. neglectus* is first made with the mandible ascribed by Thalmann (1994) to
1104 this species. It is slightly larger than *P. gaudryi*, resulting in being significantly larger than the
1105 specimens of Cos. In its molars, it has long and narrow paralophids, which are closer to those
1106 at Cos (those without swellings), however on m/2 the paralophid joins the base of the
1107 metaconid, which has a slight premetacristid and realizes more continuity than at Cos, and
1108 this link with the metaconid base is present on m/1, where the paralophid curves slightly
1109 posteriorly, whereas such a closing is never observed on the m/1s of Cos. In lingual view, the
1110 m/1 of *P. neglectus* has an entoconid lower and less pointed than on the m/1s of Cos. In
1111 occlusal view, the m/3 of *P. neglectus* has an entoconid salient lingually, which is not the case
1112 on the two m/3s from Cos. For premolars, *P. neglectus* differs more strongly by the absence
1113 of p/1 and complete absence of metaconid on p/4. Its p/3 has a beginning of posterior cresting
1114 with two crests, one of them becoming posterolingual in occlusal view, recalling those of Cos,
1115 however the posteriorly directed crest is till the dominant one, recalling the primitive
1116 morphology present on *P. gaudryi*. The p/3 also has no lingual cingulum, and on p/3 and p/4
1117 the anterior cingula are simpler, without any swelling in the paraconid shelf region. The
1118 description of the type skeleton by Thalmann (1994) confirms what is suspected from the
1119 examination of the mandible: this species had lost the first premolar, both in the upper and
1120 lower dentition. M1/ and M2/ had no lingual cingulum. From the illustrations by Thalmann

1121 and our own observations of the type specimen, we estimate that the hypocone is smaller on
1122 M1/ and M2/ than on the upper molars of *P. cosensis*. On the whole, the species of Cos is also
1123 clearly different from that of the Geiseltal, which is also divergent in its own way (loss of
1124 p/1/, no metaconid on p/4, narrow paralophid curving posteriorly on m/1. Again none of them
1125 would appear as a likely ancestral state in a specific lineage.

1126 A last comparison must be done with the very scanty material mentioned in Vielase as
1127 *Pronycticebus cf gaudryi* (Legendre et al., 1992). Comparisons were limited at that time
1128 because the upper teeth are highly worn on the cranium of *P. gaudryi*. The M2/ VIE 141
1129 appears to be extremely similar to the M2/s described above (Fig. 6S). Small differences
1130 concern a very slight flexus on the anterolingual border of the tooth, not observed in Cos, the
1131 lingual cingulum which appears slightly less complete: the prehypocrista is very short, leaving
1132 the groove between protocone and hypocone lingually open (as on some M1/s from Cos),
1133 whereas this crest is longer on the two well preserved M2/ of Cos, almost completing the
1134 lingual cingulum (on the pathological one, the crest is very low and the groove quite open).

1135 Another difference is the complete absence of paraconule on this tooth, whereas it is well
1136 formed on the M2/s from Cos. However, the difference is very small with the M2/ of Cos 258,
1137 which has the smallest paraconule in the Cos assemblage. The centrocrista is straight on VIE
1138 141, as on the M2/ of Cos 258. The M2/ from Vielase has strongly crenulated enamel, and its
1139 mesostyle is larger than in all the teeth from Cos, accompanied by a low crest joining the
1140 bottom of the notch of the centrocrista. Polarities appear opposed for these morphological
1141 differences. The M2/ from Vielase could appear more primitive through its less complete
1142 lingual cingulum, and more derived through the complete loss of the paraconule and the larger
1143 mesostyle. Because there are strong variations among lingual cingular characters, may be that
1144 the two others are a first indication of the Vielase species being slightly more advanced?

1145 Clearly, this hypothesis needs more quantitative data to be strengthened. Another fragmentary

1146 tooth from Vielase, VIE 142, is an incomplete m/2 or m/3, which has a paralophid thin and
1147 straight as on Cos 271 (Fig. 6T). The tooth seems to posteriorly broaden as would an m/3, and
1148 the reach of the cristid obliqua on the trigonid wall, relatively low and labial, also fits with an
1149 m/3. This tooth does not add any difference with those of Cos. Pending the recovery of more
1150 specimens, the species from Vielase is best be referred to the new species *P. cosensis*.

1151

1152 Genus *Anchomomys* Stehlin 1916

1153 4.3. *Anchomomys* sp.

1154 Material: One incomplete M2/, Cos 290 and one upper canine, Cos 297.

1155 Measurements: C sup Cos 297, 1.50 x 1.14; M2/ Cos 290, > 2.20 x >= 3.10.

1156 Description and remarks

1157 This M2/ Cos 290 is very close in morphology to the M2/ of the type specimen of
1158 *Anchomomys gaillardi* from Lissieu, described by Stehlin (1916) and Szalay (1974). The
1159 main differences are: a significantly larger size, a slightly larger hypocone, more cuspidated,
1160 associated with a slightly more quadrangular lingual border of the crown. The tooth seems to
1161 be slightly more transversally elongated, which is corroborated by the slope of the paracone,
1162 which is extremely steep in anterior view in *A. gaillardi*, whereas the same slope is more
1163 lingually extended on the tooth of Cos. These differences are enough to consider this
1164 specimen as belonging to a different species, however from the available evidence also a very
1165 close one. Because it is more transversally elongated, it might be primitive in relation to *A.*
1166 *gaillardi*. However, upper molars in the *Anchomomys* clade are quite conservative. This tooth
1167 is also very close to one upper molar of *A. frontanyensis* from Sant Jaume de Frontanyà
1168 (Marigo et al., 2011). The hypocone is closer in size in the latter species, however the tooth
1169 seems to be also more transversely short in *A. frontanyensis*, with a paracone not lingually

1170 extended (see Figure 1J in Marigo et al., 2011). More teeth are needed to further elaborate the
1171 significance of the Cos *Anchomomys*.
1172 The small tooth Cos 297 is not easy to identify. It is relatively simple, moderately longer than
1173 broad, and it seems very slightly procumbent (Fig. 7B). On its lingual side, a cingulum is
1174 present, weak anteriorly, more salient posteriorly, absent in-between. The root is complete
1175 and in posterior view somewhat labially shifted at its extremity, which fits with an upper, and
1176 not with a lower canine. The global shape is not far away from the upper canines which were
1177 described for *A. frontanyensis* and *Mazateronodon endemicus* (Marigo et al., 2010, 2011),
1178 however it differs from them in being less pointed and much smaller in relation to the upper
1179 molars. Nothing else in the fauna would suggest the presence of a second smaller species of
1180 *Anchomomys*. We consider more likely that these two teeth belong to the same species, which
1181 in turn suggests that a marked evolution in upper canine size took place within *Anchomomys*
1182 lineages.

1183

1184 Infraorder Omomyiformes Schmid 1982

1185 Family Microchoeridae Lydekker 1887

1186 4.4. Genus *Quercyloris* Godinot & Vidalenc, nov. gen.

1187 Figure

1188 Derivation of name: from the Quercy region and the living genus *Loris*, a small insectivorous
1189 strepsirrhine from Asia

1190 Type species: *Quercyloris eloisae* Godinot & Vidalenc, nov. sp.

1191 Included species : the type species only

1192 Occurrence and diagnosis: see type species

1193

1194 *Quercyloris eloisae* Godinot & Vidalenc, nov. sp.

1195 Figure 7

1196 Derivation of name : in honor of Eloïse Lande-Zoukouba, in recognition of her dedication to
1197 sorting small fossils in washing and screening residues of Quercy localities during many
1198 years.

1199 Holotype: the right M1/ Cos 288;

1200 Paratypes: two other upper molars, the right M1/ Cos 287 and the left M2/ Cos 289;

1201 Material: one upper incisor Cos 304, one upper canine Cos 294, three upper premolars left P4/
1202 Cos 291, Cos 292 and right P4/ Cos 293, one p/3 Cos 298, an m/2 Cos 295, and an incomplete
1203 m/1 Cos 301.

1204 Type Locality: Cos in the Quercy region, France.

1205 Occurrence: the type locality only;

1206 Measurements: I1/ Cos 304, length perpendicular to the root (H in Godinot 2003, Fig 2), 1.31,
1207 width 0.92, length along the crown base in lingual view, 1.88; upper canine Cos 294, length
1208 1.35 x width 0.89 x height 0.78; P4/ Cos 291, 1.48 x 2.12; P4/ Cos 292, 1.37 x 1.86; P4/ Cos
1209 293, 1.49 x 1.94; M1/ Cos 287, 1.76 x 2.43; M1/ Cos 288, 1.65 x 2.38; M2/ Cos 289, 1.53 x
1210 2.26; p/3 Cos 298, 1.20 x 0.91 x 0.59; m/1 Cos 301, 1.55 x 1.33; m/2 Cos 295, 1.75 x 1.44.

1211 Diagnosis: Small microchoerid with transversely elongated upper molars, without hypocone
1212 or *Nannopithec*-fold, and with a long postmetaconule crista and variably elongated
1213 premetaconule crista forming a crescent around the metacone base; P4/ with an elongated and
1214 narrow lingual lobe, low protocone, and isolated metastylar swelling; upper incisor elongated,
1215 with a strongly bulging posterolingual eminence, and a crown without the global curvature
1216 present in *Pseudoloris*; lower molars with relatively low relief, big cuspidated paraconid
1217 isolated from the metaconid by a groove, making a lingually open trigonid on m/1-2.

1218

1219 4.4.1. Description

1220 The p/3 Cos 298 is typical of small microchoerid premolars, single rooted with the crown
1221 markedly anteriorly inclined, having in lingual view an elongated and rectilinear cingulum
1222 (see Godinot, 2003, Figure 1a,h,i); anteriorly, the protoconid is not high above the cingulum,
1223 a character accentuated here by a strong wear of the protoconid summit (Fig. 7K1). In
1224 occlusal view, the posterior part of the crown is very broad, producing a subtriangular outline,
1225 despite a long vertical wear facet has affected the posterolingual border and slightly
1226 diminished the posterior breadth. This posteriorly broad outline is the reason to consider this
1227 tooth a p/3 instead of a p/2. There is only one posterior crest on the posterior side of the
1228 protoconid, which is median and not salient; it joins the posterior cingulum. In posterior view,
1229 the cingulum extends only on the lingual side of this junction, until it is interrupted by the
1230 above mentioned wear facet.

1231 The two lower molars are uneasy to identify, because the best preserved, with its large
1232 paraconid resembles m/1s and the other is incomplete, its entirely broken away protoconid
1233 rendering its interpretation difficult. However, because they have similar talonids and similar
1234 low relief in lingual view, we place them in the same species. The slightly smaller one, Cos
1235 301, despite its broken away protoconid, has a well preserved paraconid, which is very salient
1236 anteriorly, median instead of lingual on the other; also what remains of its outline shows the
1237 anterior half of the crown to be much narrower than the posterior half (Fig. 7L1). For these
1238 reasons, Cos 301 is probably an m/1, and the complete one, Cos 295, is probably an m/2. Both
1239 share in posterior view a low entoconid and a much higher hypoconid, with enamel more
1240 ventrally extended (some exodaenodonty); this explains why the labial slope of the protoconid
1241 is extended on Cos 295, as is often the case in microchoerids (Fig. 7M1). Both have a similar
1242 cristid obliqua joining the back of the trigonid, clearly below the protoconid summit on Cos
1243 295. They also have similar metaconids, that of Cos 301 being slightly worn, with a wear
1244 facet extending on its side of the protocristid. The paraconid of the m/1 Cos 301 is cuspidated,

1245 slightly more crestiform than on Cos 295; it is anteriorly placed, median, and isolated from
1246 the metaconid by a deep valley (Fig. 7L2). On Cos 295, the paraconid is more bulbous, more
1247 linguallly placed, also isolated from the metaconid by a groove, however a shallower one.
1248 Both paraconid and metaconid have on Cos 295 blunt edges directed toward each other in
1249 occlusal view, however they do not meet, the groove between them is continuous, the overall
1250 appearance is still of two bulbous cusps and a linguallly open trigonid basin (Fig. 7M2). On
1251 the labial side, there is no cingulum around the hypoconid (a crack in the crown just below
1252 could be misleading); a rounded cingulum starts at the opening of the postvallid, with a small
1253 bulge, an interruption just in front of the valley, and a cingulum extending forward, then
1254 strongly dorsally curving, and then interrupted by the breakage of the antero-ventrolabial part
1255 of the crown. On Cos 301, one sees only an unusual rounded bulge of enamel toward the
1256 opening of the postvallid, and anteriorly the crown is damaged.

1257 The right I1/ Cos 304 has a convex and smooth labial face, and a flatter lingual face entirely
1258 surrounded by a crest (Fig. 7C1): anterior and posterior crests on both sides of the protoconid,
1259 continuous on both sides with the cingulum, which forms two ventrally inflated parts
1260 separated by a concavity; the anterior part first follows an almost straight line, then it fades
1261 through the concave part, possibly due to some degree of wear (difficult to recognize), then
1262 the posterior part is shorter and strongly bulging linguallly; the tip of this bulging is affected
1263 by a lingual wear facet, which prevents to know if it would have made a salient summit
1264 (which would have been analogous with a small plesiadapid posterocone). The crown is on
1265 the whole somewhat extended, recalling the extension of lower premolars as seen in lingual
1266 view.

1267 Another isolated tooth, Cos 294, has an overall similarity with the p/3 described above (Fig.
1268 7D1-3). However, it differs by its crown more perpendicular to its root, an outline in occlusal
1269 view more rounded, less posteriorly broadened, a lingual cingulum limited to its anterior part,

1270 a posterior cingulum more cusp-like, round, isolated from the protocone by a transverse
1271 groove. On the whole, it was a less procumbent tooth, less modified to fit into a closely
1272 packed series, it may have been slightly higher, however wear of its summit also obscures that
1273 aspect. It is best interpreted as an upper canine.

1274 The three P4/ Cos 291, Cos 292 and Cos 293 (Fig. 7E-G) are transversely elongated, with a
1275 narrow protocone lobe, a well isolated metastylar crest, a preprotocrista continuous with the
1276 anterior cingulum (less continuous, thinner and sinuous, on Cos 293), reaching a cingular
1277 parastyle, a more abrupt postprotocrista quickly joining the posterior cingulum, also
1278 continuous until the metastyle. The labial cingulum is only incipient in the middle of the
1279 labial side (not visible on Cos 291 due to breakage of the base of the crown). They differ in
1280 some details. Cos 292 has a lingual lobe slightly shorter and broader than the others, giving it
1281 a more quadrangular outline, with a postprotocrista directed posteriorly. Cos 291 has a
1282 postprotocrista directed posterolingually, as Cos 293, which has a narrower protocone lobe,
1283 rounded in outline, with a slight flexus of its anterior border. There is a faint anterior
1284 cingulum below the preprotocrista on Cos 291, not on the others. The metastylar crest makes
1285 an angle with the postparacrista on Cos 291, visible in occlusal as in posterolingual view; this
1286 crest is more continuous on Cos 293, which has a slightly more inflated metastyle.

1287 The three upper molars Cos 287, Cos 288 and Cos 289 are quite similar to each other (Fig.
1288 7H-J). They are simple, transversely elongated, narrower lingually than labially. Cos 289 has
1289 a metacone smaller than the paracone, a protocone slightly lower than the two others, with a
1290 less extended lingual protocone slope; it is likely an M2/. Cos 287, with its slight waisting, is
1291 a likely M1/. Cos 288 is more ambiguous, however because it shares with Cos 287 a high
1292 protocone and long lingual slope, we identify it as a second M1/. Cos 287 and 288 have a
1293 slight ectoflexus, whereas Cos 289 has a straight labial border. All have a postmetacrista
1294 somewhat labially oriented, they have cingular parastyle and metastyle, not cuspidated. The

1295 posterior cingulum is well formed on Cos 289, being continuous and staying low in its lingual
1296 part. On the two others, the posterior cingulum moderately ascends lingually, the crown
1297 becomes salient beyond it in occlusal view, which gives the impression of an incipient
1298 hypocone. Cos 287 and Cos 288 have a distinct paraconule, with a summit visible in anterior
1299 or posterior view, Cos 289 has no real paraconule, only a very faint broadening of the base of
1300 the preprotocrista. All have a paracone which has a long lingual edge, which becomes more
1301 crested toward its base (and is slightly longer on Cos 289); this extension (hypoparacrista not
1302 salient) is always separated from the preprotocrista or preparaconule-crista by a groove; none
1303 of them has a post-paraconule crista which would make the link between paraconule and
1304 paracone often encountered in *Nannopithec* species. The metaconule is only crestiform on
1305 Cos 287, crestiform with a low summit on Cos 289, and crestiform with a well formed
1306 summit, that is cuspidated, on Cos 288. It has a long postmetaconule crista joining the
1307 posterior cingulum when there is one (and still continuing until the metastyle when the
1308 posterior cingulum is interrupted, as on Cos 287). The premetaconule crista is broadly
1309 divergent from the latter, lowering and going around the metacone base on Cos 287; on Cos
1310 288, the premetaconule crista is less divergent, it turns and joins the base of the metacone; and
1311 on Cos 289, the premetaconule crista goes more toward the metacone; it is also much less
1312 abrupt, realizing a continuity between the metaconule and the metacone lingual edge.

1313

1314 4.4.2. Remarks

1315 These new fossils do not fit in any of the microchoerid genera described until now. They
1316 would most closely compare with the most primitive species of the family, *Melaneremia* from
1317 the early Eocene and early *Nannopithec*. The upper molars are close, however the sole
1318 M1/described in *Melaneremia* has a small metaconule and a direct link from protocone to
1319 metastyle (Hooker, 2007); it does not present the strong metaconule with crescentiform crests

1320 of *Quercyloris*. The lower molars also would appear close, however the p/3s are markedly
1321 different. Whereas *Melaneremia* still has a two-rooted p/3 relatively similar to p/4, as in
1322 primitive omomyids (Hooker, 2012), *Quercyloris* has a single-rooted one with the
1323 anterodorsally oriented crown typical of more advanced microchoerids (Fig. 7K1). This
1324 reflects a higher degree of premolar compaction, clearly indicating a different genus. The
1325 most primitive species of *Nannopithec*, *N. zuccolae* from Prémontré, has transversely
1326 elongated upper molars and P4/, and no hypocone (Godinot et al., 1992). However, here again
1327 there are differences: the postprotocrista presents a more or less expressed *Nannopithec*-fold,
1328 the M2/ is lingually more dissymmetrical, and the metaconule does not present the long
1329 postmetaconule crista present at Cos as on the upper molars of *Pseudoloris* species.
1330 Furthermore, the tendency of the two labial metaconule cristae to make a crescent around the
1331 metacone base, as in *Pseudoloris*, is well expressed on Cos 287, less on Cos 288, not on Cos
1332 289, which is more similar to *Nannopithec* for this character. On the paraconule side, the
1333 upper molars of Prémontré frequently have the link between paraconule and hypoparacrista
1334 usually present in *Nannopithec* species, whereas all the upper molars from Cos have a groove
1335 separating the paraconule from the hypoparacrista. Differences also occur on the lower
1336 molars. The m/2s of Prémontré have much more acute crests than Cos 301. They also have a
1337 much deeper protocristid notch and a deeper trigonid basin; the trigonid crests are higher,
1338 there is a true premetacristid, the paraconid is less lingually placed, and the trigonid crests are
1339 starting to lingually close the trigonid basin (in the way which is more advanced on the m/3s,
1340 with their narrow triangular trigonid typical of *Nannopithec*). In contrast, the trigonid basin is
1341 shallower, lingually open, and the paraconid more lingual on Cos 301. In sum, the molars
1342 from Cos resemble those of *N. zuccolae* by their primitive proportions and characters (large
1343 paraconid on the lower molars, lack of hypocone on the uppers), however they belong to a
1344 different lineage which did not develop a *Nannopithec*-fold and a crest linking paraconule and

1345 paracone on the uppers, which did not develop the closing of the trigonid in the *Nannopithec*
1346 way on the lowers, and which shares with *Pseudoloris* the tendency to build a metaconule
1347 crescent on the upper molars. It is very probably a primitive member of the *Pseudoloris*
1348 clade. It cannot be ascribed to a primitive species of *Pseudoloris* because there are still too
1349 many differences in major characters between them: *Pseudoloris* lower molars never have a
1350 large cuspidated paraconid, they have a high pointed entoconid in lingual view; its upper
1351 incisors have a different shape, being more pointed and curved; added to the fact that
1352 *Pseudoloris* upper molars and premolars are transversely shorter, all these differences justify
1353 the erection of a new genus. Its only known species, *Quercyloris eloisae* gen. nov. sp. nov.,
1354 appears primitive relative to *Pseudoloris* in many of its known characters, so that it could
1355 represent an early member of the *Pseudoloris* lineage. This will have to be tested by further
1356 discoveries (e.g. intermediate I1/ morphology, intermediate trigonid shapes, etc.).

1357 Another poorly documented genus, *Pivetonia*, often has been considered a synonym of
1358 *Pseudoloris* (e.g. Szalay & Delson, 1979; Godinot, 1983; Minwer-Barakat et al., 2010, 2012).
1359 However, we consider it as a valid genus, represented by its type species *P. isabena* from
1360 Capella (Crusafont-Pairo, 1967), and by *P. saalae* from the Geiseltal (Thalmann, 1994).

1361 *Pivetonia* has also been mentioned as possibly present in Lissieu (Godinot, 1983), Cuzal
1362 (Marandat et al., 1992), and Vielase (Legendre et al., 1992). The teeth of the type specimen of
1363 *P. isabena*, a mandible bearing p/3 to m/2, show a remarkable overall similarity with the
1364 teeth of *Q. eloisae*. Their p/3s are similar; their lower molars have the same size and low
1365 relief. However, on the m/1 of *Pivetonia*, a lingual crest joins the paraconid to the metaconid,
1366 lingually closing the trigonid basin; on m/2, the difference is strongly accentuated because the
1367 paraconid, more crestiform but still voluminous, is shifted labially, and the closing of the
1368 trigonid basin is more complete. The trigonid is made of a triangle, the paraconid summit
1369 being closer to the protoconid than to the metaconid. This means that *P. isabena* is advanced

1370 in a process of a trigonid closing. This process is more advanced on *P. saalae* from the
1371 Geiseltal, which has on m/2 and m/3 a trigonid made of three crests in triangle. Such a process
1372 appears apomorphic, and difficult to reconcile with the morphology of an early assemblage of
1373 *Pseudoloris* as illustrated in Le Bretou (Godinot, 1988). On the latter's m/1 and m/2, the
1374 trigonid is lingually open, and we think that such a morphology is unlikely to be derived from
1375 a closed trigonid morphology. In the different processes of trigonid evolution, *Pivetonia* is
1376 already advanced toward a triangular trigonid closing, which distantly recalls the trigonid
1377 closing found among *Nannopithec* species. We consider as unparsimonious, unlikely, a
1378 secondary loss of the lingual crest joining the paraconid to the metaconid, i.e. a secondary
1379 reopening of the trigonid basin in the *Pseudoloris* lineage. In this view, *Pivetonia* is evolving
1380 in its own way, divergent from *Pseudoloris*, whereas *Quercyloris* is still a candidate for a
1381 morphology possibly ancestral to that of *Pseudoloris*. More material will help to test these
1382 hypotheses. For example, *P. saalae* has an enlarged p/4 which also recalls *Nannopithec* and
1383 might be associated with enlarged anterior incisors. A p/4 of *Quercyloris* would help to test
1384 this scenario, as would an m/3 (posteriorly broadened as in *Nannopithec*, or not, as in
1385 *Pseudoloris*?).

1386 In this context, the significance of *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà
1387 (MP 14-15; Minwer-Barakat et al., 2010) will be important. On one hand, its incompletely
1388 lingually closed trigonid and its variations might appear intermediate between those of
1389 *Pivetonia* and *Pseudoloris*. On the other hand, the lower incisors attributed to this species, as
1390 those attributed to *P. cuestai* (Minwer-Barakat et al., 2012) are so different from those of *P.*
1391 *parvulus* and from those of microchoerids in general, that they would indicate a different
1392 lineage (*Pivetonia*?) or be misattributed to those species. Further analyses are requested to
1393 better settle these questions.

1394 Comparisons also must be made with the two fragmentary teeth from Vielase previously
1395 mentioned as *Pivetonia* n. sp. (Legendre et al., 1992). The trigonid of m/1 VIE 144 appears
1396 very similar to the parts preserved in the incomplete m/1 from Cos. The cusps are low and it
1397 possesses a very large paraconid separated from the metaconid by a wide space. It resembles a
1398 lot the m/1 of *Quercyloris moniquae*, despite a small difference in paraconid shape. However
1399 the fragmentary M1/ VIE 143 is transversely shorter than the upper molars from Cos, it is
1400 markedly narrower in its lingual than in its labial part, and it has cingula, especially the
1401 posterior one, which are much stronger than on the teeth from Cos. This M1/ cannot belong to
1402 the same species as in Cos. Nevertheless, we can list *Quercyloris* as present in Vielase in
1403 replacement of *Pivetonia*, which is not there.

1404
1405 Order Plesiadapiformes Simons and Tattersall, in Simons 1972

1406 Family Paromomyidae Simpson, 1940

1407 Genus *Arcius* Godinot, 1984b

1408 4.5. *Arcius moniquae* Godinot & Vidalenc, nov. sp.

1409 Figure 8

1410 Derivation of the name : in honor of our colleague Monique Vianey-Liaud, in recognition of
1411 her magnificent research on fossil rodents from the Quercy.

1412 Holotype: the left M2/ Cos 300, University of Montpellier collection.

1413 Material: The P4/ Cos 299, the m/3s Cos 305 and Cos 306, the i/1 Cos 302.

1414 Type Locality: Cos, Quercy region, France.

1415 Measurements: P4/ Cos 299, 1.82 x 2.15 mm; M2/ Cos 300, holotype, 1.95 x 2.57; m/3 Cos

1416 305, > 1.95 x 1.40; m/3 Cos 306, 2.63 x 1.39; lower incisor Cos 302, total length, 7.41, height

1417 at the base of the crown, 2.58, width (in occlusal view) in the middle of the crown, 1.35.

1418 Diagnosis: Species of *Arcius* which differs from all previously described species of the genus
1419 by its reduced labial cingulum and complete absence of paraconule on the upper molars; very
1420 reduced trigonid on its m/3, without any remnant of paralophid, and with a low vestigial
1421 protocristid making the trigonid broadly open posteriorly. In addition, the upper molars are
1422 relatively transversely short and have a vast posteriorly extended posterior fossa.

1423 4.5.1. Description

1424 The partial i/1 Cos 302 is broken at its tip and at its base (Fig. 8A1-2). The remaining part is
1425 long and characteristic enough to be identified: in its preserved part, it is exactly similar to the
1426 i/1 of *Arcius rougieri*, as described in Godinot (1984) and again figured in Lopez-Torres and
1427 Silcox (2018, Figure 1). This part does not need to be described again. Breakage at the tip
1428 allows to see that the enamel is thicker on the labial and ventral side, thinner on the dorsal
1429 side and lingually above the thin crest which curves and posteriorly quickly reaches the dorsal
1430 side (Fig. 8A1). Two m/3, Cos 305 (Fig. 8D) and Cos 306, are very similar. Their trigonid is
1431 anteroposteriorly very short; no trace of paralophid can be distinguished. Their protocristid is
1432 extremely reduced: very low and blunt on the protoconid side, no more discernible on the
1433 metaconid side. The trigonid is no more a transverse wall, it is mainly an anteroposterior
1434 broad valley. Their hypoconid is low and its crests are almost anteroposterior. The third lobe
1435 is broad, the entoconid low and very little lingually salient.

1436 The P4/ Cos 299 and the M1-2/ Cos 300, the type specimen, are quite similar in overall shape,
1437 with a subquadrangular outline, weak labial cingulum, straight preprotocrista directly
1438 reaching the parastyle, postprotocingulum surrounding a vast posterior fossa, a low
1439 postprotocrista (Fig. 8B-C). They differ by the outline transversely more extended and
1440 posteriorly shortened in Cos 300, which is similar to most M1-2/ described in *Arcius* species.
1441 In labial view, the paracone and metacone summits are slightly closer, and the paracone is
1442 higher, on Cos 299, which prompts us to identify it as a P4/. The notch of the centrocrista as

1443 seen in labial view is deeper on Cos 299, extremely low on Cos 300 on which it makes a very
1444 open V and the crest appears highly situated. The trigon fossa is deeper on Cos 300 than on
1445 Cos 299, which may also confirm our identification. The paracone lingual extension is a blunt
1446 edge on Cos 299, it is more lingually extended and more crested on Cos 300 (hypoparacrista).
1447 On both teeth, a groove separates these crests from the preprotocrista; on the latter, a
1448 paraconule is completely lacking on Cos 300, and vestigial, visible only in anterior view as a
1449 very low summit of the crest on Cos 299. The labial cingulum is poorly differentiated, not
1450 isolated by grooves. In labial view, a very shallow relief allows the delineation of a parastylar
1451 and a metastylar low relief; in the middle of the labial border, there is no cingulum on Cos
1452 299, whereas on Cos 300, even if the cingulum is poorly crested, the presence of a small fossa
1453 anterolabially to the metacone underlines its presence.

1454

1455 4.5.2. Remarks

1456 When compared with all the species of *Arcius* described until now, the small material from
1457 Cos presents several original characters. Its cusps and crests are relatively low, less acute than
1458 in several species as *A. rougieri* and *A. fuscus*. In most *Arcius* species, the notch of the
1459 centrocrista is deep, whereas it is especially shallow on the M2/ of Cos. The two upper teeth
1460 also are less transversely elongated than in the primitive species of the genus, *A. zbyzewskii*
1461 and *A. fuscus*. In occlusal outline, they are close to some of the upper molars of *A. lapparenti*
1462 figured by Aumont (2003, 2004). However, the upper molars of *A. lapparenti* have a more
1463 differentiated labial cingulum, and for some of them a less posteriorly extended posterior
1464 fossa. More important, all the upper molars of these species, and *A. ilerdensis*, have a distinct
1465 paraconule and a link between the paraconule and the hypoparacrista. This is also true of the
1466 P4/s of *A. fuscus* and *A. lapparenti*. The loss of the paraconule and groove isolating the
1467 preprotocrista from the hypoparacrista, on M2/ and possibly on P4/, appears as unique to the

1468 species of *Cos*. If our identification of *Cos* 299 as a P4/ is correct, then this P4/ seems
1469 transversely shorter than the P4/s of most other *Arcius* species; it may also have the paracone
1470 and metacone the closest in size among the species of *Arcius*, which would be one more
1471 derived character relative to the others. On the lower m/3s, the species of *Cos* also appears at
1472 the end of a morphological trend, the reduction and posterior opening of the trigonid. All the
1473 figured m/3s of *Arcius* have a more or less reduced paralophid, and some kind of anterior
1474 extension of either the preprotocristid (e.g. *A. lapparenti* in Aumont 2004) or the
1475 premetacristid (*A. ilerdensis*); a paralophid crest is lacking on the m/3s of *Cos*. Furthermore,
1476 all the m/3s of other species have a well differentiated protocristid, whereas this major
1477 transverse crest is highly reduced on the m/3s of *Cos*, broadly posteriorly opening the
1478 trigonid. For all these reasons, despite the paucity of the material recovered until now in *Cos*,
1479 this *Arcius* material needs to be recognized as a new species, which appears apomorph
1480 relative to previously described species for several of its distinctive characters. An
1481 evolutionary trend toward more bunodont teeth has already been identified in *Arcius* and in
1482 other genera of paromomyids (Lopez-Torres et al., 2017). Morphological quantifications may
1483 be done in the future to test if this new species really is an advanced stage in this trend among
1484 *Arcius* species.

1485 The m/3s of *Cos* lead to comment the two m/3s from Bouxwiller which have been described
1486 by Aumont (2003) as *A. lapparenti*, and excluded from this genus and considered as possibly
1487 belonging to a *Nannopithex* by Lopez-Torres et al. (2018). Among the reasons to question
1488 their attribution to *Arcius* was the extremely short trigonid and very broad talonid basin.
1489 These characters are present on the new species from *Cos*, and moreover on the figures of
1490 Aumont (2003, Plate 15) the protocristid appears as reduced as it is on the m/3s from *Cos*.
1491 There is no doubt that the two m/3s from Bouxwiller belong to an *Arcius*, and they may best
1492 be referred to *A. cf moniquae* pending the recovery of more material from both localities. The

1493 m/3 figured by Aumont (2003) appears slightly anteroposteriorly shorter than the m/3s from
1494 Cos, and the talonid basin this way seems to be broader, however these differences are very
1495 small; they do not exceed the strong intraspecific variations illustrated in large assemblages of
1496 *Arcius* by Aumont (2003), and they do not justify to exclude the m/3s from Bouxwiller of the
1497 genus *Arcius*. These m/3s appear closer to *A. moniquae* nov. sp. than to any other *Arcius*
1498 species.

1499

1500 5. Discussion

1501 The new fauna of Cos has a very original composition. It does not include any perissodactyl
1502 nor any artiodactyl. It is rich in rodents and bats, and also in bird remains. Bones of some
1503 large prey birds have been recovered, which suggest that the assemblage may result from the
1504 accumulation of preys by raptors. The other elements of the fauna are under study.

1505 The fauna of Cos being new, it would be important to propose for it an age, which will be
1506 given by the fossil content because it is a fissure filling. However, the primates are new
1507 species and the plesiadapiform belongs to a poorly documented lineage. The biochronological
1508 considerations which follow therefore will not be precise. The fauna does not content any
1509 primate species found in Bouxwiller. The *Protoadapis* has a remarkably primitive M2/
1510 without hypocone, whereas the *Europolemur* and a possible other cercamoniine from
1511 Bouxwiller have very large hypocones. These elements suggest that the fauna is probably
1512 older than Bouxwiller, i.e. older than MP 13. If we consider that *P. brachyrhynchus*, absent in
1513 Bouxwiller, is probably older than MP 13, then *P. andrei*, which must be older than *P.*
1514 *brachyrhynchus*, would be even older, which would point toward MP 12 or before. The only
1515 species of *Pronycticebus* known outside of the Quercy is *P. neglectus* from the Geiseltal, MP
1516 12 level. No simple lineage of *Pronycticebus* has been identified, the genus seems to have had
1517 a bushy evolution, however its presence in the MP 12 reference-level is an important

1518 indication. As seen above, the presence of *P. cosensis* in the MP 10-11 fauna of Vielase, even
1519 if they have a slight difference in evolutionary stage, suggests a close age for Cos. The
1520 absence of these primates from the relatively well sampled faunas from the MP 10 level
1521 suggests that it is likely later than MP 10. The new species of *Arcius*, which seems more
1522 advanced than the MP 10 common species *A. fuscus* and *A. lapparenti*, would confirm this
1523 indication. It is very difficult to go further. Rouzilhac, which is not very far away, has
1524 different middle-sized cercamoniines and no micromammals. It is placed in the MP 10 – MP
1525 11 interval, which is broad (Godinot et al., 2018). In conclusion, the absence of well
1526 delineated lineages prevents strong biochronological statements, however many indirect
1527 arguments point toward a MP 10 – MP 12 bracket, and the presence of *P. cosensis* and a
1528 *Quercyloris* species in Vielase suggest an age close to that ascribed to this locality, in the MP
1529 10 – MP 11 interval. Based on the differences on one upper molar of *Pronycticebus* and the
1530 presence of a larger species of *Quercyloris* in Vielase, a preliminary conjecture would
1531 propose the Cos fauna as possibly older than Vielase. This first indication needs confirmation
1532 by other evidence.

1533

1534 6. Conclusion

1535 The four new species described in this paper are a significant addition to our knowledge of
1536 European Eocene primates and plesiadapiformes. The new *Protoadapis andrei*, close to *P.*
1537 (*Cercamoni*) *brachyrhynchus*, is documented by more complete material than the latter,
1538 including p/3, p/4, m/3, and more importantly for the first time upper canines, a P4/ and an
1539 M2/ which can confidently be attributed to a *Protoadapis* species. This will be very important
1540 for future phylogenetical analyses. Concerning the new *Pronycticebus*, the material also
1541 presents for the first time a lower incisor, a lower canine in place, p/2, and unworn teeth from
1542 third premolar to last molar above and below, with variations. Documenting the intraspecific

1543 variability is crucial to a sound appreciation of the value of characters in phylogenetic
1544 analyses. Our comparisons have shown us that, on isolated lower molars, it may be difficult to
1545 distinguish *Pronycticebus* from *Europolemur* species. This is illustrated by the proposal of
1546 Tattersall & Schwartz (1983) to consider the mandible from Mancy previously ascribed to
1547 *Protoadapis curvicauspiciens* (Russell et al., 1967) as a new species of *Pronycticebus*, *P.*
1548 *mancyi*. This attribution was not followed by us, and we lately thought that this species should
1549 be considered as *Europolemur mancyi*. The new material of *Pronycticebus* confirms this
1550 choice in making clear a difference between the two genera: *Europolemur* species have large
1551 canines, whereas *Pronycticebus* species have much smaller canines, above and below. Also,
1552 unworn teeth reveal that *Pronycticebus* molars are much less bunodont than those of
1553 *Europolemur*. These new characters will be crucial to enhance our understanding of the
1554 genera *Protoadapis*, *Europolemur* and *Pronycticebus*, which until now have unresolved
1555 phylogenetic relationships, in large part due to insufficient documentation. Interestingly, in
1556 both *Protoadapis* and *Pronycticebus*, our preliminary phylogenetic observations seem to point
1557 toward a bushy evolution and not to simple specific lineages easily traceable through time. It
1558 is possible that the two species *P. brachyrhynchus* and *P. andrei* will fit in a well-defined
1559 genus *Cercamonius*, however this would necessitate a good understanding of *Protoadapis*
1560 species and their evolution, which is not the case.

1561 The new genus and species *Quercyloris eloisae* is an important addition to our knowledge of
1562 the small microcheorids because it documents a very primitive form which seems closely
1563 related to *Pseudoloris*. Until now, we had only two species of *Pivetonia*, without upper
1564 dentitions, as possible relatives of *Pseudoloris*. The new form found at Cos documents a new
1565 lineage which at the same time appears as suitably ancestral for *Pseudoloris* and leads to place
1566 aside the species of *Pivetonia* in a lineage parallel to *Nannopithecus* instead of directly ancestral
1567 to *Pseudoloris*. More material of these tiny forms will be needed to complete the scenario, and

1568 confirm or invalidate our hypothesis. Nevertheless, the new species demonstrates a very early
1569 separation between a *Nannopithecus* clade, including later *Necrolemur* and *Microchoerus*, and
1570 the clade leading to *Pseudoloris*.

1571 The new species of *Arcius* is the first discovery of a plesiadapiform in the Quercy fossil
1572 record. Its large incisor is exactly similar to those found in the earliest Eocene, showing the
1573 remarkable stability of this tooth in the genus *Arcius*. Furthermore, it illustrates an
1574 evolutionary trend in *Arcius*, an increasing bunodonty, linking the early Eocene forms to the
1575 latest occurring European plesiadapiform in Bouxwiller, late Lutetian (MP 13). This confirms
1576 the relatively late survival of paromomyids in Europe, which was recently questioned by
1577 Lopez-Torres et al. (2018).

1578

1579 7. Acknowledgements

1580 We are happy to dedicate this contribution to the memory of Gregg Gunnell, a competent,
1581 very friendly, and helpful colleague. He greatly facilitated visits in An Arbor and Duke
1582 University. M.G. thanks Oliver Wings in Halle-a.d.-Saale and Loïc Costeur in Basel for the
1583 possibility to study fossil primates in their care. J. Marigo provided casts of *A. ilerdensis*. D.
1584 V. thanks the owners of the Cos locus for their kind permission to look for fossils on their
1585 land, during many years. M.G. thanks O. Béthoux for his advice in taking macro photographs,
1586 P. Loubry for advice with Photoshop, and A. Lethiers for his work in mounting the figures.
1587 M.G. thanks Y. Larabi-Godinot for her continuous patience with paleontological research.

1588

1589 8. References

1590 Aumont, A., 2003. Systématique et phylogénie des Paromomyidés européens (Eocène –
1591 Plésiadapiformes, Mammifères). Ph.D. thesis, Paris, Muséum National d’Histoire Naturelle (unpubl.).

- 1592 Aumont, A., 2004. Première découverte d'espèces sympatriques de Paromomyidés (Plésiadapiformes,
1593 Mammifères) en Europe. *Comptes Rendus Palevol* 3, 27-34.
- 1594 Bacon, A.-M., Godinot, M., 1998. Analyse morphofonctionnelle des fémurs et des tibias des "*Adapis*"
1595 du Quercy: mise en évidence de cinq types morphologiques. *Folia Primatologica* 69,1-21.
- 1596 Boyer, D.M., Seiffert, E.R., Gladman, J.T., Bloch, J.I., 2013. Evolution and allometry of calcaneal
1597 elongation in living and extinct primates. *Plos One* 8, (7) e67792.
- 1598 Crochet, J.-Y., Hartenberger, J.-L., Rage, J.-C., Remy, J.A., Sigé, B., Sudre, J., Vianey-Liaud, M.,
1599 1981. Les nouvelles faunes de vertébrés antérieures à la « Grande Coupure » découvertes dans les
1600 phosphorites du Quercy. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4^e Série 3, 245-266.
- 1601 Crusafont-Pairo, M., 1967. Sur quelques Prosimiens de la zone préaxiale pyrénéenne et un essai
1602 provisoire de reclassification, in: *Evolution des Vertébrés*, Editions du C.N.R.S., Paris, pp 611-632.
- 1603 Cuvier, G., 1822. *Recherches sur les ossements fossiles* (2^e édition). Dufour et d'Ocagne, Paris.
- 1604 Dagosto, M. 1983. Postcranium of *Adapis parisiensis* and *Leptadapis magnus* (Adapiformes,
1605 Primates). *Folia Primatologica* 41, 49-101.
- 1606 Delfortrie, M., 1873. Un Singe de la famille des Lémuriens dans les phosphates de chaux quaternaires
1607 du département du Lot. *Actes de la Société Linnéenne de Bordeaux* 29, 87-95.
- 1608 Filhol, H., 1874. Nouvelles observations sur les Mammifères des gisements de phosphates de chaux
1609 (Lémuriens et Pachylémuriens). *Annales des Sciences Géologiques* 5, 1-36.
- 1610 Gingerich, P.D., 1975. A new genus of Adapidae (Mammalia, Primates) from the late Eocene of
1611 southern France, and its significance for the origin of higher primates. *Contributions from the Museum*
1612 *of Paleontology, The University of Michigan* 24, 163-170.
- 1613 Gingerich, P.D., 1977. New species of Eocene primates and the phylogeny of European Adapidae.
1614 *Folia Primatologica* 28, 60-80.

1615 Godinot, M., 1983. Contribution à l'étude des primates paléogènes d'Europe – Systématique,
1616 locomotion. Thèse d'Etat, Université des Sciences et Techniques du Languedoc, Montpellier
1617 (unpubl.).

1618 Godinot, M., 1984a. Un nouveau genre témoignant de la diversité des Adapinés (Primates, Adapidae)
1619 à l'Eocène terminal. Comptes-Rendus de l'Académie des Sciences, Paris 299, 1291-1296.

1620 Godinot, M., 1984b. Un nouveau genre de Paromomyidae (Primates) de l'Eocène Inférieur d'Europe.
1621 Folia Primatologica 43, 84-96.

1622 Godinot, M., 1985. Evolutionary implications of morphological changes in Palaeogene primates.
1623 Special Papers in Palaeontology 33, 39-47.

1624 Godinot, M., 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa
1625 faune de Vertébrés de l'Eocène Supérieur. VI. Primates. Palaeontographica A 205, 113-127.

1626 Godinot, M., 1992. Toward the locomotion of two contemporaneous *Adapis* species. Zeitschrift für
1627 Morphologie und Anthropologie 78, 387-405.

1628 Godinot, M., 2003. Variabilité morphologique et évolution des *Necrolemur* (Primates,
1629 Omomyiformes) des niveaux-repères MP 17 à MP 20 du sud de la France. Coloquios de Paleontologia
1630 Volume Extra 1, 203-235.

1631 Godinot, M., Dagosto, M., 1983. The astragalus of *Necrolemur* (Primates, Microchoerinae). Journal of
1632 Paleontology 57, 1321-1324.

1633 Godinot, M., Couette, S., 2008. Morphological diversity in the skulls of large adapines (Primates,
1634 Adapiformes) and its systematic implications, in: Sargis, E.J., Dagosto, M. (Eds.), Mammalian
1635 Evolutionary Morphology: A Tribute to Frederick S. Szalay. Springer, Dordrecht, pp 285-313.

1636 Godinot, M., Russell, D.E., Louis, P., 1992. Oldest known *Nannopithec* (Primates, Omomyiformes)
1637 from the early Eocene of France. Folia Primatologica 58, 32-40.

1638 Godinot, M., Labarrère, H.-P., Erfurt, J., Franzen, J.L., Lange-Badré, B., Lapparent de Broin, F. de,
1639 Vidalenc, D., 2018. Un nouveau gisement à vertébrés éocènes, Rouzilhac (MP 10-11), dans la série
1640 molassique d'Issel (Aude, France). *Revue de Paléobiologie, Genève* 37, 141-333.

1641 Grandidier, G., 1904. Un nouveau Lémurien fossile de France, le *Pronycticebus Gaudryi*. *Bulletin du*
1642 *Muséum National d'Histoire Naturelle* 10, 9-13.

1643 Gregory, W.K., 1920. On the structure and relations of *Notharctus*, an American Eocene primate.
1644 *Memoirs of the American Museum of Natural History* 3, 51-243.

1645 Hooker, J.J., 2007. A new microchoerine omomyid (Primates, Mammalia) from the English early
1646 Eocene and its palaeobiogeographical implications. *Palaeontology* 50, 739-756.

1647 Hooker, J.J., 2012. A new omomyid primate from the earliest Eocene of southern England: First phase
1648 of microchoerine evolution. *Acta Palaeontologica Polonica* 57, 449-462.

1649 Legendre, S., Marandat, B., Sigé, B., Crochet, J.-Y., Godinot, M., Hartenberger, J.-L., Sudre, J.,
1650 Vianey-Liaud, M., Muratet, B., Astruc, J.-G., 1992. La faune de mammifères de Vielase (phosphorites
1651 du Quercy, Sud de la France) : Preuve paléontologique d'une karstification du Quercy dès l'Eocène
1652 inférieur. *Neues Jahrbuch für Geologie, Paläontologie H.7*, 414-428.

1653 Lopez-Torres, S., Silcox, M., 2018. The European Paromomyidae (Primates, Mammalia): taxonomy,
1654 phylogeny, and biogeographic implications. *Journal of Paleontology* (doi 10.1017/jpa.2018.10)

1655 Lopez-Torres, S., Silcox, M.T., Holroyd, P.A., 2018. New omomyoids (Euprimates, Mammalia) from
1656 the late Uintan of Southern California, USA, and the question of the extinction of the Paromomyidae
1657 (Plesiadapiformes, Primates). *Palaeontologia Electronica* 21.3.37A (28 pp).

1658 Lopez-Torres, S., Selig, K.R., Prufrock, K.A., Lin, D., Silcox, M.T., 2017. Dental topographic analysis
1659 of paromomyid (Plesiadapiformes, Primates) cheek teeth: more than 15 million years of changing
1660 surfaces and shifting ecologies. *Historical Biology* (doi 10.1080/08912963.2017.1289378)

1661 Marandat, B., Crochet, J.-Y., Godinot, M., Hartenberger, J.-L., Legendre, S., Remy, J.A., Sigé, B.,
1662 Sudre, J., Vianey-Liaud, M., 1992. Une nouvelle faune à Mammifères d'âge éocène moyen (Lutétien
1663 Supérieur) dans les Phosphorites du Quercy. *Geobios* 26, 617-623.

1664 Marigo, J., Minwer-Barakat, R., Moyà-Solà, S., 2010. New *Anchomomyini* (Adapoidea, Primates)
1665 from the Mazateron Middle Eocene locality (Almazan Basin, Soria, Spain). *Journal of Human*
1666 *Evolution* 58, 353-361.

1667 Marigo, J., Minwer-Barakat, R., Moyà-Solà, S., 2011. New *Anchomomys* (Adapoidea, Primates) from
1668 the Robiacian (Middle Eocene) of northeastern Spain). Taxonomic and evolutionary implications.
1669 *Journal of Human Evolution* 60, 665-672.

1670 Marigo, J., Verrières, N., Godinot, M., 2019. Systematic and locomotor diversification of the Adapis
1671 group (Primates, Adapiformes) in the late Eocene of the Quercy (Southwest France) revealed by
1672 hueral remains. *Journal of Human Evolution* 64, 473-485.

1673 Minwer-Barakat, R., Marigo, J., Moyà-Solà, S., 2010. A new species of *Pseudoloris* (Omomyidae,
1674 Primates) from the middle Eocene of Sant Jaume de Frontanyà (Eastern Pyrenees, Spain). *American*
1675 *Journal of Physical Anthropology* 143, 92-99.

1676 Minwer-Barakat, R., Marigo, J., Moyà-Solà, S., 2012. *Pseudoloris cuestai*, a new microchoerine
1677 (Primates, Omomyidae) from the middle Eocene of the Iberian Peninsula. *Journal of Vertebrate*
1678 *Paleontology* 32, 407-418.

1679 Mourer-Chauviré, C., 2006. The avifauna of the Eocene and Oligocene phosphorites du Quercy
1680 (France): an updated list. *Strata (Toulouse)* 13: 135-149.

1681 Pulou, R., 1980. Jean-André Poumarède et l'industrie des phosphates du Quercy au XIXe siècle.
1682 *Mémoires de l'Académie des Sciences, Inscriptions et Belles Lettres de Toulouse* 16, 83-92.

1683 Rage, J.-C., 2006. The lower Vertebrates from the Eocene and Oligocene of the phosphorites du
1684 Quercy (France): an overview. *Strata (Toulouse)* 13, 161-173.

- 1685 Remy, J.A., Crochet, J.-Y., Sigé, B., Sudre, J., Bonis, L. de, Vianey-Liaud, M., Godinot, M.,
1686 Hartenberger, J.-L., Lange-Badré, B., Comte, B., 1987. Biochronologie des phosphorites du Quercy :
1687 Mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. Münchner
1688 Geowissenschaftliche Abhandlungen A 10, 169-188.
- 1689 Russell, D.E., Louis, P., Savage, D.E., 1967. Primates of the French early Eocene. University of
1690 California Publications in Geological Science 73, 1-46.
- 1691 Schlosser, M., 1907. Beitrag zur Osteologie und systematischen Stellung der Gattung *Necrolemur*,
1692 sowie zur Stammesgeschichte der Primaten überhaupt. Neues Jahrbuch für Mineralogie, Geologie und
1693 Paläontologie, (Festband) 197-226.
- 1694 Schmid, P., 1982. Die systematische Revision der europäischen Microchoeridae Lydekker, 1887
1695 (Omomyiformes, Primates). Juris Druck + Verlag, Zürich.
- 1696 Sigé, B., Crochet, J.-Y., 2006. Marsupiaux, Insectivores s. l., Chiroptères, Créodontes et Carnivores
1697 paléogènes d'Europe décrits ou révisés d'après les nouvelles collections du Quercy (SW France).
1698 Strata (Toulouse) 13 : 189-205.
- 1699 Sigé, B., Hugueney, M., 2006. Les micromammifères des gisements à phosphates du Quercy (SW
1700 France). Strata (Toulouse) 13, 207-227.
- 1701 Simons, E.L., 1972. Primate Evolution – An Introduction to Man's Place in Nature. Macmillan, New
1702 York.
- 1703 Simpson, G.G., 1940. Studies on the earliest primates. Bulletin of the American Museum of Natural
1704 History 77, 185-212.
- 1705 Stehlin, H.G., 1912. Die Säugetiere des schweizerischen Eocaens. Siebenter Teil, erste Hälfte: *Adapis*.
1706 Abhandlungen der Schweizerische Paläontologische Gesellschaft 38, 1163-1298.
- 1707 Stehlin, H.G., 1916. Die Säugetiere des schweizerischen Eocaens. Siebenter Teil, zweite Hälfte.
1708 Abhandlungen der Schweizerische Paläontologische Gesellschaft 41, 1299-1552.

- 1709 Szalay, F.S., 1974. New genera of European Eocene Adapid Primates. *Folia Primatologica* 22, 116-
1710 133.
- 1711 Szalay, F.S., Delson, E.D., 1979. *Evolutionary History of the Primates*. Academic Press, New York.
- 1712 Tattersall, I., Schwartz, J.H., 1983. A revision of the European Eocene primate genus *Protoadapis* and
1713 some allied forms. *American Museum Novitates* 2762, 1-16.
- 1714 Teilhard de Chardin, P., 1922. Les Mammifères de l'Eocène inférieur français et leurs gisements.
1715 *Annales de Paléontologie* 10-11, 1-116.
- 1716 Thalmann, U., 1994. Die Primaten aus dem eozänen Geiseltal bei Halle/Saale (Deutschland). *Courier*
1717 *Forschungsinstitut Senckenberg* 175, 1-161.
- 1718
- 1719
- 1720 Figure captions
- 1721
- 1722 Figure 1. Left, view of the Cos fossiliferous outcrop, at the rim of a large fissure covered with
1723 vegetation; it shows the superposition of beds. Right, a closer view after some excavation; the beds
1724 appear affected by sliding; hammer and bag give the scale.
- 1725
- 1726 Figure 2. Mandibles of *Protoadapis andrei* nov. sp. A-B, the right mandible Cos 253, the type
1727 mandible, in occlusal (A) and lingual (B) views; C-E, the left mandible Cos 254 in occlusal (C),
1728 lingual (D) and labial (E) views. Scale bar is 1 cm.
- 1729
- 1730 Figure 3. Teeth of *Protoadapis andrei* nov. sp. A1-2, the upper canine Cos 753 in lingual (A1) and
1731 labial (A2) views; B-E, occlusal views of the P4/ Cos 77 (B), the M2/ Cos 247 (C), the M3/ Cos 248

1732 (D), and the m/3 Cos 246 €; F, H, p/3 to m/3 of the type mandible Cos 253 in occlusal (F) and lingual
1733 (H) views; G, the p/3 Cos 254 in lingual view. Scale bar is 1 cm.

1734

1735 Figure 4. Mandibles of *Pronycticebus cosensis* sp. nov. A1-3, type mandible Cos 271 in labial (A1),
1736 lingual (A2) and occlusal (A3) views; B1-2, posterior fragment bearing m/3 Cos 269 in lingual (B1)
1737 and labial (B2) views; C1-2, fragmentary juvenile mandible with anterior alveoli and p/3 germ in place
1738 in lingual (C1) and occlusal (C2) views. Scale bar is 5 mm.

1739

1740 Figure 5. Lower teeth of *Pronycticebus cosensis* nov. sp. The type specimen Cos 271 is on A1-2 and
1741 L-P. A1-2, L, , anterior teeth, i/2 to p/4 of Cos 271 in labial (A1), lingual (A2) and occlusal (L) views;
1742 B, p/1 Cos 278 in lingual vie; C1-2, p/3 Cos 277 in occlusal (C1) and lingual (C2) views; D1-2, p/3
1743 Cos 276 in occlusal (D1) and lingual (D2) views; E, p/4 Cos 860 in occlusal view; F, p/4 and m/1 of
1744 Cos 270 in occlusal view; G1-2, p/4 Cos 859 in occlusal (G1) and lingual (G2) views; H1-3, the m/1
1745 Cos 755 in Occlusal (H1), labial (H2), and lingual (H3) views; I-K, m/1 Cos 272 (I), m/2 Cos 273 (J),
1746 m/3 Cos 269 (K) all in occlusal views; M-P, posterior teeth of Cos 271 in occlusal (M-N), labial (O),
1747 and lingual (P) views. Scale bar is 5 mm.

1748

1749 Figure 6. Maxillary fragment and upper teeth of *Pronycticebus cosensis* nov. sp. A1-2, maxillary
1750 fragment bearing P4/ cos 265 in occlusal (A1) and labial (A2) views (scale bar 5 mm); B1-2, upper
1751 canine Cos 863 in lingual (B1) and labial (B2) views; C, P1/ Cos 279 in lingual view; D1-2, P2/ Cos
1752 281 in lingual (D1) ad labial (D2) views; E1-2, P3/ Cos 858 in anterior (E1) and occlusal (E2) views;
1753 F1-2, P3/ Cos 264 in occlusal (F1) and anterior (F2) views; G1-2, P4/ Cos 262 in occlusal (G1) and
1754 anterior (G2) views; H, P4/ of Cos 265 in occlusal view; I1-2, P4/ Cos 263 in occlusal (I1) and
1755 anterior (I2) views; J, M1/ Cos 861 in occlusal view; K1-2, M1/ Cos 257 in occlusal (K1) and
1756 posterior (K2) views; L, M1/ Cos 832 in occlusal view; M, M1/ and M2/ on a fragment of maxilla Cos

1757 258 in occlusal view; N1-2, M2/ Cos 255 in occlusal (N1) and posterior (N2) views; O-P, M2/ Cos
1758 256 and M3/ Cos 259 (cast) in occlusal view; Q-R, milk teeth, DP4/ Cos 266 and dp/4 Cos 274 both I
1759 occlusal views; S-T, two teeth from another Quercy locality, Vielase, the M2/ VIE 141 (S) and the
1760 anterior part of a right m/2 or m/3, both in occlusal views. Scale bar for all teeth from B1 to T is 5 mm.

1761

1762 Figure 7. Teeth of *Anchomomys* sp. (A-B) and of *Quercyloris eloisae* nov. gen. nov. sp. (C1-M2). A,
1763 incomplete M1-2/ Cos 290 in occlusal view; B, Upper canine Cos 297 in lingual view; C1-2, upper
1764 anterior incisor Cos 304 in lingual (C1) and posterior (C2) views; D1-3, upper canine Cos 294 in
1765 lingual (D1), posterior (D2) and labial (D3) views; E-G, three P4/s in occlusal views, Cos 291 (E), Cos
1766 292 (F), and Cos 293 (G); H-J, three upper molars in occlusal views, M1/ Cos 287 (H), M1/ Cos 288,
1767 type specimen (I), M2/ Cos 289 (J); K1-3, p/3 Cos 298 in lingual (K1), posterolingual (K2), and
1768 posterolabial (K3) views; L1-2, incomplete m/1 Cos 301, missing its protoconid, in occlusal (L1) and
1769 lingual (L2) views; M1-2, m/2 Cos 295 in occlusal (M1) and lingual (M2) views. Scale bar is 2 mm.

1770

1771 Figure 8. Teeth of *Arcius moniquae* nov. sp. A1-2, Lower anterior incisor Cos 302 in lingual (A1) and
1772 labial (A2) views; B, P4/Cos 299, C, M2/ Cos 300, type specimen, and D, m/3 Cos 305, all in occlusal
1773 view. Scale bar is 2 mm.

1774

1775 Table caption

1776 Table 1. Measurements of the teeth of *Pronycticebus cosensis* nov. sp., all in mm.

1777

1778

1779

1780

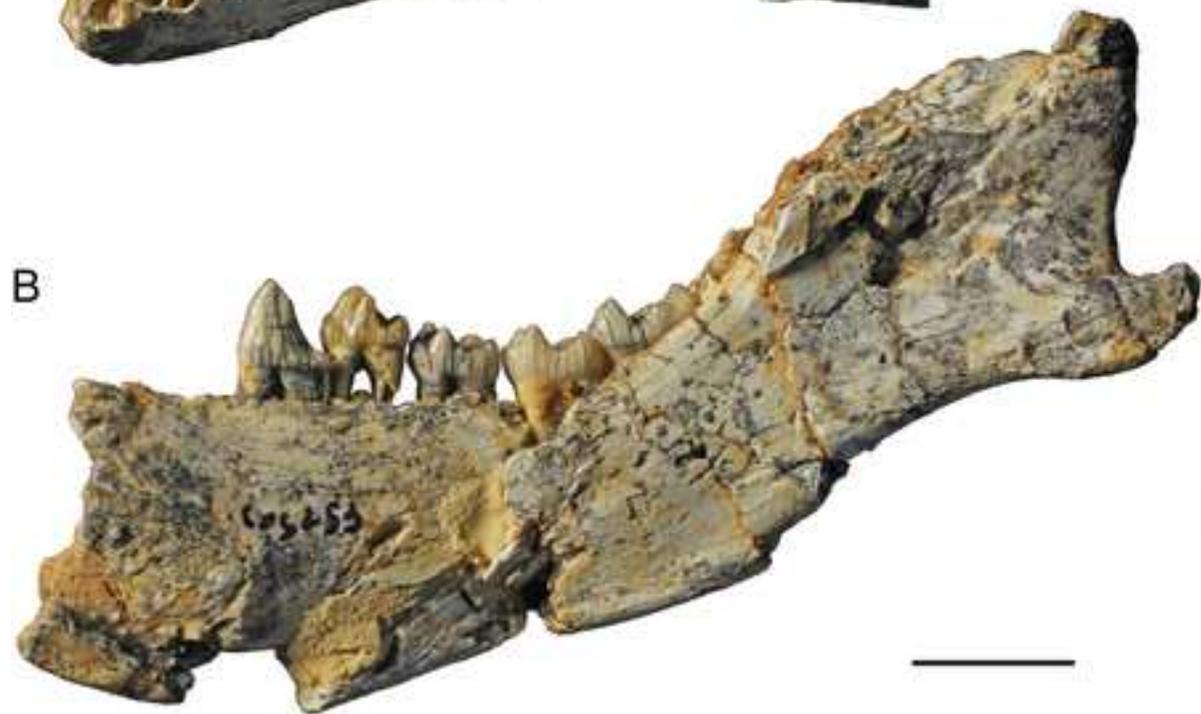
1781

1782

Table 1

Tooth	Length	Width	Tooth	Length	Width	Tooth	Length	Width
Cos 271 C	2.07	1.61	p/4 Cos 860	3.02	2.23	P4/ Cos 262	3.14	4.21
--- p/1	1.30	1.06	Cos 270 p/4	3.21	2.15	P4/ Cos 263	2.62	3.73
--- p/2	1.83	1.20	--- m/1	3.66	2.52	P4/ Cos 265	3.03	3.89
--- p/3	2.86	2.44	m/1 Cos 272	4.05	2.87	M1/ Cos 257	3.35	4.00
--- p/4	3.25	2.41	m/1 Cos 755	3.99	2.79	M1/ Cos 832	3.59	4.43
--- m/1	3.69	2.73	m/2 Cos 273	3.39	2.36	M1/ Cos 861	3.56	4.51
--- m/2	3.71	2.97	m/3 Cos 269	4.82	2.73	M1/ Cos 862	3.69	--
--- m/3	4.79	2.80	dp/4 Cos 274	3.07	2.84	Cos 258 M1/	3.92	5.00
p/1 Cos 278	1.43	1.34	C sup Cos 863	2.46	1.93	--- M2/	4.00	5.43
p/3 Cos 275	> 2.46	1.69	C sup Cos 864	2.51	1.83	M2/ Cos 255	3.89	5.20
p/3 Cos 276	2.84	1.72	P1/ Cos 279	1.43	1.09	M2/ Cos 256	3.67	5.08
p/3 Cos 277	2.73	1.85	P2/ Cos 281	2.26	1.68	M3/ Cos 259	3.20	4.78
p/3 Cos 280	2.99	>= 1.80	P3/ Cos 264	2.75	2.65	M3/ Cos 261	3.31	--
p/4 Cos 859	3.30	1.98	P3/ Cos 858	2.89	2.91	DP4/ Cos 266	3.53	3.64





A1



A2



B



C



D



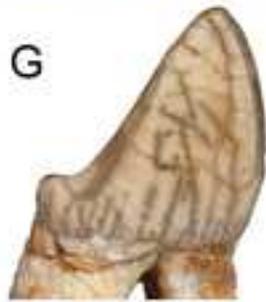
E



F



G



H



A1



A2



A3



B1



B2



C1



C2



