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1 Can Pallars i Llobateres: A new hominoid-bearing locality from the late Miocene of the  
2 Vallès-Penedès Basin (NE Iberian Peninsula)  
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31

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33

#### 34 **Abstract**

35 In the Iberian Peninsula, Miocene apes (Hominoidea) are generally rare and mostly  
36 restricted to the Vallès-Penedès Basin. Here we report a new hominoid maxillary fragment  
37 with M<sup>2</sup> from this basin. It was surface-collected in March 2017 from the site of Can Pallars i  
38 Llobateres (CPL, Sant Quirze del Vallès), where fossil apes had not been previously recorded.  
39 The locality of provenance (CPL-M), which has delivered no further fossil remains, is located  
40 very close (ca. 50 m) to previously known CPL outcrops, and not very far (ca. 500 m in NW  
41 direction) from the classical hominoid-bearing locality of Can Poncic 1. Here we describe the  
42 new fossil and, based on the size and proportions of the M<sup>2</sup>, justify its taxonomic attribution  
43 to *Hispanopithecus* cf. *laietanus*, a species previously recorded from several Vallesian sites of  
44 the Vallès-Penedès Basin. Based on the associated mammal fauna from CPL, we also provide  
45 a biochronological dating and a paleoenvironmental reconstruction for the site. The  
46 associated fauna enables an unambiguous correlation to the *Cricetulodon hartenbergeri* –  
47 *Progonomys hispanicus* interval local subzone, with an estimated age of 9.98–9.73 Ma (late

48 Vallesian, MN10). Therefore, CPL-M is roughly coeval with the *H. laietanus*-bearing localities  
49 of Can Llobateres 1 and Can Feu 1, and minimally older than those of La Tarumba 1 and Can  
50 Llobateres 2. In contrast, CPL-M is younger than the early Vallesian (MN9) localities of Can  
51 Poncic 1 (the type locality of *Hispanopithecus crusafonti*) as well as Polinyà 2 (Gabarró) and  
52 Estació Depuradora d'Aigües Residuals–Riu Ripoll 13, where *Hispanopithecus* sp. is recorded.  
53 The associated fauna from CPL indicates a densely forested and humid paleoenvironment  
54 with nearby freshwater. This supports the view that *Hispanopithecus* might have been  
55 restricted to dense wetland forests soon before its extinction during the late Vallesian, due  
56 to progressive climatic deterioration. Coupled with the existence of other fossiliferous  
57 outcrops in the area, this find is most promising for the prospect of discovering additional  
58 fossil hominoid remains in the future.

59

## 60 **1. Introduction**

### 61 *1.1 The hominoid find from Can Pallars i Llobateres*

62 Miocene apes (Primates: Hominoidea) from Iberia are geographically restricted to  
63 Catalonia (NE Iberian Peninsula), mostly coming from multiple sites in the Vallès-Penedès  
64 Basin (Alba, 2012), near Barcelona (Casanovas-Vilar et al., 2016a). Although several partial  
65 hominoid skeletons have been recovered there (Moyà-Solà and Köhler, 1996; Moyà-Solà et  
66 al., 2004; Alba, 2012; Alba et al., 2012b, 2015), hominoid remains are generally scarce and  
67 mostly consist of isolated specimens, being considered 'rare' or uncommon taxa that require  
68 a large sampling effort to be adequately documented (e.g., Alba, 2012; Alba et al., 2017a).  
69 This notwithstanding, sometimes hominoid finds are the result of fortunate circumstances  
70 (e.g., the partial skeleton of *Hispanopithecus laietanus* from Can Feu 1; Alba et al., 2012b).

71 Here we report a maxillary fragment from the site of Can Pallars i Llobateres<sup>1</sup> (CPL, Sant  
72 Quirze del Vallès; Llenas Avellaneda, 1999; Furió et al., 2015; Casanovas-Vilar et al.,  
73 2016a,b), which was surface-collected by J. Manel Méndez in March 2017. We describe and  
74 figure this specimen, and compare it with previously known hominoid remains from the  
75 Vallès-Penedès Basin, in order to justify its taxonomic assignment. Based on the study of the  
76 unpublished associated vertebrate fauna, we further contextualize this find from both  
77 chronological and paleoenvironmental viewpoints.

78

## 79 1.2 *Can Pallars i Llobateres*

80 CPL is located ca. 500–600 m NW from the site of Can Poncic<sup>2</sup> (CP, Sant Quirze del Vallès;  
81 Crusafont Pairó and Truyols Santonja, 1947; Figs. 1 and 2). The exact location of CP localities  
82 (Crusafont Pairó and Golpe Posse, 1972; Golpe Posse, 1974) is uncertain due to the  
83 insufficient published documentation (Crusafont Pairó and Truyols Santonja, 1947; Santafé  
84 Llopis, 1978; Llenas i Avellaneda, 1996). However, based on published photographs  
85 (Crusafont Pairó and Truyols Santonja, 1947), orthophotos from 1946 (ICGC, 2017), and  
86 recent surveys (Alba and Almécija, 2017), CP can be confidently located within an area of  
87 about 0.7 ha (Fig. 2). Hominoid remains were recovered at the locality of Can Poncic 1 (CP1)  
88 from the early 1950s to the early 1970s (Crusafont Pairó, 1958; Crusafont Pairó and  
89 Hürzeler, 1969; Crusafont-Pairó and Golpe-Posse, 1973; Moyà-Solà et al., 1990; Harrison,  
90 1991; Golpe Posse, 1993; Alba, 2012; Alba et al., 2012a, 2013; Pérez de los Ríos et al., 2013).  
91 CP1 is the type locality of the extinct great ape *Hispanopithecus crusafonti* (Begun, 1992),

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<sup>1</sup> Formerly spelled ‘Can Pallàs de Llobateres’ or ‘Can Pallars de Llobateres.’

<sup>2</sup> Formerly spelled ‘Can Ponsic’ or ‘Can Ponsich.’

92 otherwise only recorded from Teuleria del Firal (Begun, 1992; Alba, 2012) in the Seu d'Urgell  
93 Basin (Catalan Pyrenees).

94 The site of CPL was discovered in 1999, when urbanization works unearthed several  
95 Miocene large mammal remains within an area smaller than 1.5 ha (Fig. 2). These were  
96 excavated by a team from the former Institut de Paleontologia M. Crusafont in Sabadell  
97 (IPS), which also screen-washed some sediment samples. The exact provenance of most  
98 remains was not documented, but those subsequently surface-collected came from different  
99 spots (Fig. 2): CPL-A, CPL-B, CPL-P1 (=CPL-C), CPL-P3, CPL-P2, and CPL-P4. The more  
100 abundant small mammal material came from two consecutive stratigraphic horizons (CPL s.s.  
101 and CPL3) within the classical CPL area (M. Llenas Avellaneda, pers. comm. to D.M.A.; see  
102 also Llenas Avellaneda, 1999). Except for a provisional faunal list provided in the field report  
103 (Llenas Avellaneda, 1999) and a few subsequent emendations (Casanovas-Vilar et al.,  
104 2016b), the fossils from CPL remained mostly unpublished (but see Furió et al., 2015). The  
105 hominoid maxillary fragment described here was found embedded within a small sediment  
106 block of carbonated claystone in locality CPL-M (Alba et al., 2017b), within an uncultivated  
107 land parcel (Fig. 2) very close to the classical CPL outcrops (roughly equivalent to CPL-B). The  
108 find was immediately reported to the Archaeological and Paleontological Survey of the  
109 Generalitat de Catalunya, and is currently housed at the Institut Català de Paleontologia  
110 Miquel Crusafont (ICP) with catalog No. IPS102942.

111

## 112 **2. Materials and methods**

### 113 *2.1 Comparisons with other hominoids*

114 IPS102942 was compared with upper molars of other Vallès-Penedès dryopithecines  
115 (Begun et al., 1990; Begun, 1992; Golpe Posse, 1993; Moyà-Solà and Köhler, 1995, 1996;

116 Moyà-Solà et al., 2004, 2009a,b; Alba, 2012; Alba et al., 2012a, 2013; Pérez de los Ríos et al.,  
117 2013), with particular emphasis on those from CP1 (*H. crusafonti*) and Can Llobateres 1 and  
118 2 (CLL1 and CLL2, respectively; tooth locus identifications of *H. laietanus* from CLL1 after  
119 Alba et al., 2012a). No upper molars are available from the other Vallès-Penedès localities  
120 with *H. laietanus*, namely: La Tarumba 1 (LT1, type locality; Villalta Comella and Crusafont  
121 Pairó, 1944; Golpe Posse, 1993), Polinyà 2 (Gabarró; PO2; Crusafont-Pairó and Golpe-Posse,  
122 1973; Golpe Posse, 1993), Estació Depuradora d'Aigües Residuals–Riu Ripoll 13 (EDAR13;  
123 Checa Soler and Rius Font, 2003) and Can Feu 1 (CF1; Alba et al., 2012b). All specimens were  
124 measured with digital calipers to the nearest 0.1 mm by one of the authors (D.M.A.). The  
125 following measurements were taken: BL, buccolingual breadth (in mm, taken both at the  
126 mesial and the distal crown portions); MD, mesiodistal length (in mm); and BLI,  
127 breadth/length index (in %, computed as maximum BL/MD×100). Dental terminology follows  
128 Alba et al. (2013:Fig. 1).

129

## 130 2.2 Associated fauna

131 Large vertebrate remains from CPL are very scarce, including 52 specimens from CPL, CPL-  
132 B, CPL-A, CPL-P1, CPL-P3 and CPL-P4—see Supplementary Online Material (SOM) S1 for  
133 further details. The associated small mammal fauna is represented by a collection of 384  
134 micromammal teeth from CPL and CPL3 (see SOM S1). All of the fossils are housed at the  
135 ICP.

136

## 137 2.3 Coordinates

138 Geographic coordinates for paleontological localities are given in the Universal Transverse  
139 Mercator (UTM) system, based on the European Terrestrial Reference System 1989

140 (ETRS89). They were verified with the aid of topographic maps and orthophotos from the  
141 web application VISSIR v3.26 of the Institut Cartogràfic i Geològic de Catalunya (ICGC, 2017).

142

### 143 **3. Results**

#### 144 *3.1 Description of the hominoid maxilla*

145 IPS102942 is a left maxillary fragment (ca. 1.5 × 2.0 cm), still partially embedded in matrix,  
146 that preserves an alveolus with broken roots and a socketed molar crown (Fig. 3A–C). The  
147 specimen is poorly preserved, displaying multiple diagenetic cracks filled with sediment.  
148 Given the poor preservation, little can be said about the comparative anatomy of the  
149 maxilla, although the position of the preserved portion of the palatine process relative to the  
150 alveolar margin suggests that the palate was deep.

151 Alba et al. (2017b) originally identified the near-complete, socketed tooth as M<sup>1</sup>, but  
152 closer examination suggests it is M<sup>2</sup>. The missing crown, anterior to the molar crown, is  
153 broken at or slightly below the cervix. The lingual root of this tooth, visible along most of its  
154 length (because the maxillary bone lacks its lingual side), is mesiodistally broad and  
155 resembles the single fused root of the socketed molar (which is slightly exposed below the  
156 cervix). The cross-section of the roots close to the alveolar plane, in occlusal view, reveals  
157 two buccal root canals, indicating that two distinct buccal roots were likely present, as it is  
158 typical of hominoid upper molars. Although the presence of one or two buccal roots in  
159 hominoid P<sup>4</sup> is variable (Emoret and Kullmer, 2014), the aforementioned morphology of the  
160 lingual root enables us to rule out an identification of the missing crown as a P<sup>4</sup>, meaning  
161 that the missing crown is a molar. Given that the well-developed metacone and only  
162 moderate distal tapering of the molar crown are not consistent with an M<sup>3</sup>, the socketed  
163 molar must belong to an M<sup>2</sup>, and the missing crown was an M<sup>1</sup>.



164 The molar crown is well preserved, except for a missing enamel chip that would have  
165 included the lingual and distal aspects of the hypocone, as well as most of the distal marginal  
166 ridge—which nevertheless does not preclude taking reliable crown measurements. The  
167 crown is quite worn, with extensive dentine exposure at the protocone and the preserved  
168 portion of the hypocone. It displays a subrectangular to suboval and distally tapering  
169 occlusal contour, being buccolingually broader (BL = 9.8 mm) than mesiodistally long  
170 (estimated MD = 8.7 mm; BLI = 112.6%), and much broader on the mesial than on the distal  
171 (BL = 8.7 mm) portions of the crown. The mesial contour of the crown is rather straight,  
172 whereas the buccal and distal contours are convex, and the lingual contour is more clearly  
173 biconvex. The crown displays quite vertical walls and is not particularly inflated toward its  
174 base. There are four main cusps, the protocone being the most extensive, the hypocone  
175 being the smallest, and the paracone and metacone being similar in size to one another  
176 (although the former is somewhat higher). The buccal cusps are more mesially located than  
177 the corresponding lingual cusps, and very peripheral. The hypocone is located on the  
178 distolingual corner of the crown. Mesiobuccally from the protocone, at approximately the  
179 crown midline behind the mesial marginal ridge, there is a small dentine exposure that  
180 seemingly represents a completely worn protoconule located at the end of the similarly  
181 worn preprotocrista. A short and slit-like mesial fovea is still discernible on the buccal moiety  
182 of the crown in spite of wear. This fovea, which originally likely ran to the protoconule base,  
183 is distally delimited by a rather straight and transverse hypoparacrista directed toward the  
184 former protoconule. Two occlusal grooves can be still observed in spite of wear: a transverse  
185 one, separating the bases of the protocone and the hypocone, and a more obliquely  
186 oriented one, which runs from the buccal crown wall to the center of the trigon basin,  
187 separating the bases of the paracone and the metacone, and further transecting the merging

188 point of the long postparacrista with the shorter premetacrista. The postmetacrista and the  
189 preparacrista progressively curve in a lingual direction until merging with the distal and  
190 mesial marginal ridges, respectively. A straight crista obliqua apparently linked the  
191 protocone with the metacone, although the postprotocrista portion has been completely  
192 obliterated by wear. Similarly, a somewhat developed hypocone-metacone crista might have  
193 crossed the distal fovea, although it has been largely obscured by wear and it is not possible  
194 to ascertain whether it would have been continuous or not. No secondary enamel folds or  
195 wrinkling can be discerned, but this might be simply attributable to wear. No buccal or  
196 lingual cingular remnants are present.

197

### 198 3.2 Comparisons with other Vallès-Penedès hominoids

199 Compared with the available M<sup>1</sup> and M<sup>2</sup> sample of Vallès-Penedès hominoids, IPS102942  
200 (Fig. 4a) fits well with the occlusal morphology of previously known specimens of  
201 *Hispanopithecus* spp. (Fig. 4b–h, k–p). In particular, like the specimens of *Hispanopithecus*  
202 (Alba et al., 2013; Pérez de los Ríos et al., 2013), IPS102942 differs from the upper molars of  
203 the middle Miocene taxa—*Dryopithecus* (Fig. 4i), *Pierolapithecus* (Fig. 4j), and *Anoiapithecus*  
204 (Fig. 4q–s)—in the more peripheralized cusps, the less bulging crown base, the apparently  
205 lesser developed metacone-hypocone crista (even if blurred by wear in IPS102942), and the  
206 more reduced cingula (although their development is variable in *Hispanopithecus*; Alba et  
207 al., 2012b). Compared to the two species of *Hispanopithecus* from the Vallès-Penedès, the  
208 slightly tapering occlusal profile of IPS102942 more closely resembles that of the M<sup>2</sup> (Fig.  
209 4e–g,k,n–p) than the squarer profile of the M<sup>1</sup> (Fig. 4b–f,k–m), even though IPS102942  
210 appears smaller and mesiodistally shorter than the previously recorded M<sup>2</sup>. The hypocone in  
211 IPS102942 appears mesiodistally aligned with the protocone, as in the M<sup>2</sup> of *H. laietanus*

212 (Fig. 4f–h), whereas in the M<sup>2</sup> of *H. crusafonti* (Fig. 4k,n) the hypocone is more lingually  
213 situated relative to the protocone, as in the M<sup>2</sup> of *Anoiapithecus* (Fig. 4r,s).

214 With regard to metric comparisons, IPS102942 more closely resembles in both size and  
215 proportions the smaller (presumably female) M<sup>1</sup> of *H. laietanus* (Fig. 5a), being somewhat  
216 smaller than all available M<sup>2</sup> (Fig. 5b). Thus, the MD (8.7 mm) and BL (9.7 mm) of IPS102942  
217 fall somewhat below the known M<sup>2</sup> size ranges of both *H. laietanus* (MD mean = 10.18 mm,  
218 range = 8.8, 11.2 mm; BL mean = 11.18 mm, range = 10.0, 11.6 mm; *n* = 5) and *H. crusafonti*  
219 (MD mean = 10.10 mm, range = 8.8, 11.1 mm; BL mean = 11.50 mm, range = 10.9, 12.2 mm;  
220 *n* = 4; data from Alba et al., 2012a:Table 4). In turn, the BLI (112.6%) of IPS102942 falls well  
221 within the M<sup>2</sup> range of both *H. laietanus* (BLI mean = 110.54%, range = 101.8%, 130.7%; *n* =  
222 5) and *H. crusafonti* (BLI mean = 114.58%, range = 105.4%, 127.3%; *n* = 4; data from Alba et  
223 al., 2012a:Table 4).

224

## 225 4. Discussion

### 226 4.1 Taxonomic assignment

227 Even before the erection of *H. crusafonti* by Begun (1992), the distinction of the CP1  
228 hominoid sample at the species rank advocated by Begun et al. (1990) was already  
229 controversial (Harrison, 1991; Ribot et al., 1996; Andrews et al., 1996). However, the  
230 taxonomic validity of *H. crusafonti* has been subsequently supported by multiple researchers  
231 (e.g., Cameron, 1999; Begun, 2002, 2009, 2015; Moyà-Solà et al., 2009a; Casanovas-Vilar et  
232 al., 2011; Pickford, 2012; Alba, 2012; Alba et al., 2012a). Alba et al. (2012a) concurred with  
233 Ribot et al. (1996) that the development of upper molar cingula is too variable to be  
234 diagnostic (contra Begun, 1992, 2002), but confirmed that *H. crusafonti* tends to display  
235 broader M<sup>1</sup> and M<sup>2</sup> than *H. laietanus* (Begun, 1992, 2002). However, based on available

236 sample, such differences in occlusal proportions are only significant for the M<sup>1</sup> (Alba et al.,  
237 2012), so that this diagnostic criterion is not useful in the case of IPS102942, which  
238 moreover falls in the extensive overlap zone between the two species. This notwithstanding,  
239 an assignment to *H. laietanus* is supported by some subtleties of occlusal morphology  
240 (hypocone position), for which *H. crusafonti* differs from *H. laietanus* and more closely  
241 approaches the condition of *Anoiapithecus* (see Alba et al., 2013). Additional remains—the I<sup>1</sup>  
242 is particularly diagnostic (Begun, 1992; Alba et al., 2012a)—would be required to further  
243 substantiate the attribution of IPS102942 to *H. laietanus*. Given that a single tooth is  
244 available, we prefer to be cautious and provide a tentative assignment to this species, i.e., *H.*  
245 *cf. laietanus*.

246

#### 247 4.2 Age

248 An updated faunal list from CPL is reported in Table 1 (see also SOM S2 and SOM Figs. S1–  
249 S2). The presence of the three-toed horse *Hippotherium* conclusively demonstrates the  
250 Vallesian age of CPL, being first recorded in the Vallès-Penedès Basin at 11.2 Ma (Garcés et  
251 al., 1997, 2003; Agustí et al., 1997; Casanovas-Vilar et al., 2016a,b). This agrees with the  
252 presence of the boselaphin antelope *Miotragocerus* aff. *pannoniae* sensu Moyà-Solà (1983)  
253 and the lagomorph *Prolagus crusafonti*, which apparently replaced *Miotragocerus*  
254 *monnacensis* (Moyà-Solà, 1983; Fuss et al., 2015) and *Prolagus oeningensis* (López Martínez,  
255 2001; Angelone and Veitschegger, 2015), respectively, in the Vallesian. Rodents (Fig. 6) and  
256 insectivores enable a more precise dating, the assemblage being dominated by *Cricetulodon*  
257 *sabadellensis*, as in other Vallesian hominoid-bearing localities (CLL1 and CFE1; Casanovas-  
258 Vilar et al., 2012). The presence of this species (instead of its putative ancestor, *Cricetulodon*  
259 *hartenbergeri*), coupled with that of *Democricetodon* cf. *nemoralis* and *Keramidomys*

260 *pertesunatoi*, and the absence of *Progonomys hispanicus*, indicates an unambiguous  
261 correlation to the *C. hartenbergeri* – *P. hispanicus* interval local subzone of the Vallès-  
262 Penedès Basin (Casanovas-Vilar et al., 2011, 2012, 2016a,b), with an estimated age of 9.98–  
263 9.73 Ma (Casanovas-Vilar et al., 2016a,b). This is consistent with the presence of *Dinosorex*  
264 (which became extinct in the Vallès-Penedès Basin shortly after the MN9/MN10 transition;  
265 Furió et al., 2015) and the co-occurrence between *Lantanotherium sanmigueli* and  
266 *Crusafontina endemica* (characteristic of this subzone; Casanovas-Vilar et al., 2012).

267 CPL is therefore roughly coeval with CFE1 (same subzone; Casanovas-Vilar et al., 2012,  
268 2016a,b) and CLL1 (with a magnetostratigraphically interpolated age of 9.76 Ma; Agustí et  
269 al., 1996, updated by Casanovas-Vilar et al., 2016b after new chron boundaries in Hilgen et  
270 al., 2012), where *H. laietanus* is also recorded (Crusafont Pairó, 1958, 1965; Crusafont Pairó  
271 and Hürzeler, 1969; Crusafont-Pairó and Golpe-Posse, 1973; Begun et al., 1990; Moyà-Solà  
272 et al., 1990; Harrison, 1991; Golpe Posse, 1993; Alba, 2012; Alba et al., 2012a,b). Because of  
273 the absence of *Progonomys*, these localities have been classically correlated to MN9 (early  
274 Vallesian; e.g., Agustí et al., 1996, 1997; Furió et al., 2015; Casanovas-Vilar et al., 2011, 2012,  
275 2016a)—unlike the slightly younger locality of CLL2, which has also yielded remains of *H.*  
276 *laietanus* (Moyà-Solà and Köhler, 1993, 1995, 1996; Almécija et al., 2007; Alba, 2012) and is  
277 correlated to the *C. sabadellensis* + *P. hispanicus* concurrent range subzone (i.e., to MN10,  
278 late Vallesian), with an interpolated age of 9.62 Ma (updated by Casanovas-Vilar et al.,  
279 2016b, after Agustí et al., 1996). Under the ‘faunal’ concept of MN units, CLL1 was even  
280 selected by some authors (Fahlbusch, 1976; De Bruijn et al., 1992; Mein, 1999) as the  
281 reference locality for MN9. However, *Progonomys* already commonly occurs in roughly  
282 coeval sites from other Iberian basins (Hilgen et al., 2012; Van Dam et al., 2014; Casanovas-  
283 Vilar et al., 2016b), with the lower boundary of MN10 being set at 9.98 Ma. Therefore, under

284 a strictly biostratigraphic approach to MN units, MN10 would include the local subzone to  
285 which CPL, CLL1 and CFE1 are correlated (Casanovas-Vilar et al., 2016b).

286 The latest occurrence of *H. laietanus* corresponds to its type locality (LT1; Villalta Comella  
287 and Crusafont Pairó, 1944; Golpe Posse, 1993; Alba, 2012), correlated to the local  
288 *Rotundomys montisrotundi* lineage subzone (MN10) and with a magnetostratigraphically  
289 interpolated age of 9.57 Ma (Casanovas-Vilar et al., 2016a). In turn, the oldest possible  
290 occurrence of *Hispanopithecus* in the basin is documented at PO2 and EDAR13 (Crusafont-  
291 Pairó and Golpe-Posse, 1973; Golpe Posse, 1982, 1993; Moyà Solà et al. 1990; Harrison,  
292 1991; Begun, 2002; Checa Soler and Rius Font, 2003; Alba, 2012). The former is correlated to  
293 MN9 in a strict sense (11.2–10.0 Ma; Casanovas-Vilar et al., 2011, 2016a), whereas EDAR13  
294 is correlated to the *C. hartenbergeri* range subzone (10.3–9.98 Ma; Casanovas-Vilar et al.,  
295 2011, 2016a, b) and therefore older than CLL1. Even though the material from PO2 and  
296 EDAR13 has been classically assigned to *H. laietanus* (Crusafont-Pairó and Golpe-Posse,  
297 1973; Golpe Posse, 1982, 1993; Moyà Solà et al., 1990; Harrison, 1991; Ribot et al., 1996;  
298 Checa Soler and Rius Font, 2003; Casanovas-Vilar et al., 2011; Alba, 2012), the scarce  
299 available remains are arguably undiagnostic at the species level: the female C<sup>1</sup> from PO2 was  
300 assigned to *H. laietanus* based on its similarities to those from CLL1 (Crusafont-Pairó and  
301 Golpe-Posse, 1973; Golpe Posse, 1982, 1993), but this tooth type is unknown for *H.*  
302 *crusafonti* (e.g., Begun, 1992), and the same applies to the fragmentary manual phalanges  
303 from EDAR13 (Checa Soler and Rius Font, 2003), even if they resemble those of *H. laietanus*  
304 from CLL2 (Moyà-Solà and Köhler, 1996; Almécija et al., 2007).

305 If the PO2 and EDAR13 remains are removed from the hypodigm of *H. laietanus* and  
306 assigned to *Hispanopithecus* sp. (contra Alba, 2012), the known stratigraphic range of *H.*  
307 *laietanus* is circumscribed to ca. 10 to 9.57 Ma. This is younger than CP1—the type locality of

308 *H. crusafonti* (Begun, 1992; Alba, 2012; Alba et al., 2012a), correlated with the C.  
309 *hartenbergeri* range subzone (10.30–9.98 Ma; Casanovas-Vilar et al., 2016a,b)—suggesting  
310 that *H. laietanus* might have postdated *H. crusafonti*. Unfortunately, the lack of diagnostic  
311 remains from EDAR13 (roughly coeval to CP1) and dating uncertainties for PO2 do not allow  
312 us to conclusively discard some overlap between the stratigraphic ranges of *H. crusafonti*  
313 and the younger *H. laietanus* during the latest early Vallesian (MN9).

314

#### 315 4.3 Paleoenvironment

316 Based on its postcranial morphology (Moyà-Solà and Köhler, 1996; Almécija et al., 2007,  
317 2013, 2015; Alba et al., 2010, 2012b; Alba, 2012; Pina et al., 2012) and microwear analyses  
318 (Ungar, 1996; DeMiguel et al., 2014), *H. laietanus* can be considered an arboreal orthograde  
319 primate with specific adaptations to below-branch suspension and frugivory—thereby being  
320 indicative of densely forested environments, in agreement with the paleoenvironmental  
321 evidence provided by the CPL associated fauna (Table 1; SOM S2 and SOM Figs. S1–S2).

322 The tridactyl horse *Hippotherium (primigenium)* does not necessarily indicate an open,  
323 grassland habitat, given mesowear evidence that it displayed a wide dietary spectrum  
324 (Kaiser et al., 2000; Kaiser, 2003). In contrast, the antelope *Miotragocerus* is considered a  
325 browser (Merceron et al., 2007) and semiaquatic animal that inhabited closed and swampy  
326 areas (Köhler, 1993). The latter is consistent with the nearby presence of freshwater, as  
327 further indicated by the beaver *Euroxenomys* and the geoemydid turtle *Ptychogaster*.

328 Several small mammals are also indicative of a forested environment, including the  
329 remarkable diversity of arboreal dormice, the presence of two eomyids, and the more  
330 abundant cricetids *Eumyarion* and *Anomalomys* (Casanovas-Vilar and Agustí, 2007)—the  
331 latter interpreted as a burrower that would have preferred moist soils (Casanovas-Vilar and

332 Agustí, 2007). The diverse insectivore assemblage from CPL is similarly indicative of moist  
333 and warm conditions, as further shown by the presence *Dinosorex* (a typical forest dweller;  
334 Furió et al., 2015), *Talpa* (a burrower linked to constantly humid soils; Furió et al., 2011),  
335 *Plesiodimylus* (a malacophagous taxon indicative of an abundant presence of gastropods;  
336 Crespo et al., 2018), and *Lantanotherium* and *Crusafontina* (whose extant relatives are  
337 restricted to the rainforests of southeastern Asia).

338 Most of the small mammal taxa apparently associated with humid forest environments  
339 are not recorded in coeval sites from the inner Iberian Peninsula, which during the Vallesian  
340 were typically characterized by more arid environments (Casanovas-Vilar and Agustí, 2007;  
341 Casanovas-Vilar et al., 2008). This applies to most of the insectivores (with the exception of  
342 *Crusafontina*; Furió et al., 2011) and multiple rodent taxa (the eomyids, most of the glirids,  
343 and the cricetids *Eumyarion* and *Anomalomys*; Casanovas-Vilar and Agustí, 2007; Casanovas-  
344 Vilar et al., 2008). This paleobiogeographical evidence suggests that, during the Vallesian,  
345 Vallès-Penedès habitats were moister and more densely forested than other areas of the  
346 Iberian Peninsula, thus being closer to those from France and Central Europe, as previously  
347 noted for the late Aragonian (Casanovas-Vilar et al., 2008). Such environmental differences  
348 would account for the observed geographical distribution of Miocene hominoids in the  
349 Iberian Peninsula, being only recorded from the more humid and closed environments from  
350 the Vallès-Penedès and Seu d'Urgell basins in NE Iberia (e.g., Alba, 2012).

351 Based on the associated fauna, the paleoenvironment of CPL can be inferred as a densely  
352 forested and humid environment with nearby water, similar to that of CLL1. The latter has  
353 further yielded plant remains, which together with the fauna allow us to reconstruct its  
354 paleoenvironment as a very humid marshy area with nearby dense wetland forests with  
355 some (sub)tropical plant elements (Marmi et al., 2012). The newly reported maxillary



356 fragment of *Hispanopithecus* from CPL-M therefore supports the view that this taxon would  
357 have been restricted to forested humid habitats providing a year-round fruit supply (Marmi  
358 et al., 2012, and references therein). These habitats apparently persisted in the Vallès-  
359 Penedès Basin until the early late Vallesian—even if they were progressively becoming more  
360 fragmentary, due to an ongoing trend of climatic deterioration that ultimately presumably  
361 led to their extinction (Agustí et al., 2003; Casanovas-Vilar et al., 2011; Marmi et al., 2012;  
362 DeMiguel et al., 2014).

363

## 364 **5. Summary and conclusions**

365 We describe a new hominoid maxillary fragment with M<sup>2</sup> recovered from a new locality  
366 from the site of CPL, where Miocene apes had not been previously reported. Although CPL is  
367 relatively close (500 m) to the type locality of *H. crusafonti* (10.30–9.98 Ma, MN9, early  
368 Vallesian), based on occlusal morphology the new find is tentatively assigned to *H. cf.*  
369 *laietanus*. The associated fauna from CPL further indicates a younger age (9.98–9.73 Ma),  
370 being roughly coeval with other Vallès-Penedès localities with *H. laietanus* (CLL1 and CFE1),  
371 correlated to earliest MN10 (late Vallesian) on biostratigraphic grounds. Although some  
372 temporal overlap between the two species cannot be completely ruled out, currently  
373 available evidence is consistent with a replacement of *H. crusafonti* by *H. laietanus* close to  
374 the MN9/MN10 transition (ca. 10.0 Ma). The associated fauna from CPL indicates a densely  
375 forested and humid paleoenvironment with nearby freshwater (as in CLL1), thereby  
376 strengthening the view that *Hispanopithecus* might have been restricted to dense wetland  
377 forests soon before it went extinct in the late Vallesian. Given the existence of other  
378 fossiliferous outcrops in CPL, the find reported here is most promising for the prospect of  
379 finding additional fossil hominoid remains in this area.

380

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403

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625

## 626 **Figure captions**

627

628 **Figure 1.** Geological map of the Vallès sector of the Vallès-Penedès Basin (NE Iberian  
629 Peninsula), indicating the location of all the Vallesian localities that have delivered fossil  
630 remains of *Hispanopithecus* spp. Abbreviations (municipalities indicated within brackets):  
631 CFE1 = Can Feu 1 [Sant Quirze del Vallès]; CLL1 = Can Llobateres 1 [Sabadell]; CLL2 = Can  
632 Llobateres 2 [Sabadell]; CP1 = Can Poncic 1 [Sant Quirze del Vallès]; CPL-M = Can Pallars i  
633 Llobateres-M [Sant Quirze del Vallès]; EDAR13 = Estació Depuradora d’Aigües Residuals–Riu  
634 Ripoll 13 [Sabadell]; LT1 = La Tarumba 1 [Viladecavalls]; PO2 = Polinyà 2 (Gabarró) [Polinyà].

635

636 **Figure 2.** Aerial photograph showing various fossiliferous outcrops from Can Pallars i  
637 Llobateres (CPL) and the approximate location of the classical site of Can Poncic (CP). Dotted  
638 white rectangles denote loosely defined sites, whereas red asterisks denote the exact  
639 location of paleontological localities. The location of the Can Poncic farmhouse and other  
640 local toponyms are also indicated. North is toward the top. Coordinates are indicated below  
641 (for details on the system of geographical coordinates used, please see the Materials and  
642 methods). Legend: CPL = Can Pallars i Llobateres (central coordinates: 31N 421450 E –  
643 4598750 N, including CPL-A and CPL3); CPL-M (=CPL-B) = Location of the hominoid find by  
644 Méndez (31N 421380 E – 4598702 N); CPL-P2 = Spot 2 of CPL (31N 421610 E – 4598607 N);  
645 CPL-P3 = Spot 3 of CPL (31N 421423 E – 4598424 N); CPL-P4 = Spot 4 of CPL (31N 421672 E –  
646 4598609 N); CP = Can Poncic (approximate coordinates 31N 421900 – 4598475). Other CPL  
647 localities not depicted in the figure include CPL-B (31N 421410 E – 4598675 N) and CPL-P1  
648 (=CPL-C; 31N 421470 E – 4598485 N). Figure modified from base orthophotos downloaded  
649 from VISSIR v3.26 (ICGC, 2017: sheets 286-119 and 287-119, scale 1:2500), ©Institut  
650 Cartogràfic i Geològic de Catalunya, with permission allowed by licence Creative Commons  
651 (CC) – Attribution 4.0 International (CC BY 4.0; see <http://www.icgc.cat/Ajuda/Avis-legal> for  
652 the reuse policies allowed for ICGC web contents).

653

654 **Figure 3.** Left maxillary fragment with M<sup>2</sup> (IPS102942) of *Hispanopithecus* cf. *laietanus* from  
655 CPL-M in occlusal (a), buccal (b) and lingual (c) views.

656

657 **Figure 4.** Comparison of the occlusal morphology of the left M<sup>2</sup> (IPS102942) of  
658 *Hispanopithecus* cf. *laietanus* from CPL-M (a) with the M<sup>1</sup> and/or M<sup>2</sup> of other Vallès-Penedès  
659 hominoids: b) left M<sup>1</sup> (IPS1781) of *H. laietanus* from CCL1; c) right M<sup>1</sup> (IPS1844, reversed) of

660 *H. laietanus* from CLL1; d) left M<sup>1</sup> (IPS1788) of *H. laietanus* from CLL1; e) left M<sup>1</sup>–M<sup>2</sup>  
661 (IPS58338–IPS58338) of *H. laietanus* from CCL1; f) right M<sup>1</sup>–M<sup>2</sup> (IPS18000.5) of *H. laietanus*  
662 from CLL2; g) left M<sup>2</sup> IPS1794 of *H. laietanus* from CLL1; h) left ?M<sup>2</sup> (IPS1771) of *H. laietanus*  
663 from CLL1; i) left M<sup>1</sup>–M<sup>2</sup> (IPS35026) of *Dryopithecus fontani* from ACM/C3-Ae; j) left M<sup>1</sup>–M<sup>2</sup>  
664 (IPS21350, holotype) of *Pierolapithecus catalaunicus* from ACM/BCV1; k) left M<sup>1</sup>–M<sup>2</sup>  
665 (IPS1798, holotype) of *Hispanopithecus crusafonti* from CP1; l) left M<sup>1</sup> (IPS1815) of *H.*  
666 *crusafonti* from CP1; m) left M<sup>1</sup> (IPS1818) of *H. crusafonti* from CP1; n) left M<sup>2</sup> (IPS1820 of *H.*  
667 *crusafonti* from CP1; o) right M<sup>3</sup> or M<sup>2</sup> (IPS1812, reversed) of *H. crusafonti* from CP1; p) right  
668 M<sup>2</sup> (IPS1821, reversed) of *H. crusafonti* from CP1; q) left M<sup>1</sup> (IPS41712) of *Anoiapithecus*  
669 *brevirostris* from ACM/C3-Aj; r) left M<sup>1</sup>–M<sup>2</sup> (IPS43000, holotype) of *A. brevisrostris* from  
670 ACM/C3-Aj; s) right M<sup>1</sup>–M<sup>2</sup> (IPS35027, reversed) of *A. brevisrostris* from ACM/C1-E\*. Locality  
671 abbreviations: ACM = Abocador de Can Mata (els Hostalets de Pierola); C1 = Cel·la 1 (ACM  
672 sector); C3 = Cel·la 3 (ACM sector); for other abbreviations, see Figure 1 caption.

673

674 **Figure 5.** Bivariate plots of buccolingual breadth (BL, in mm) vs. mesiodistal length (MD, in  
675 mm) of the M<sup>2</sup> (IPS102942) of *Hispanopithecus cf. laietanus* from CPL-M, as compared to the  
676 M<sup>1</sup> (a) and M<sup>2</sup> (b) of Vallès-Penedès hominoids.

677

678 **Figure 6.** Stratigraphic ranges of the biochronologically most significant rodent species and  
679 situation of the Vallès-Penedès localities that have previously yielded fossil remains of  
680 *Hispanopithecus*. Rodent species present at CPL-M are indicated in bold. Dashed lines  
681 between rodent species indicate phylogenetic relationships. Local biozonation of the Vallès-  
682 Penedès Basin is after Casanovas-Vilar et al. (2016b) while Neogene timescale follows Hilgen  
683 et al. (2012). In the case of MN (Mammal Neogene) zones, their boundaries are indicated as

684 defined by selected first appearance events (after Hilgen et al., 2012). The reference sites for  
685 MN9 (CLL1) and MN10 (Masía del Barbo, Spain) are denoted with asterisks. Note that CLL1 is  
686 herein placed within MN10 when MN zones are defined according to first appearance  
687 events. For locality abbreviations, see Figure 1 caption. Other abbreviations: *C. harten.* =  
688 *Cricetulodon hartenbergeri* range subzone; *C. h. – P. h.* = *Cricetulodon hartenbergeri* –  
689 *Progonomys hispanicus* interval subzone; *C + P* = *Cricetulodon sabadellensis* + *Progonomys*  
690 *hispanicus* concurrent range zone. *Rot. montis.* = *Rotundomys montisrotundi* lineage  
691 subzone; *Rot. bressa.* = *Rotundomys bressanus* lineage subzone.  
692

1 **Table 1**

2 Updated list of the faunal assemblage from Can Pallars i Llobateres (CPL, including those  
 3 small mammal specimens labelled as CPL3, as well as the large mammal specimens from  
 4 CPL, CPL-A, CPL-B, CPL-P1, CPL-P3, CPL-P4 and CPL-M).

Order	Family	Taxonomic assignment
Testudines	Geoemydidae	<i>Ptychogaster</i> sp.
Testudines	Testudinidae	<i>Testudo</i> sp.
Testudines	Testudinidae	<i>Titanochelon</i> cf. <i>richardi</i>
Squatama	Indet.	Serpentes indet.
Primates	Hominidae	<i>Hispanopithecus</i> cf. <i>laietanus</i>
Proboscidea	Indet. <sup>a</sup>	Proboscidea indet. <sup>a</sup>
Artiodactyla	Cervidae	Cervidae indet.
Artiodactyla	Bovidae	<i>Miotragocerus</i> aff. <i>pannoniae</i>
Perissodactyla	Equidae	<i>Hippotherium (primigenium)</i> cf. <i>catalaunicum</i> <sup>b</sup>
Perissodactyla	Rhinocerotidae	Rhinocerotidae indet.
Eulipotyphla	Soricidae	<i>Crusafontina</i> <i>endemica</i>
Eulipotyphla	Erinaceidae	<i>Lantanothereum</i> <i>sanmigueli</i>
Eulipotyphla	Heterosoricidae	<i>Dinosorex</i> <i>grycivensis</i>
Eulipotyphla	Dimylidae	<i>Plesiodimylus</i> <i>chantrei</i>
Eulipotyphla	Talpidae	<i>Talpa</i> <i>minuta</i>
Lagomorpha	Ochotonidae	<i>Prolagus</i> <i>crusafonti</i>
Rodentia	Cricetidae	<i>Cricetulodon</i> <i>sabadellensis</i>
Rodentia	Cricetidae	<i>Eumyarion</i> <i>leemanni</i>



Rodentia	Cricetidae	<i>Democricetodon cf. nemoralis</i>
Rodentia	Cricetidae	<i>Hispanomys thaleri</i>
Rodentia	Cricetidae	<i>Anomalomys gaillardi</i>
Rodentia	Eomyidae	<i>Eomyops catalaunicus</i>
Rodentia	Eomyidae	<i>Keramidomys pertesunatoi</i>
Rodentia	Gliridae	<i>Muscardinus hispanicus</i>
Rodentia	Gliridae	<i>Muscardinus vallesiensis</i>
Rodentia	Gliridae	<i>Glirulus lissiensis</i>
Rodentia	Gliridae	<i>Paraglrulus werenfelsi</i>
Rodentia	Gliridae	<i>Myoglis meini</i>
Rodentia	Sciuridae	<i>Spermophilinus bredai</i>
Rodentia	Sciuridae	<i>Heteroxerus grivensis</i>
Rodentia	Castoridae	<i>Euroxenomys minutus</i>

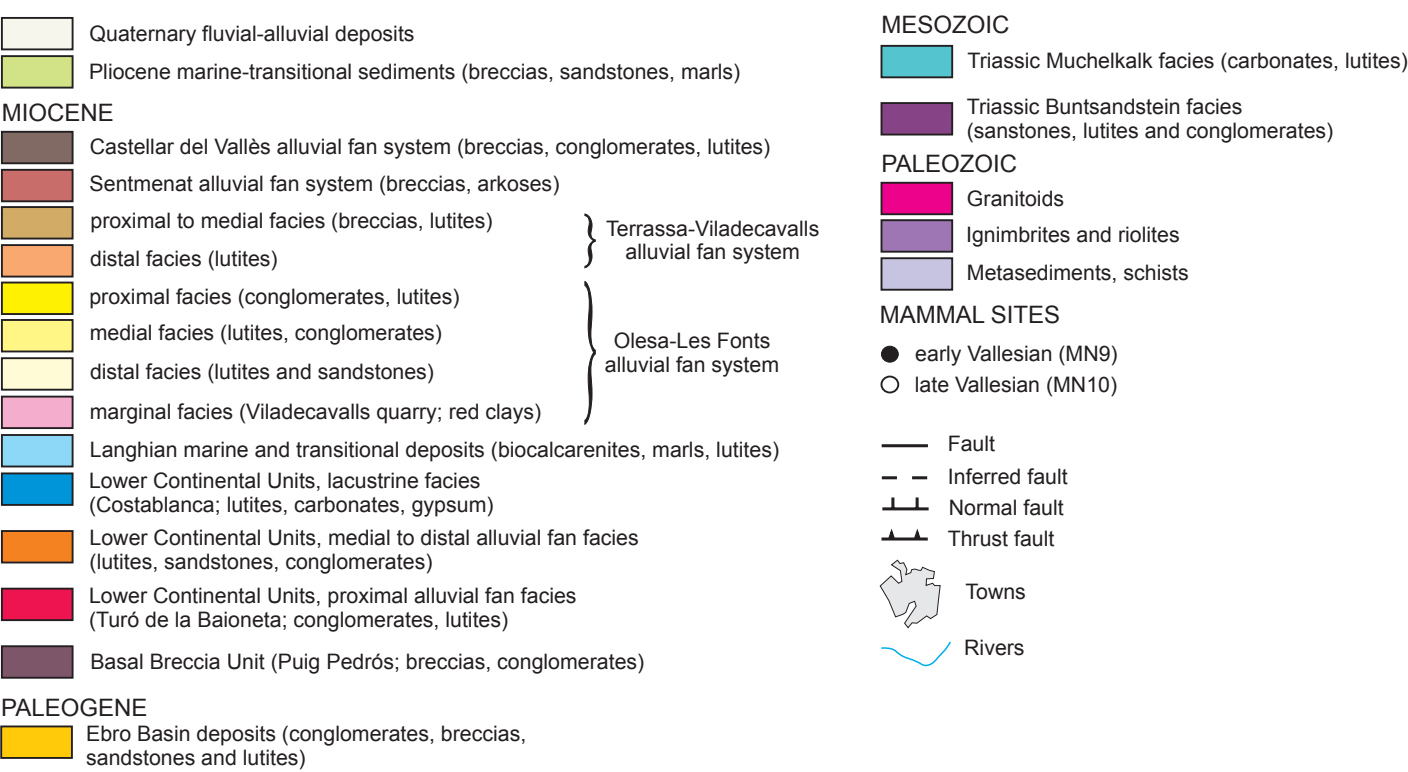
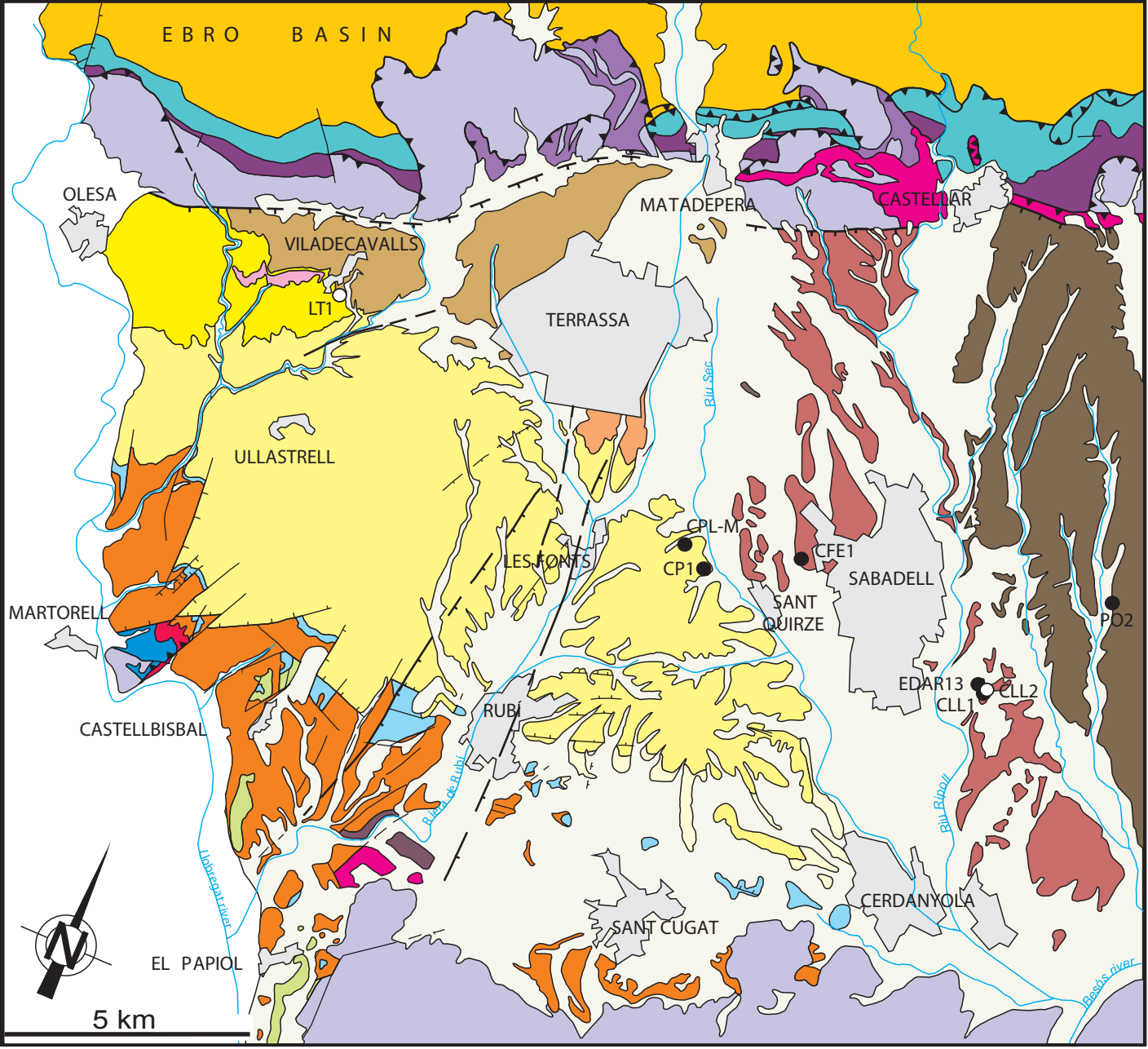
5

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6       <sup>a</sup> Llenas i Avellaneda (1999) mentioned the recovery of a cervical vertebra of  
7 *Tetraolophodon longirostris*, but we were unable to find such a material. All the available  
8 proboscidean remains from CPL localities are too fragmentary to enable their identification  
9 even at the family rank.

10       <sup>b</sup> Following Bernor et al. (1996), we consider *Hippotherium (primigenium)* as a species  
11 complex (as denoted by the name interpolated within parentheses; see ICZN, 1999:Art. 6.2).

12







Can Pallars  
i Llobateres

Can Pallars  
i Llobateres

CPL

CPL-M

Can  
Llobateres

CPL-P2

CPL-P4

Torrent de la Betzuca

Can Poncic  
(farmhouse)

Residència  
Assis

CP

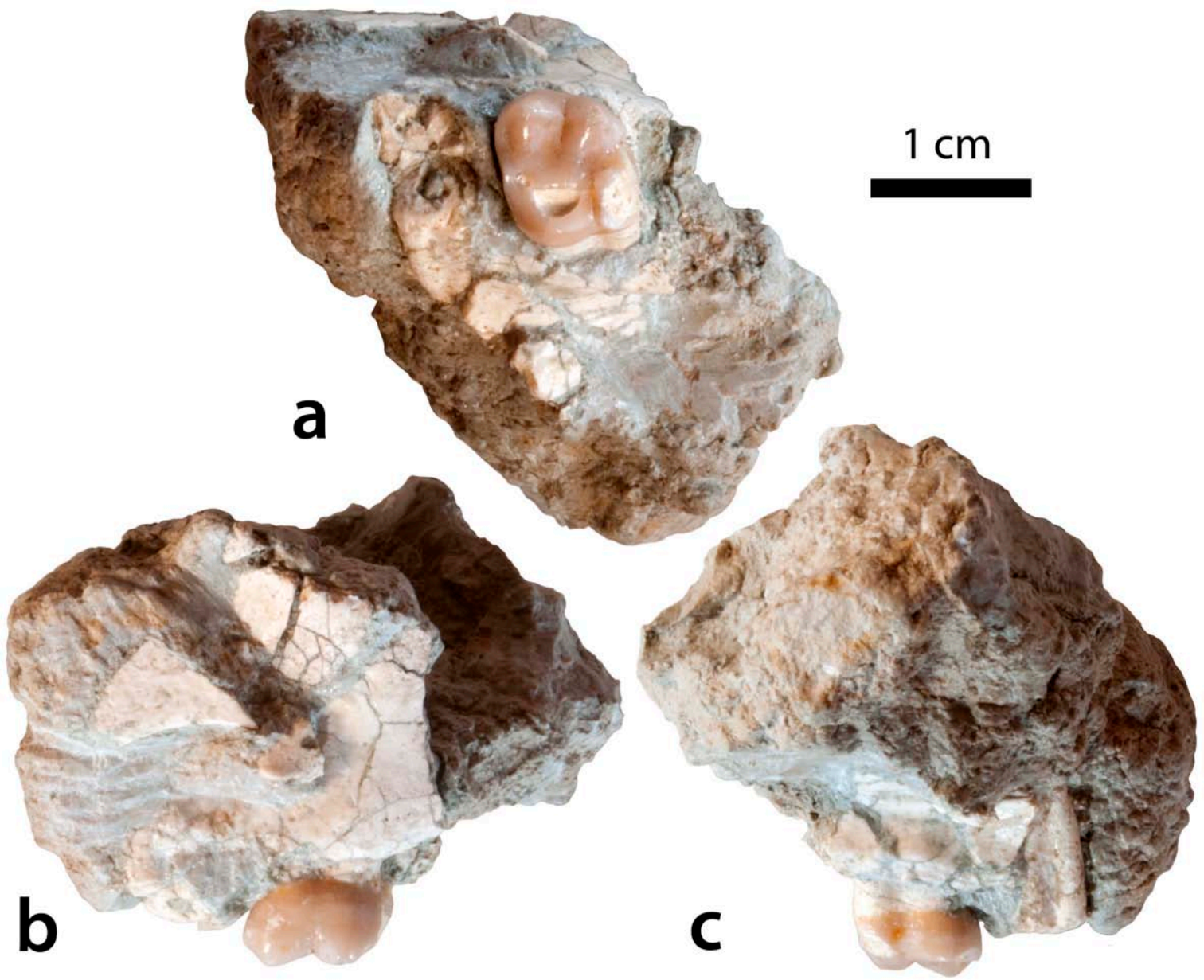
CPL-P3

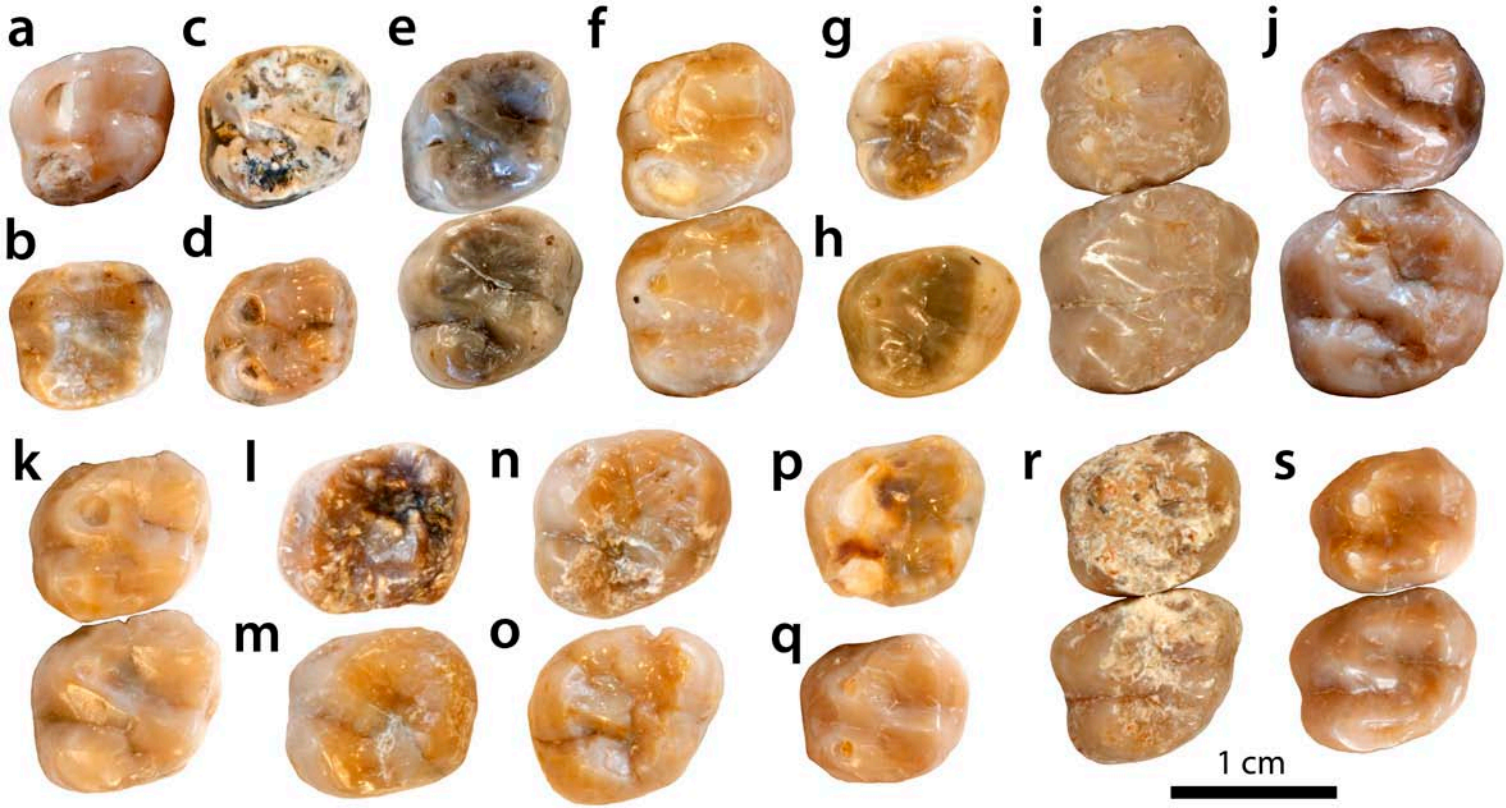
Can Poncic  
(area)

Camí del Mig

100 m











## Supplementary Online Material

Can Pallars i Llobateres: A new hominoid-bearing locality from the late Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula)

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## SOM S1

### Supplementary materials and methods

#### *Associated fauna*

The large vertebrate remains from CPL include the following specimens:

- 20 specimens recovered in 1999 from CPL (IPS13989 to IPS13994, IPS13996, IPS103684 to IPS103688, and IPS105907 to IPS105914, of which IPS13993 and IPS105908 come from CPL-B).
- 29 specimens surface-collected, apparently at a later time, from CPL-A (IPS104303 to IPS104322), CPL-B (IPS104294 to IPS104299, and IPS104302) and CPL-P1 (=CPL-C; IPS104299, IPS104300).
- Three specimens most recently recovered in 2017 from CPL-P3 (IPS104355) and CPL-P4 (IPS104348 to IPS104350).

The associated small mammal fauna from CPL includes the following micromammal teeth:

- 279 rodent teeth labeled as coming from CPL (IPS66320 to IPS66598) and 73 from CPL3 (IPS14948, IPS66604 to IPS66638, IPS69519 to IPS69555).
- 30 eulipotyphlan teeth from CPL (IPS65589 to IPS65615, IPS66599 to IPS66601).
- Two lagomorph teeth from CPL3 (IPS66639 and IPS66640).

## SOM S2

### Supplementary results

#### *Associated fauna*

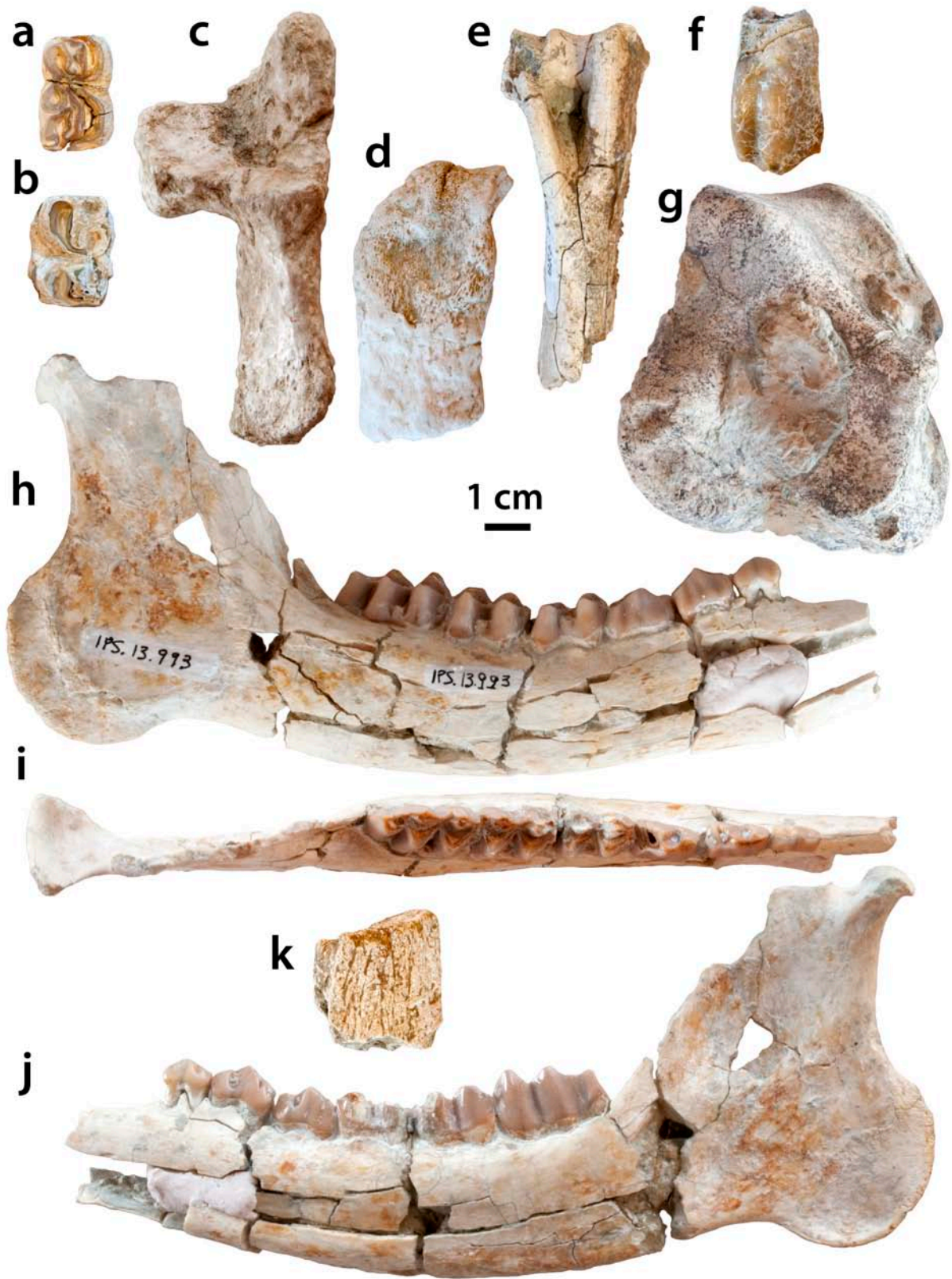
The presence of an indeterminate snake can be ascertained based on a fragmentary vertebra (IPS140320), and the scarce and fragmentary testudine remains allow us to determinate the presence of three different species: a medium-sized tortoise of genus *Testudo*, based on a couple of peripherals (IPS104299 and IPS104302); a giant tortoise that we assign to *Titanochelon* cf. *richardi*, based on another peripheral (IPS104318) and a costal fragment (IPS104348); and a freshwater geoemydid turtle, based on a peripheral (IPS104300) and a costal fragment (IPS104313), the former attributable to genus *Ptychogaster*.

Owing to the lack of a fossiliferous layer amenable to systematic excavations, large mammals from CPL are insufficiently sampled, so that only a few species can be identified.

Equids are rather abundantly represented by the three-toed horse *Hippotherium (primigenium) cf. catalaunicum*, including two lower cheek teeth (IPS13994 and IPS104305; SOM Fig. S1a, b), fragments of metacarpal III (IPS104308 and IPS104315; SOM Fig. S1d), a distal phalanx III (IPS104310), a distal fragment of lateral metapodial (IPS104311), and a calcaneus (IPS104355; SOM Fig. S1c). Some other available remains might belong to the same taxon, but do not preserve enough information so as to be sure. In turn, boselaphin bovids are represented by a small horn core fragment (IPS104349; SOM Fig. S1k), a lumbar vertebral body (IPS13991), a P<sup>3</sup> crown fragment (IPS103686), and a hemimandible with P<sub>2</sub>–M<sub>3</sub> (IPS13993; Fig. 6h–j). The dentognathic material, in particular the mandible, is attributable to the antelope *Miotragocerus aff. pannoniae* sensu Moyà-Solà (1983). Even though the diagnostic metatarsal morphology of this species (Moyà-Solà, 1983; Fuss et al., 2015) cannot be ascertained from this material, several features, such the size of the dentition, rule out an attribution to either *Miotragocerus monacensis* or *Protragocerus chantrei*, which are smaller and display shorter and more molarized lower premolars (Moyà-Solà, 1983). Following Moyà-Solà (1983), the species assignment is made with open nomenclature, because the available remains correspond to a form smaller than *M. pannoniae* s.s. from similarly-aged localities from the basin, such as Can Llobateres. Due to the scarcity of the material, other large mammals can be only identified to family rank, including: a proboscidean, based on fragments of a long bone (IPS13996), ribs (IPS104316, IPS105913), and indeterminate bones (IPS104314, IPS105914); a rhinocerotid, based on an upper cheek tooth fragment (IPS104304; SOM Fig. S1f), a patella (IPS13990; SOM Fig. S1g), a fragmentary metapodial (IPS105908), and fragments of a long bone (IPS103685) and ribs (IPS104306, IPS105905), among other remains of more dubious taxonomic ascription; and a cervid, based on a distal fragment of humerus (IPS103687; SOM Fig. S1e). Llenas i Avellaneda (1999) reported the presence at CPL of the gomphothere *Tetraolophodon longirostris*, as recorded by a cervical vertebra. However, we were unable to find this specimen among the ICP collections and, therefore, this species is not included on the faunal list reported in Table 1.

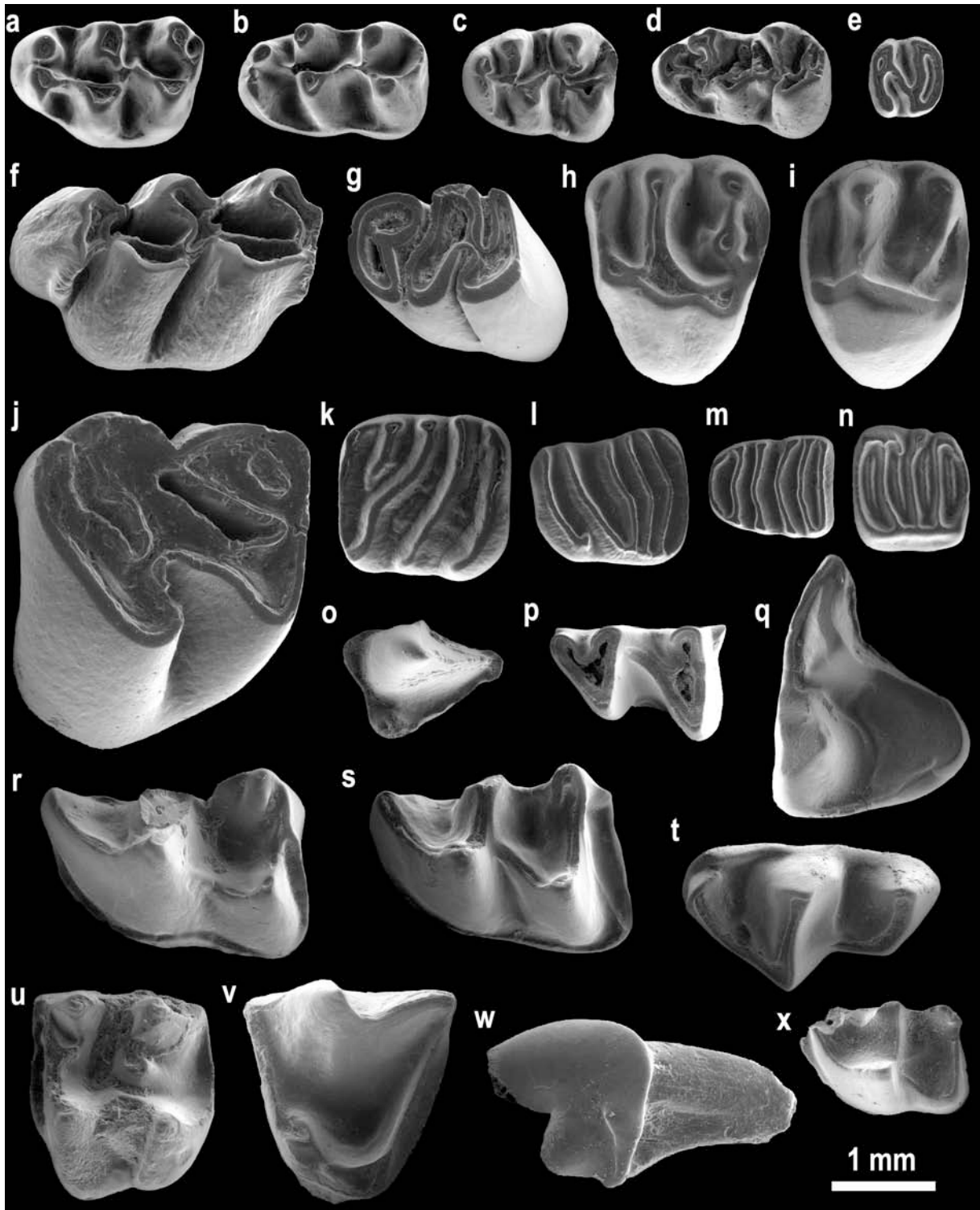
In contrast to the scarcity of large mammal remains, micromammals are well represented by a sample of 384 identifiable teeth (SOM Fig. S2). Rodent are represented by 15 out of 21 species, including: five cricetids (*Cricetulodon sabadellensis*, SOM Fig. S2a, b; *Eumyarion leemanni*, SOM Fig. S2d; *Democricetodon cf. nemoralis*, SOM Fig. S2c; *Hispanomys thaleri*,

SOM Fig. S2f; and *Anomalomys gaillardi*, SOM Fig. S2g), two eomyids (*Eomyops catalaunicus*; and *Keramidomys pertesunatoi*, SOM Fig. S2e), five glirids (*Muscardinus hispanicus*, SOM Fig. S2m; *Muscardinus vallesiensis*, SOM Fig. S2l; *Glirulus lissiensis*; *Paraglrulus werenfelsi*, SOM Fig. S2n; and *Myoglis meini*, SOM Fig. S2k), two sciurids (*Spermophilinus bredai*, SOM Fig. S2i; and *Heteroxerus grivensis*, SOM Fig. S2h), and a castorid (*Euroxenomys minutus*, SOM Fig. S2j). Eulipotyphlans (24%) include a soricid (*Crusafontina endemica*, SOM Fig. S2w, x), an erinaceid (*Lantanothereium sanmigueli*, SOM Fig. S2r, u), a heterosoricid (*Dinosorex grycivensis*, SOM Fig. S2s, v), a dimylid (*Plesiodimylus chantrei*, SOM Fig. S2q, t) and a talpid (*Talpa minuta*, SOM Fig. S2o, p), whereas lagomorphs (5%) are represented by the ochotonid *Prolagus crusafonti*.



**SOM Figure S1.** Large mammal remains from CPL: a) right lower cheek tooth ( $P_4$  or  $M_1$ ; IPS13994) of *Hippotherium (primigenium) cf. catalaunicum* from CPL, in occlusal view; b) left lower cheek tooth (? $P_4$ ; IPS103305) of *Hi. cf. catalaunicum* from CPL-A, in occlusal view; c) right calcaneus (IPS104355) of *Hi. cf. catalaunicum* from CPL-P3, in dorsal view; d) distal

fragment of metacarpal III (IPS104315) of *Hi. cf. catalaunicum* from CPL-A, in anterior view. e) distal fragment of right humerus (IPS103687) of Cervidae indet. from CPL, in posterior view; f) fragment of upper cheek tooth (IPS104304) of Rhinocerotidae indet from CPL-A, in buccal view; g) patella (IPS13990) of Rhinocerotidae indet. from CPL, in posterior view; h–j) right hemimandible with P<sub>2</sub>–M<sub>3</sub> (IPS13993) of *Miotragocerus aff. pannoniae* from CPL-B, in buccal (h), occlusal (i) and lingual (j) views; k) horn core fragment (IPS104349) of Boselaphini indet. from CPL-P4.



**SOM Figure S2.** SEM micrographs of selected small mammal remains from CPL: a) left M<sup>1</sup> (IPS66333) of *Cricetulodon sabadellensis*; b) right M<sub>1</sub> (IPS66470, reversed) of *C. sabadellensis*; c) left M<sub>1</sub> (IPS66594) of *Democricetodon cf. nemoralis*; d) right M<sub>1</sub> (IPS66574, reversed) of *Eumyarion leemanni*; e) left M<sub>1</sub> or M<sub>2</sub> (IPS66595) of *Keramidomys pertesunatoi*; f) left M<sup>1</sup> (IPS66542) of *Hispanomys thaleri*; g) left M<sub>1</sub> (IPS66607) of *Anomalomys gaillardi*; h) left M<sup>1</sup> or M<sup>2</sup> (IPS66611) of *Heteroxerus grivensis*; i) left M<sup>1</sup> or M<sup>2</sup> (IPS66622) of

*Spermophilus bredai*; j) left  $M^1$  or  $M^2$  (IPS66610) of *Euroxenomys minutus*; k) right  $M_1$  (IPS69520, reversed) of *Myoglis meini*; l) left  $M^1$  (IPS69550) of *Muscardinus vallesiensis*; m) left  $M_1$  (IPS69542) of *Muscardinus hispanicus*; n) left  $M^2$  (IPS69525) of *Paraglrulus werenfelsi*; o) left  $P^4$  (IPS65590) of *Talpa minuta*; p) left  $M_1$  (IPS65614) of *T. minuta*; q) right  $M^2$  (IPS65606, reversed) of *Plesiodimylus chantrei*; r) left  $M_1$  (IPS65612) of *Lantanothereium sanmigueli*; s) left  $M_1$  (IPS65610) of *Dinosorex grycivensis*; t) left  $M_2$  (IPS65615) of *Pl. chantrei*; u) left  $M^2$  (IPS65594) of *L. sanmigueli*; v) right  $P^4$  (IPS65604, reversed) of *D. grycivensis*; w) left  $I^1$  (IPS65593) of *Crusafontina endemica*; x) right  $M_2$  (IPS65597, reversed) of *Cr. endemica*.