

1 Paleoenvironmental inferences on the Late Miocene hominoid-bearing site of Can Llobateres
2 (NE Iberian Peninsula): An ecometric approach based on functional dental traits

3

4 **Abstract**

5 *Hispanopithecus laietanus* from the Late Miocene (9.8 Ma) of Can Llobateres 1 (CLL1;
6 Vallès-Penedès Basin, NE Iberian Peninsula) represents one of the latest occurrences of fossil
7 apes in Western mainland Europe, where they are last recorded at ~9.5 Ma. The
8 paleoenvironment of CLL1 is thus relevant for understanding the extinction of European
9 hominoids. To refine paleoenvironmental inferences for CLL1, we apply ecometric models
10 based on functional crown type (FCT) variables—a scoring scheme devised to capture
11 macroscopic functional traits of occlusal shape and wear surfaces of herbivorous large mammal
12 molars. Paleotemperature and paleoprecipitation estimates for CLL1 are provided based on
13 published regional regression models linking average FCT of large herbivorous mammal
14 communities to climatic conditions. A mapping to Whittaker’s present-day biome classification
15 is also attempted based on these estimates, as well as a case-based reasoning via canonical
16 variate analysis of FCT variables from five relevant biomes. Estimates of mean annual
17 temperature (25 °C) and mean annual precipitation (881 mm) classify CLL1 as a tropical
18 seasonal forest/savanna, only in partial agreement with the canonical variate analysis results,
19 which classify CLL1 as a tropical rainforest with a higher probability. The former biome agrees
20 better with previous inferences derived from fossil plants and mammals, as well as preliminary
21 isotopic data. The misclassification of CLL1 as a tropical forest is attributed to the mixture of
22 forest-adapted taxa with others adapted to more open environments, given that faunal and plant
23 composition indicates the presence of a dense wetland/riparian forest with more open
24 woodlands nearby. The tested FCT ecometric approaches do not provide unambiguous biome
25 classification for CLL1. Nevertheless, our results are consistent with those from other

26 approaches, thus suggesting that FCT variables are potentially useful to investigate
27 paleoenvironmental changes through time and space—including those that led to the extinction
28 of European Miocene apes.

29

30 **Key words:** Fossil apes; *Hispanopithecus*; Functional crown types; Ecometrics; Vallesian;
31 Spain.

32

33 **1. Introduction**

34 *1.1. The hominoid-bearing site of Can Llobateres*

35 Historical background The fossil site of Can Llobateres (Late Miocene), in the municipality of
36 Sabadell (Catalonia, NE Spain), has figured prominently in the study of Miocene mammals
37 from Europe—being considered the reference locality of MN9 (Mein, 1990)—with emphasis
38 on fossil hominoids. The site was discovered in 1926 (Crusafont Pairó, 1969; Alba et al., 2011a,
39 2011b) and the first accounts of its fauna were published in the 1940s (Villalta Comella and
40 Crusafont Pairó, 1943; Crusafont Pairó and Villalta Comella, 1948). Hominoid dental remains,
41 assigned to the dryopithecine¹ *Hispanopithecus laietanus*, were first discovered there in 1958
42 (Crusafont Pairó, 1958; Crusafont Pairó and Hürzeler, 1969) and additional hominoid remains
43 were subsequently recovered during the 1960s (Crusafont Pairó and Hürzeler 1961, 1969;
44 Crusafont Pairó 1965; Golpe Posse 1982, 1993; Moyà-Solà et al. 1990). Crusafont and Hürzeler
45 (1961, 1969) reported two additional species from the site—never figured or described, and

¹ Although it is currently uncertain whether the Dryopithecinae constitute a clade or a paraphyletic assemblage (Alba, 2012; Almécija et al., 2021; Pugh, 2022), we follow Urciuoli and Alba (2023) in provisionally distinguishing this group at the subfamily rank until its phylogenetic relationships are clarified further.

46 hence considered *nomina nuda* (Szalay and Delson, 1979; Alba, 2012; Alba et al., 2012a)—
47 while a fourth hominoid was subsequently reported based on an isolated male upper canine
48 (Crusafont Pairó and Golpe Posse, 1973), being attributed to *Sivapithecus indicus*.

49 In 1981, additional dental hominoid material was recovered from the lower levels of the site
50 (Begun et al., 1990; Golpe Posse, 1993), known as Can Llobateres 1 (CLL1). From 1992
51 onward, a partial cranium (Moyà-Solà and Köhler, 1993, 1995; Begun, 1994) and skeleton
52 (Moyà-Solà and Köhler, 1996; Almécija et al., 2007; Pina et al., 2012; Tallman et al., 2013;
53 Susanna et al., 2014) were discovered on the upper levels of the site, termed Can Llobateres 2
54 (CLL2), which were last excavated in 1997. In 2010, excavations were resumed again at CLL1
55 by a team led from the ICP and additional hominoid teeth were found (Alba et al., 2012a), along
56 with plant remains that enabled a better characterization of the paleoenvironment (Marmi et al.,
57 2012). The locality of CLL1 was last excavated in 2015, owing to the paucity of the fossiliferous
58 levels that delivered most of the hominoid dental remains in previous years. Begun et al. (1990)
59 and most subsequent authors attributed the whole hominoid sample from Can Llobateres to
60 *Dryopithecus laietanus* (Harrison, 1991; Moyà-Solà and Köhler, 1993, 1995, 1996; Begun,
61 1994; Ribot et al., 1996) or, more recently, *Hispanopithecus laietanus* (Almécija et al., 2007;
62 Cameron, 1997, 1998, 1999, 2004; Moyà-Solà et al., 2009; Begun, 2009; Alba, 2012; Alba et
63 al., 2012a).

64 Geological background and taphonomical remarks Can Llobateres is located in the Vallès
65 sector of the Vallès-Penedès Basin (Catalonia, Spain; Fig. 1), an elongated half-graben about
66 100 km in length and 12–14 km in width, parallel to the Catalan coastline near Barcelona, and
67 bounded by the Catalan Coastal Ranges (for an updated review, see Casanovas-Vilar et al.,
68 2016a). The Miocene sedimentary infill of the Vallès-Penedès Basin has been divided into four
69 main lithostratigraphic units, Can Llobateres belonging to the Upper Continental Units, which
70 range from the Middle to the Late Miocene (Casanovas-Vilar et al., 2016a). In particular, Can

71 Llobateres is located within distal facies of the alluvial fan system of Castellar del Vallès
72 (Agustí et al., 1996, 1997), consisting of a short sequence ~20 m thick mostly defined by
73 mudstones (claystones and siltstones), as well as polymictic breccias and conglomerates
74 (Marmi et al., 2012; Alba et al., 2012a). The locality of CLL1 is located in the lower section of
75 the sequence, characterized by organic matter and abundant mudstones, indicating a poorly
76 drained alluvial plain that would have favored the development of small shallow lakes and
77 ponds (Agustí et al., 1996; Alba et al., 2011a, 2011b, 2012a).

78 No taphonomic study has been performed at CLL1, but Begun et al. (1990) made some
79 sedimentological and taphonomic remarks based on the 1981 campaign, while Marmi et al.
80 (2012) and Alba et al. (2012a) provided far more detailed sedimentological descriptions and
81 additional taphonomic details based on the 2010–2011 campaigns. The former authors
82 distinguished two 'sedimentary units' at CLL1, which they interpreted as corresponding to two
83 different 'fluvial cycles' (Begun et al., 1990): the lower one, characterized by finer sediments
84 indicative of a low energy depositional environment, would have yielded taxa associated with
85 humid and forested environments (such as primates and suids); the upper one, in turn, would
86 be characterized by coarser sediments (including channel deposits) indicative of a higher energy
87 depositional environment and, according to these authors, would have yielded taxa indicative
88 of more open conditions (such as hipparionin equids) that could have been transported from
89 greater distances. Subsequent fieldwork at the site (Alba et al., 2012a) confirmed that primates
90 are apparently restricted to the lower 'unit' recognized by Begun et al. (1990) but evinced a
91 greater stratigraphic and taphonomic complexity (Alba et al., 2012a; Marmi et al., 2012), in
92 which four stratigraphic bodies may be discerned.

93 The bottom of the CLL1 sequence (not available to Begun et al., 1990) is composed by layers
94 of reddish to brown silts, sands, and conglomerates, indicative of less humid conditions than
95 the 'classical' layers of CLL1, probably representing the end of a preceding depositional cycle

96 (Alba et al., 2012a). The lower 'unit' of Begun et al. (1990), in turn, comprises variously colored
97 mudstones (mostly fine-grained clays) with abundant micromammal and some macromammal
98 remains (including the hominoid teeth recovered in 1981 and 2011), plus mollusk shells,
99 silicified figs, and other fragmentary and poorly preserved plant remains. The lower layers (1a
100 and 1b) are blackish and become lighter in color (light gray to greenish) toward the top (layer
101 2), although at different locations layers 1b and 2—the ones that yielded primate remains—are
102 completely light brown (Alba et al., 2012a; Marmi et al., 2012). The top layers (3a and 3b)
103 consist of greenish to yellowish clays with some coarser sediments, in which gastropod shells
104 are poorly preserved and vertebrate remains sparser than in the underlying layers. The upper
105 'unit' of Begun et al. (1990) begins with a paleochannel (layer 4a) of varying thickness
106 composed of much coarser sediments (with decreasing granulometry from bottom to top),
107 which at some point erodes some or all of the aforementioned layers and which locally yielded
108 more abundant large mammal remains. Overlying these channel deposits there is a thick (>2.5
109 m) sedimentary package (layer 4b/4p) of alternating green clays, greenish to orange silts, and
110 conglomerates, which locally preserve abundant plant macroremains (Marmi et al., 2012). A
111 fourth sedimentary body can be distinguished at the top of the CLL1 sequence, including a
112 paleochannel (layer 5a) that erodes layer 4b and an overlying 6.5 m-thick package (layer 5b) of
113 multiple episodes of ocher to red clays, silts, and conglomerates, indicative of paleosol
114 formation and well-aerated conditions (Marmi et al., 2012).

115 Pending more detailed analyses, and contrary to Begun et al.'s (1990) previous assessment,
116 the 2010–2015 fieldwork campaigns (author#15 unpublished data) failed to confirm differences
117 in faunal composition between the primate-bearing layers and the paleochannel deposits (other
118 than the apparent lack of primates in the latter). For example, suids are not restricted to the
119 primate-bearing layers (contra Begun et al., 1990) but also present in the paleochannel deposits
120 (layer 4a) and in the layer 4b that overlies them. Similarly, *Hippotherium* remains are more

121 abundant in layer 4a but are also present in most of the remaining layers, both above (4b) and
122 below (3b, 2, and 1b), thus including the primate-bearing ones. Finally, that forest-adapted taxa
123 are not restricted to the latter is best exemplified by the recovery of a *Tapirus* tooth from the
124 bottom of layer 4a (author#15 unpublished data). Coupled with the fact that detailed
125 stratigraphic provenance is not recorded for most of the remains recovered before 2010, this
126 makes impossible to conclusively ascertain whether CLL1 as a whole mixes faunal elements
127 from different environments due to differential transport among various fossiliferous layers.

128 On the other hand, different degrees of transport depending on the layer are confirmed by
129 available data. In particular, the presence of isolated teeth from two single individuals
130 (hominoid and cervid) scattered over a few square meters in one of the clay layers that yielded
131 primate remains suggests minimal transport, probably under water (Alba et al., 2012a). In
132 contrast, the paleochannel combines fragmentary and rounded remains of multiple large
133 mammals with better preserved and larger macromammal remains (including disarticulated
134 dentognathic and postcranial remains of a single *Hippotherium* individual; author#15,
135 unpublished data)—overall indicative of transport in higher energy conditions from longer
136 distances, than in the primate-bearing layers as previously concluded by Begun et al. (1990).
137 Finally, the plant remains from layer 4p (Marmi et al., 2012) are interpreted as a
138 parautochthonous assemblage accumulated by wind and short water transport in a shallow-water
139 epositional environment. All this preliminary taphonomic evidence combined suggests that the
140 fossil assemblages from CLL1 are representative of the fauna and flora present at and near the
141 depositional environment, although it cannot be discounted that some taxa preferentially
142 inhabited farther from it, as some fossiliferous layers evince greater degrees of transport than
143 others.

144 Chronological and paleoenvironmental background On biostratigraphic grounds, CLL1 is
145 correlated to the *Cricetulodon hartenbergeri*–*Progonomys hispanicus* interval local subzone,

146 while CLL2 is correlated to the *Cricetulodon sabadellensis* + *Progonomys hispanicus*
147 concurrent range local subzone (Casanovas-Vilar, 2016b). In turn, the Can Llobateres sequence
148 records three magnetozones, with reverse polarity in the lower and upper part, and normal
149 polarity in the middle (Agustí et al., 1996, 1997). In particular, CLL1 is correlated to C4Ar.3r
150 while CLL2 is correlated to C4Ar.2r (Agustí et al., 1996, 1997), with interpolated ages of 9.76
151 and 9.62 Ma, respectively (Casanovas-Vilar et al., 2016b). Based on the absence of
152 *Progonomys* from CLL1, it has traditionally been considered that the Can Llobateres sequence
153 records the early to the late Vallesian transition, with CLL1 and CLL2 being correlated to MN9
154 and MN10, respectively (Agustí et al., 1996, 1997; Alba et al., 2012a); indeed, CLL1 is
155 considered the reference locality for MN9 (Mein, 1990; de Bruijn et al., 1992; Casanovas-Vilar
156 et al., 2016b). However, *Progonomys* remains have been found in older sites from other Iberian
157 basins, placing the lower boundary of MN10 (as defined by the first common occurrence of this
158 genus) at 9.98 Ma (Hilgen et al., 2012; Van Dam et al., 2014). Accordingly, under a strictly
159 biostratigraphic approach to MN units, CLL1 must be correlated to MN10 instead of MN9
160 (Casanovas-Vilar et al., 2016b; Alba et al., 2018). It is unlikely that the paleobiodiversity of
161 CLL1 is inflated by time averaging, as most of the remains come from a short stratigraphic
162 interval of ~2 m (Alba et al., 2012a). Based on the average sedimentation rate for the Vallesian
163 of the Vallès-Penedès Basin (20 cm/kyr; Garcés et al., 1996) this would merely represent a time
164 interval of ~10 kyr—in rough agreement with the difference between the interpolated ages of
165 CLL1 and CLL2 (~140 kyr; Casanovas-Vilar et al., 2016b), which are separated by less than
166 20 m of stratigraphic distance.

167 Paleoenvironmental inferences have previously been drawn for CLL1 based on both
168 mammals and plants, using different methods—see summary in Table 1 and the Discussion for
169 additional details. The plant remains (Sanz de Siria Catalán, 1993, 1994; Álvarez Ramis, 1975;
170 Alba et al., 2011b; Marmi et al., 2012), which enable a reliable reconstruction of the

171 paleoenvironment where *H. laietanus* inhabited, are generally in agreement with the
172 conclusions drawn from the large and/or small mammals (Nagatoshi, 1987; Köhler, 1993;
173 Andrews, 1996; Hernández Fernández et al., 2003; Casanovas-Vilar and Agustí, 2007; Costeur,
174 2005), which indicate the presence of a humid and closed forest paleoenvironment at the
175 depositional area but further hint at the existence of relatively more open woodlands nearby
176 (Marmi et al., 2012). Some paleoenvironmental conclusions have also been derived for CLL1
177 from the numerical analyses of its mammalian assemblage composition (Andrews, 1996;
178 Hernández Fernández et al., 2003) and ecometrics in general have been applied to this site as
179 part of studies that aimed to reconstruct continental patterns of Neogene paleoprecipitation
180 (Fortelius et al., 2002; Eronen et al., 2009, 2010a; Kaya et al., 2018) or net primary production
181 (Toivonen et al., 2022). However, no dedicated ecometric approaches to paleoenvironment
182 reconstruction have been performed thus far. Given that *H. laietanus* is the latest hominoid
183 recorded from mainland Western Europe, the reconstruction of its paleoenvironment is highly
184 significant for understanding the local extinction of hominoids and other mammalian taxa in
185 Europe during the Late Miocene (Casanovas-Vilar et al., 2011).

186

187 *1.2. Ecometrics and functional crown types*

188 Ecometrics is a trait-based approach based on the study of functional morphological features
189 of organisms that attempts to quantify links between the distribution of those traits across biotic
190 communities and specific environmental factors as well as to analyze their dynamics through
191 space and time in the fossil record (Fortelius et al., 2002; Eronen et al., 2010b; Vermillion et
192 al., 2018). Ecometric traits are measurable macroscopic features that are known to represent
193 their function in relation to local environmental conditions (Eronen et al., 2010b)—either due
194 to adaptive reasons or to use/plasticity (ecophenotypic features). The most typical ecometric
195 traits of vertebrates describe dental morphology, limb proportions, and body mass. Candidate

196 traits for ecometric modeling must be at least preliminarily associated through their functional
197 relationship with the local environmental conditions, including the dominant temperature,
198 precipitation, or dominant vegetation type (Eronen et al., 2010b; Vermillion et al., 2018).
199 However, the exact associations are captured computationally when fitting statistical models to
200 link the traits of communities with their environmental conditions. Due to its functional
201 perspective, ecometrics has sometimes been referred to as a taxon-free approach, to highlight
202 that the ecology of fossil organisms is not inferred from that of their nearest living relatives and
203 that ecometric approaches neither rely on presence or absence of any individual taxa.
204 Theoretically, ecometric approaches can be completely taxon blind—e.g., analyzing random
205 samples of teeth that are found at localities without considering any taxonomic information.
206 However, in practice, for robustness and potentially larger samples, most ecometric studies,
207 including the present work, analyze the distribution of traits over species at localities,
208 sometimes on global datasets (e.g., Liu et al., 2012; Žliobaitė et al., 2018). Ecometrics, thus,
209 does not focus on individual organisms, but deals with the functional composition of
210 communities, thereby enabling comparisons between present and past communities. Of course,
211 there is no way to statistically test for predictions about the past (retrodictions), which makes it
212 necessary to use different approaches and see how they compare.

213 Because of its relatively fast and non-destructive sampling, dental ecometrics has been
214 particularly used to make large-scale inferences about paleoenvironmental and biotic changes
215 across different geographic and temporal scales, and different tailored global and regional
216 models have been developed for different types of analysis (Eronen et al., 2010b; Liu et al.,
217 2012; Fortelius et al., 2016; Žliobaitė et al., 2016; Oksanen et al., 2019). In this study, we aim
218 at predicting multiple climatic characteristics of CLL1, for which we use the dental trait scoring
219 scheme reported in Žliobaitė et al. (2016), termed functional crown types (FCT). This scheme
220 was devised to potentially increase the scope of environmental predictions particularly in the

221 Late Miocene and Plio-Pleistocene. The scheme is based on a modular system called crown
222 types (Jernvall, 1995), which was designed to be applicable to mammals generally, primarily
223 focusing on the shape of unworn teeth. The FCT scheme includes seven variables (Žliobaitė et
224 al., 2016; Galbrun et al., 2018). Ecometric approaches based on hypsodonty (HYP; relative
225 crown height) and loph count (Fortelius et al., 2002, 2016; Eronen et al., 2010a, 2010c; Liu et
226 al., 2012; Oksanen et al., 2019) have been used to estimate paleoprecipitation and productivity
227 in the Old World from the Miocene through the Pleistocene, as well as temperature in the
228 Pleistocene. However, the set of seven variables of the FCT scheme offers potential for
229 estimating a broader set of climatic conditions, including seasonality characteristics, among
230 others (Žliobaitė et al., 2016). Here we apply regional and global ecometric approaches based
231 on the FCT of herbivorous large mammals from CLL1 to refine the previous
232 paleoenvironmental inferences on the habitat of *H. laietanus*.

233

234 **2. Materials and methods**

235 *2.1. Studied material*

236 As in Žliobaitė et al. (2016), the study was restricted to herbivorous large mammals of the
237 orders Artiodactyla, Perissodactyla, Proboscidea, and Primates, and focused on M²s (see also
238 Galbrun et al., 2018). We scored at the species level. An updated faunal list of the mammals
239 recorded at CLL1, including 20 species of the aforementioned orders (Table 2), was compiled
240 based on the information available from the Vallès-Penedès Miocene Vertebrates –
241 Paleobiodiversity Database (Casanovas-Vilar et al., 2018; Alba et al., 2022a), which includes
242 specimen identification and provenance information for Miocene vertebrate remains from the
243 Vallès-Penedès Basin and is maintained by ICP researchers, not yet openly accessible. The
244 identification of multiple species was also revised in the course of this work by examining
245 original material housed in the ICP and comparing it with that from published sources.

246 Functional crown type variables were scored by visual inspection from M²s in all species of
247 large herbivorous mammals. Žliobaitė et al. (2016) scored these variables from M³s in the case
248 of Suidae, because in the studied species there was a great difference between M³ and M².
249 However, this was not necessary in the case of the Miocene suid species recorded at CLL1.
250 When the identification of a taxon was well-documented in the literature and M²s were
251 available from CLL1, we focused on this material to score the FCT variables. When any of
252 these conditions did not apply, other dental (or even postcranial) remains were studied to
253 confirm or refine the taxonomic identifications. When no M²s were available from CLL1 for a
254 particular taxon, FCT variables were based on those of the same species or higher taxonomic
255 ranks from elsewhere as reported in the literature.

256

257 *2.2. Ecometric analysis*

258 Functional crown types The FCT dental trait scoring scheme was designed to capture main
259 functional traits (durability, cutting, and other occlusal properties, as well as dental tissues) of
260 tooth shape and worn occlusal surfaces of herbivorous large mammal teeth, based on seven
261 (two ordinal and five binary) variables (Žliobaitė et al., 2016; Galbrun et al., 2018) that are
262 summarized in Table 3. The two ordinal variables, HYP and horizodonty (HOD; length of the
263 functional occlusal surface in terms of main cusp pairs) are related to tooth durability and have
264 three states each (Table 3). In turn, the binary variables record three additional functional
265 aspects, namely (Table 3): cutting structures (acute lophs [AL] and obtuse, or basin-like, lophs
266 [OL]); occlusion characteristics (structural fortification of cusps [SF] and occlusal topography
267 [OT]); and material properties (coronal cementum; CM). Based on data from extant
268 environments (national parks) from Kenya, these variables have been shown to be correlated
269 with environmental (climatic and ecological) parameters—such as precipitation (PREC),
270 temperature (TEMP), net primary productivity (NPP), and normalized difference vegetation

271 index (NDVI; i.e., the greenness of the vegetation)—thus being promising for making
272 paleoenvironmental inferences based on fossil data (Žliobaitė et al., 2016).

273 To retrodict the paleoenvironmental conditions of CLL1, we scored the seven FCT variables
274 for the herbivorous large mammal species present at this locality and, based on the average for
275 each variable, we followed the two different approaches described below. While FCT scoring
276 scheme has remained fixed over the years, scoring conventions of selenodonts have changed
277 from Oksanen et al. (2019) onward. For compatibility with the predictive models employed in
278 our first approach, here we use the scoring conventions as they were defined in Žliobaitė et al.
279 (2016), scoring all selenodonts with obtuse lophs and the Furchen of suids as fortified.

280 First approach Based on the seven FCT variables scored for 13 sites in Kenyan national parks,
281 Žliobaitė et al. (2016) derived predictive models for 23 environmental (climatic and ecological)
282 variables using least angle regression, which uses an iterative procedure to select the most
283 informative dental trait predictors (while avoiding redundancies). The resulting regression
284 models, to be used for predictive purposes, take the same functional form as ordinary linear
285 regression (a linear combination of input variables). In our first approach, we used the 23
286 regression models (based on three FCT variables each) reported by Žliobaitė et al. (2016: Table
287 2; see our Supplementary Online Material [SOM] Table S1) to estimate 23 paleoenvironmental
288 variables at CLL1. These regression models were not optimized for predictive purposes but
289 rather for comparability of information content in different seasonality indices using a constant
290 number of trait variables in each model. Yet, those models were tested for predictive accuracy
291 at present day, and in principle can be used for analysis of the fossil record.

292 An obvious limitation of this approach is that the regression models are regional, calibrated
293 on present day Kenya—no comparable models are available from elsewhere—which must not
294 necessarily be representative of past environments during the Iberian Miocene. On the other
295 hand, the geographically restricted nature of the dataset could also potentially result in a greater

296 optimization of the regression equations used to estimate the paleoenvironmental parameters.
297 In any event, we consider that the scope of the environments covered by the Kenyan localities
298 used to derived the models is compatible with a range of environments that can potentially be
299 expected at CLL1 and, thus, applicable to this fossil locality. Furthermore, precisely because of
300 the aforementioned limitation, we also followed an alternative approach that was not based on
301 such models but on the covariation between FCT variables and biomes in a much less
302 geographically restricted dataset (see next).

303 Second approach As an alternative approach, we used principal component analysis (PCA) and
304 canonical variate analysis (CVA) performed with R v. 4.1.1 (2021-08-10; R Core Team, 2021)
305 through Rstudio v. 2021.9.0.351 (Rstudio Team, 2021) to evaluate to what extent FCT variables
306 discriminate among different types of biomes and can be reliably used to make such inferences.

307 First, we used the Whittaker's system of present-day biomes to classify the 13 sites in Kenyan
308 national parks from Žliobaitė et al. (2016) based on their mean annual temperature (MAT) and
309 mean annual precipitation (MAP) into the different biomes of the world characterized according
310 to the distribution of vegetation types (Whittaker, 1975). We plotted them in the Whittaker
311 biomes diagram using the R packages ‘devtools’ v. 2.4.3 (Wickham et al., 2021), ‘plotbiomes’
312 v. 0.0.0.9001 (Stefan and Levin, 2022) and ‘ggplot2’ v. 3.3.5 (Wickham, 2016), and performed
313 a PCA with not normalized input variables (i.e., the average values for each FCT variable at
314 each locality) using the R packages ‘ade4’ v. 1.7.18 (Chessel et al., 2004; Dray and Dufour,
315 2007; Dray et al., 2007; Bougeard and Dray, 2018; Thioulouse et al., 2018), ‘factoextra’ v. 1.0.7
316 (Kassambara and Mundt, 2020), and ‘ggplot2’ v. 3.3.5 (Wickham, 2016).

317 Second, we also relied on a geographically much wider dataset of FCT variables to further
318 asses if they are useful to correctly classify extant localities according to Whittaker biomes
319 using a CVA based on FCT data. In particular, we used Galbrun et al.’s (2018) dataset (available
320 online at <https://github.com/zliobaite/teeth-redescription>), which contains data from 28,886

321 localities around the world on environmental variables, species composition, and FCT variables
322 for each species. We extracted the average of each FCT variable for those localities that,
323 according to the Whittaker diagram, correspond to certain biomes that, based on previous
324 literature (see Table 1), seem relevant to compare with CLL1 (temperate rainforest, temperate
325 seasonal forest, tropical rainforest, tropical seasonal forest/savanna, and woodland/shrubland).
326 The FCT variables mean hypsodonty and mean horisodonty were provided as three separate
327 binary variables each in Galbrun et al.'s (2018) dataset but were transformed back to ordinal
328 variables for this study. Once the localities were classified, we performed a cross-validated
329 CVA on the same data, using biomes to distinguish a priori groups, with the R packages
330 'Morpho' v. 2.9 (Schlager, 2017) and 'ggplot2' v. 3.3.5 (Wickham, 2016). To better evaluate
331 the structuration of the data and be able to discount spurious group separation, we computed
332 the amount of variance (r^2) explained by group differences in the raw data and the CVA (with
333 and without cross-validation) using a permutational multivariate analysis of variance (1000
334 pertumations) with the R package 'RRPP' v. 1.3.1. (Collyer and Adams, 2018, 2019).
335 Percentages of correct classification were computed based on the cross-validated CVA.

336 Finally, based on the CVA, CLL1 and the Kenyan localities were classified according to
337 Whittaker's biomes. The probability that each locality belongs to one of the biomes
338 distinguished a priori was evaluated based on the standard posterior probabilities of group
339 membership (which add up to 1 when all the biomes distinguished a priori are considered) as
340 well as the typicality probabilities (which test if a given locality falls outside the variation of
341 each biome independently). To evaluate the consistency of the results for CLL1, the biome
342 classification favored by the CVA posterior probabilities was compared with that obtained from
343 the estimates of paleotemperature and paleoprecipitation yielded by the regressions based on
344 FCT average values in our first approach. To further assess the reliability of the classification
345 provided by the CVA for CLL1, the classification for the nine Kenyan sites from Žliobaitė et

346 al. (2016) corresponding to the five relevant biomes included in the CVA was also compared
347 with that obtained from actual data on temperature and precipitation.

348

349 **3. Results**

350 Species identification An updated list of mammals from CLL1 is reported in Table 2. The
351 herbivorous large mammals included in FCT analyses include 20 species from 19 genera and
352 13 families, while the complete mammal list includes 78 species (39 small and 39 large
353 mammals). While a few small mammal species are added here, the number of large mammal
354 species from CLL1 (39) reported in Table 2 is lower than the figure of 47 species reported by
355 Alba et al. (2011a), and even the figure of 41 currently recognized by the NOW database (The
356 NOW Community, 2023). All these changes are not attributable recovery of new taxa during
357 the new campaigns since 2010, but rather to the ongoing revision of the collections recovered
358 in previous decades.

359 With regard to micromammals, the most updated list of eulipotyphlans from CLL1 is
360 probably that reported by van den Hoek Ostende and Furió (2005). The current list differs in
361 the following regards: (1) the erinaceid previously attributed to *Postpalerinaceus vireti* by
362 Crusafont Pairó and Gibert Clols (1974) is considered to represent a different species
363 (tentatively referred to cf. *Postpalerinaceus* sp.); (2) besides *Talpa vallesiensis*, two additional
364 talpids (*Desmanella* sp. and *Talpa* sp.) are recorded; (3) heterosoricid present at the site is
365 *Dinosorex grycivensis* instead of *Dinosorex sansaniensis* (see Furió et al., 2015); (4) an
366 additional dimylid (*Metacordylodon schlosseri*) and three additional soricids (*Miosorex*
367 *grivensis*, *Lartetium* sp., and *Paenelimnoecus* sp.) are identified. An indeterminate chiropteran
368 and a single lagomorph (contra Alba et al., 2011a) are also identified at CLL1. As for the
369 rodents, the list is taken from Casanovas-Vilar et al. (2016b), and only the genus ascription of
370 *Csakvaromys bredai* has been updated following Sinitisa et al. (2022).

371 Regarding the macromammals from CLL1 not included in the FCT computations, the
372 hyracoid is assigned to *Pliohyrax rossignoli* following Pickford et al. (1997)—although more
373 detailed comparisons of the scarce material available would be required to confirm such an
374 attribution—while most changes correspond to carnivorans. The list of the latter is based on the
375 review by Robles et al. (2014), with several subsequent updates: (1) no material of *Promephitis*
376 *pristinidens* has been identified, and it is thus considered that previous citations of this genus
377 from CLL1 correspond to *Mesomephitis medius*; (2) *Hoplictis petteri* is considered a junior
378 subjective synonym of *Eomellivora fricki* following Valenciano et al. (2019); (3) a single
379 hyaenid (*Protictitherium crassum*) is recognized from CLL1; (4) the two amphicyonids from
380 the site, currently under study, are provisionally attributed to *Amphicyon* sp. and *Ammitocyon*
381 sp.; (5) three ursids are recorded, but instead of two *Ursavus* species, only *Ursavus brevirhinus*
382 is present at the site, with scarce dental material being attributable instead to *Miomaci* sp.—an
383 indarctin ursid genus present at Rudabánya and Can Poncic (de Bonis et al., 2017). The
384 remaining large mammals are those included in the FCT analyses and hence discussed in greater
385 detail in the following paragraphs.

386 Two proboscidean species are recorded, a deinotherid and a gomphotherid. The deinotheriid
387 remains from CLL1 were described by Bergounioux and Crouzel (1962), who attributed them
388 to *Deinotherium giganteum*, which is currently considered the only deinotheriid species present
389 in MN9 of Europe (e.g., Pickford and Pourabrishami, 2013; Alba et al., 2020). The
390 gomphotheriid remains were described by Mazo (1977), who attributed them *Tetralophodon*
391 *longirostris*, which replaced *Gomphotherium angustidens* in late MN7+8 (Mazo and Van der
392 Made, 2012).

393 Perissodactyls are represented at CLL1 by six species (a chalicotherid, a horse, three
394 rhinoceroses, and a tapir). The chalicotheriid remains are unpublished but were reported as
395 *Chalicotherium grande* (currently *Anisodon grande*) by Mein (1990), being later reassigned to

396 *Chalicotherium goldfussi* by Heissig (1999). The latter assignment is confirmed here based on
397 the position of the M¹ and M² metacones (see Anquetin et al., 2007), in further agreement with
398 the MN9 age of the site (the two species only overlap in late MN7+8; Anquetin et al., 2007).
399 The equid remains were described by Alberdi (1974), being attributed to *Hipparion*
400 *primigenium primigenium*. Following Bernor et al. (1980, 1996, 2021), these remains could be
401 assigned to a distinct species endemic of the Vallès-Penedès Basin (*Hippotherium*
402 *catalaunicum*). However, a long needed revision of the Vallès-Penedès *Hippotherium* remains
403 has been undertaken by some of the authors of this paper and, on this basis, we prefer to
404 tentatively assign the CLL1 remains to *Hippotherium* cf. *primigenium*. This is because
405 differences with the vast sample of this species from Höwenegg (Bernor et al., 1997, 2022), at
406 present time, do not seem to warrant a species distinction. The rhinocerotid remains from CLL1,
407 in turn, were described by Santafé Llopis (1978), being attributed to four species, whose genus
408 attribution has been updated based on Sanisidro and Cantalapiedra (2022). Although these
409 authors reported four species from CLL1, we refrained from including *Lartetotherium*
410 *sansaniense*, whose identification by Santafé Llopis (1978), which relies on a single damaged
411 scaphoid, is doubtful. A preliminary revision of the remains from the other rhinocerotid species
412 by one of the authors of this paper further indicates that more in-depth revision is required. On
413 the one hand, the species attribution of the *Dihoplus* remains must be considered tentative,
414 because they show some dental differences as compared with *Dihoplus schleiermacheri* from
415 Central Europe. For the same reason, the identification of *Aceratherium incisivum* is even more
416 tentative and the remains might even belong to a different genus, as they display some dental
417 features that fall outside the normal variation of the genus as recorded in Central Europe. Finally,
418 the tapirid remains were described by Golpe-Posse and Crusafont-Pairó (1982), who attributed
419 them to *Tapirus priscus*, an attribution that is confirmed here.

420 Artiodactyls are more diverse than perissodactyls, being represented at CLL1 by 11 species
421 (four suids, a tragulid, a moschid, two bovids, two cervids, and a giraffid), although only the
422 suid *Parachleuastochoerus crusafonti*, the bovid *Miotragocerus pannoniae*, and at least one of
423 the cervids are common faunal elements. The suid remains were described by Golpe-Posse
424 (1971, 1972), who recognized four different species: *Listriodon splendens*, *Pa. crusafonti*,
425 *Hyotherium soemmeringi*, and ?*Hyotherium* sp. Pickford (1981, 2014) provided additional
426 descriptions of the *Pa. crusafonti* sample from CLL1, which is the type locality of the species.
427 The identification of *L. splendens* at CLL1 by Golpe-Posse (1971, 1972) was based on two
428 teeth, a purported molar and a premolar, the latter being assigned by the same author to
429 ?*Hyotherium* sp. The revision of the material indicates that the former belongs in fact to *T.*
430 *priscus* and the latter to *Pa. crusafonti*. However, two infantile specimens reported by Van der
431 Made (1996) and a few additional unpublished deciduous teeth confirms the presence of *L.*
432 *splendens* at CLL1, representing the last well-dated occurrence of the genus in Europe (Van der
433 Made et al., 2022). The larger-bodied tetraconodontine from CLL1 identified by Golpe-Posse
434 (1971, 1972) as *Hy. soemmeringi* was later reassigned to *Conohyus steinheimensis* by Van der
435 Made (1990). The species was later included in *Parachleuastochoerus steinheimensis* and,
436 more recently, split into *Versoporcus steinheimensis* and *Versoporcus grivensis* by Pickford
437 (2014, 2016). However, the revision of the single premolar attributed by Golpe-Posse (1971,
438 1972) to *Hy. soemmeringi* indicates that, together with an incisor, it belongs to the larger
439 tetraconodontine referred by Pickford (2014, 2016) to *Parachleuastochoerus valentini* (see also
440 McKenzie et al., 2023). The presence of a suine at CLL1 was first reported by de Bruijn et al.
441 (1992) as *Korynochoerus palaeochoerus* (currently *Propotamochoerus palaeochoerus*; e.g.,
442 Van der Made et al., 1999; McKenzie et al., 2023), apparently based on unpublished material
443 not yet available to Golpe-Posse (1971, 1972). The revision of the suid remains from CLL1
444 unambiguously confirms the presence of the species based on diagnostic dentognathic material.

445 The tragulid remains from CLL1, originally reported as *Dorcatherium* sp. (Crusafont Pairó,
446 1958), were subsequently identified as *Dorcatherium nawi* by Moyà-Solà (1979; see also Alba
447 et al., 2011c). The material is scanty and consists of a few tarsal bones and an upper canine.
448 The even scarcer moschid remains from CLL1 are unpublished, but referable to *Micromeryx*
449 aff. *flourensianus* based on their small size and some details of occlusal morphology, probably
450 belonging to a different and as yet undescribed species. The bovid remains from CLL1 were
451 described by Moyà-Solà (1983), being attributed to *Protragocerus* aff. *chantrei* and
452 *Miotragocerus* aff. *pannoniae*, but we concur with previous authors (e.g., Alba et al., 2011a)
453 that open nomenclature (aff.) is unnecessary for these attributions, which are not tentative. The
454 cervid remains from CLL1 have not been described in detail but were assigned to *Amphiprox*
455 *anocerus* by Azanza and Menéndez (1990). Our review of the abundant material available from
456 CLL1 indicates that dental variation would be compatible with the presence of a single species.
457 However, the variation displayed by the antler material strongly suggests the presence of a
458 second species, whose taxonomic identity cannot be clarified at the moment—although an
459 assignment to *Euprox dicranoceros*, present in earlier Vallesian sites (Azanza and Menéndez,
460 1990), seems unlikely. The giraffid remains from CLL1 were described by Crusafont Pairó
461 (1952), who assigned them to *Palaeotragus* sp. However, they are here merely referred to
462 Giraffidae indet. because the available material merely consists of a few isolated postcranial
463 elements that do not allow for a species or genus attribution, particularly taking into account
464 the taxonomic uncertainties about the MN9 giraffids from the Vallès-Penedès Basin (Alba et
465 al., 2022b).

466 Finally, as explained in greater detail in the Introduction, the hominid remains from CLL1
467 were first reported by Crusafont-Pairó (1958). The material currently available was described
468 in detail by Begun et al. (1990), Golpe-Posse (1993), and Alba et al. (2012a). Although
469 Crusafont Pairó and Hürzeler (1961, 1969) and subsequently Golpe-Posse (1993) recognized

470 the presence of various species, currently the whole sample is attributed to *Hispanopithecus*
471 *laietanus* (Alba, 2012; Alba et al., 2012a)—although, based on enamel–dentine shape, the
472 presence of a second hominoid species at CLL1 cannot be entirely ruled out (Zanolli et al.,
473 2023).

474 Paleoenvironmental estimates based on the first approach The values for the FCT variables for
475 the investigated species recorded at CLL1 are reported in Table 4, while the 23 estimated
476 environmental variables for this site are reported in Table 5. Most noteworthy are the estimated
477 values of paleotemperature (MAT = 25 °C) and paleoprecipitation (MAP = 881 mm), which
478 indicate a Whittaker’s biome of tropical seasonal forest/savanna for CLL1 (Fig. 2).

479 Paleoenvironmental estimates based on the second approach The first two principal
480 components of a PCA based on FCT variables for 13 extant localities from Kenyan national
481 parks (Fig. 3) summarize more than 75% of the variance. The first principal component (56%
482 of the variance) is mostly driven by SF and AL toward negative scores, and the remaining FCT
483 variables toward positive scores. The site of CLL1 displays very high scores along this axis,
484 most similar to the extant localities of Shimba Hills (tropical seasonal forest/savanna) as well
485 as Elgon and Kakamega (temperate seasonal forests). Along PC1, these three extant localities
486 fall far from the rest of extant localities, which cluster close to one another despite
487 corresponding to the four different biomes included in the analysis. The second principal
488 component (21% of the variance) is mostly driven by SF (and, to a lesser extent, CM and HYP)
489 toward negative scores, and by AL (and, to a much lesser extent, OT and OL) toward positive
490 scores. Extant Kenyan localities corresponding to the temperate seasonal forest and
491 woodland/shrubland biomes tend to display lower PC2 scores than those representing the
492 tropical seasonal forest/savanna and subtropical desert biomes. The site of CLL1 displays an
493 extremely positive score along this axis, well beyond any of the extant localities, suggesting
494 relevant environmental differences even compared with the closest extant localities in PC1.

495 The CVA based on 18,671 extant localities from five different biomes accounts for 33.7%
496 of the differences among the groups, which are significant at $p < 0.001$, both with and without
497 cross-validation. Differences among the groups are also significant ($p < 0.001$) based on the
498 raw data—indicating that grouping structure is not spurious—although they explain a lower
499 amount of variance (13.9%). The cross-validated CVA has a low classification accuracy (49.5%
500 after cross validation; Table 6) because there is a considerable overlap among several biomes
501 (Fig. 4). The first canonical variate summarizes most of the variance (96%), being mostly
502 determined by OL and, to a lesser extent, CM toward positive scores, and in decreasing order
503 of importance, HOD, AL, and HYP toward negative scores. The analysis discriminates well
504 between woodland/shrubland and tropical rainforest localities, and also quite well between the
505 former and tropical seasonal forest/savanna localities (only with slight overlap of their 95%
506 confidence ellipses). However, there is considerable overlap among these and other biomes,
507 with the ellipse of the tropical rainforest biome being totally included within those of both the
508 temperate rainforest and the tropical seasonal forest/savanna biomes, and further partly
509 overlapping with that of the temperate seasonal forest biome. The second canonical variate is
510 positively driven by most of the variables to some extent, except OL (which has no influence)
511 and AL (which has a moderate influence toward negative scores). Given the small amount of
512 variance summarized by CV2 (3.5%), it is questionable whether it needs to be interpreted, as
513 further confirmed by the fact that all the five investigated biomes overlap along this axis.
514 However, it is noteworthy that the tropical rainforest biome shows a lower range of variation
515 than the remaining ones, with all the localities included displaying negative scores for both CV1
516 and CV2. The locality of CLL1 also displays moderately negative scores for both axes, falling
517 within the overlap zone among the ellipses of tropical seasonal forest/savanna, temperate
518 rainforest, and tropical rainforest, and at the fringe of temperate seasonal forest.

519 However, based on the posterior probabilities (Table 7)—which hold assuming that the
520 distribution of possible climatic conditions in the past is similar to that of the reference dataset
521 of the present day—CLL1 is classified as a tropical rainforest as a first option (63%) and as a
522 tropical seasonal forest/savanna as second option (30%). The typicality probabilities (Table 7)
523 are consistent with such classifications and confirm that, based on FCT variables, CLL1
524 significantly differs from all the remaining biomes at least with $p < 0.05$. The second
525 classification option for CLL1 (tropical seasonal forest/savanna) according to the CVA based
526 on FCT variables coincides with the biome attribution of our first approach—i.e., based on
527 estimated paleotemperature and paleoprecipitation using Žliobaitė et al.’s (2016) regressions.
528 Estimates of paleotemperature and paleoprecipitation are based on different sets of variables
529 (OL, SF, and OT vs. HOD, SF, and OT, respectively) than those that have greater loadings on
530 CV1 (OL, HOD and, to a lesser extent, AL and HYP), so it is not surprising that the
531 classification results yielded by these two different approaches do not completely match.
532 However, it is remarkable that the second classification option obtained from the CVA, with a
533 lower posterior probability (30%), does coincide with the biome classification obtained from
534 paleotemperature and paleoprecipitation estimates based on FCT variables. The biome
535 classification results for the extant Kenyan localities based on the CVA only coincide with
536 those based on actual data of temperature and precipitation in five out of nine cases (Table 8),
537 which is not surprising given the classification accuracy of the analysis around 50%. The
538 mismatches correspond to localities from the temperate seasonal forest biome that are
539 erroneously classified by the CVA as tropical seasonal forest/savanna, whereas the four
540 localities actually corresponding to tropical seasonal forest/savanna are (like CLL1) correctly
541 classified as such. It must be taken into account, however, that none of the localities from
542 Kenyan national parks correspond to the tropical rainforest biome. The percentages of correctly
543 classified cases for the 18,671 localities included in the CVA (Table 6) indicate that localities

544 from the tropical seasonal forest/savanna biome are frequently erroneously classified as tropical
545 rainforest (indeed, which the same frequency as the former are correctly classified, 42%),
546 whereas tropical rainforest localities are most frequently correctly classified as such (82% of
547 the cases) and misclassified as tropical rainforest/savanna with a low frequency (9%).

548

549 **4. Discussion**

550 Environmental estimates and biome classification based on functional crown type variables The

551 23 prediction equations for environmental variables reported by Žliobaitė et al. (2016) vary in
552 both accuracy (r^2 , measuring the goodness of fit) and predictive power (r^{2*} , as measured by
553 cross-validation). The former values vary from ~ 0.6 – 0.8 in the most reliable variables to less
554 than 0.3 in the least ones, resulting in highly divergent equations in terms of predictive power.

555 While these models were not optimized to maximize the predictive accuracy, the calibration
556 accuracy is reasonable for trying them for predictive purposes on the fossil record. Probably,
557 more accurate equations could be derived in the future based on a higher number of extant
558 localities, as they would increase statistical power. In the meantime, the paleoenvironmental
559 estimates derived from these equations for CLL1 should be taken with care as rough
560 approximations whose reliability depends on the accuracy of the equations used to derive them.

561 In other words, these estimates should not be taken at face value, because the model calibration
562 accuracy (or goodness of fit, r^2) and, especially, the predictive power of these equations
563 (calibration accuracy as measured by cross-validation, r^{2*}) are quite low and there is no
564 guarantee that the Kenyan extant localities used to derive the models are representative of
565 European environments during the Miocene. Nevertheless, the estimated parameters could be
566 useful in relative terms to compare CLL1 with other well-sampled fossil localities of the Vallès-
567 Penedès Basin in the future.

568 For the purposes of this work, estimates of paleotemperature (especially MAT) and
569 paleoprecipitation (MAP) will be mainly discussed here. Neither MAT nor MAP estimates
570 appear particularly accurate, with $r^2 = 0.57$ and 0.68 , and $r^{2*} = -0.05$ and 0.38 , respectively.
571 Based on the equations' accuracy, the paleoprecipitation estimate would be a priori more
572 reliable, but this is uncertain because Žliobaitė et al. (2016) provided no method for computing
573 the confidence intervals of such estimates. In any event, the biome classification based on the
574 paleotemperature (MAT) and paleoprecipitation (MAP) estimates for CLL1 should be
575 contrasted with other independent sources of evidence, such as those derived from stable
576 isotope composition of mammalian tooth enamel (e.g., Koch, 1998; Kohn et al., 1998; Domingo
577 et al., 2013; Higgins, 2018). These analyses are currently underway, but only preliminary
578 results have been published so far (see below for further details). In the meantime, an alternative
579 approach based on a multivariate analysis of FCT average values was undertaken to contrast
580 the biome classification for CLL1 with that discussed above based on the regression equations.

581 Based on the estimated values for paleotemperature ($25\text{ }^{\circ}\text{C}$) and paleoprecipitation (881
582 mm), CLL1 would correspond to a tropical seasonal forest/savanna according to Whittaker's
583 biome scheme. The biome classification based on the CVA is not entirely coincident, as CLL1
584 is classified as a tropical rainforest with a posterior probability of 63%. Such a discrepancy is
585 not surprising, as the CVA is based on the seven FCT variables, whereas the paleotemperature
586 and paleoprecipitation estimates are calculated from different subsets of three variables each,
587 overall including only four out of the seven FCT variables. Furthermore, the classification
588 accuracy of the CVA is moderately low (49.5%). Given all these caveats, it is remarkable that
589 the biome classification based on paleoenvironmental estimates (tropical seasonal
590 forest/savanna) coincides with the second most likely classification of the CVA, with a
591 posterior probability of 30%. From a purely statistical viewpoint, CLL1 falls in an area of the
592 ecomorphospace where the 95% confidence ellipses of both biomes overlap, with the tropical

593 rainforest biome displaying a much more restricted scatter than tropical seasonal
594 forest/savanna. Moreover, extant localities from the tropical seasonal forest/savanna biome are
595 as frequently misclassified as tropical rainforest as correctly classified (42% in both cases),
596 whereas tropical rainforest localities are most frequently classified correctly and only seldom
597 misclassified as tropical seasonal forest/savanna. Therefore, it seems logical to conclude that
598 CLL1 most likely belongs to the tropical seasonal forest/savanna biome. Alternatively, CLL1
599 might belong to a tropical rainforest biome, which differs from the tropical seasonal
600 forest/savanna biome by displaying much higher precipitation values. This would imply that
601 the annual precipitation estimate derived for CLL1 largely underestimates the actual value,
602 which must be more than twice the estimate (>2500 mm instead of 881 mm at 25 °C, based on
603 Whittaker's scheme). This seems unlikely even if paleotemperature is overestimated, but not
604 completely impossible, given the low accuracy of the paleoprecipitation regression equation. A
605 third possible explanation, not mutually exclusive with the first one, is that CLL1 records a
606 mosaic of habitats that, despite falling within the tropical seasonal forest/savanna biome,
607 mimics the faunal composition that would be expected in a tropical rainforest habitat—owing
608 to local paleoenvironmental conditions favoring the presence of taxa adapted to more humid
609 environments. These possibilities are evaluated in the next subsection based on the fossil flora
610 and fauna from CLL1, as well as in relation to preliminary data on tooth enamel isotopic data.

611 Whittaker's biome classification is one of the simplest schemes to distinguish terrestrial
612 biomes as it only considers MAT and MAP. While the scheme is calibrated on the present day
613 and, in all probability, does not identically apply to the deep past, to a first approximation it can
614 be applied to the Miocene. Other biome classification systems, such as Walter (1979), consider
615 seasonality in both temperature and precipitation. Since the methods used allow inferring which
616 are the coldest/warmest and wettest/driest months in the studied localities these biome
617 classification schemes can be considered as well. MAT is above 20 °C, which indicates a

618 tropical climate (according to Köppen-Geiger climate classification; see Peel et al., 2007) with
619 little temperature seasonality since it ranges from 24.4 °C in the coldest month to 26.7 °C in the
620 warmest. MAP is also high (881 mm) for a tropical environment such as savanna or desert with
621 average monthly precipitation always above 100 mm. However, inferred rainfall seasonality is
622 remarkable, with precipitation in the wettest month (2119 mm) being more than 10 times higher
623 than that recorded during the driest month (136 mm). Such precipitation seasonality is
624 consistent with a tropical seasonal biome, with a clear rainy season. Nonetheless, there is a
625 gradient between evergreen tropical forests and tropical deciduous forests depending on the
626 length and severity of the dry season, with tropical seasonal forests (also called semievergreen
627 or mixed tropical forests), corresponding to zonoecotone I/II of Walter (1979), showing an
628 intermediate composition, characterized by the presence of some deciduous tree species that
629 lose their leaves during the dry season. Vegetation structure in tropical seasonal forests includes
630 different canopy layers as in rainforests, but generally stratification is less complex, the canopy
631 is relatively more open, epiphytes and especially lianas are abundant, and ground vegetation is
632 more diverse and abundant (see Walter, 1979; Allaby, 2006). In a tropical seasonal biome, the
633 driest month typically records less than 60 mm of rainfall, which is much lower than the values
634 inferred for CLL1, suggesting that the latter might have been characterized by a tropical
635 seasonal forest somewhat intermediate between a tropical evergreen and a tropical deciduous
636 forest.

637 Comparison with previous paleoenvironmental inferences for Can Llobateres 1 The summary
638 of previous paleoenvironmental inferences for CLL1 provided in Table 1 highlights some
639 similar conclusions among authors but also some discrepancies regarding the openness of the
640 habitat and the seasonality of the climate. Nagatoshi (1987) concluded that most of the primate-
641 bearing sites of the Middle and Late Miocene of western Eurasia were characterized by the
642 presence of water and interpreted CLL1 as an open environment with some intruding marshy

643 areas based on the presence of *Hippotherium* and *Tapirus*. However, the paleobotanical
644 evidence is rather suggestive of a closed forest next to a marshy area with more open
645 environments at some distance (Fig. 5; Marmi et al., 2012). The fossil plant assemblage from
646 CLL1 (Álvarez Ramis, 1975; Sanz de Siria Catalán, 1993, 1994; Marmi et al., 2012) is
647 composed of abundant reed remains (*Phragmites* and *Typha*), coupled with palms, evergreen
648 laurels, and fig trees (*Ficus* sp.). The reeds are suggestive of a marshy area, whereas the rest of
649 the vegetation denotes the nearby presence of a dense wetland or riparian forest (Alba et al.,
650 2011a, 2011b; Marmi et al., 2012; Andrews, 2015). In turn, the presence of mega-mesothermal
651 taxa and the absence of deciduous taxa indicate a subtropical to warm-temperate climate
652 characterized by high mean annual temperatures (Marmi et al., 2012). Sanz de Siria Catalán
653 (1994) inferred subtropical conditions based on the then available flora from CLL1. Although
654 such inferences must be taken with care, given that CLL1 corresponds to an azonal plant
655 community, they are consistent with the estimated MAT of 26 °C derived in this work from
656 FCT variables. According to the Köppen-Geiger climate classification (updated by Peel et al.,
657 2007), a tropical climate is characterized by average temperatures above 18 °C in the coldest
658 month, whereas a subtropical (or temperate) climate displays average temperatures above 10
659 °C in the hottest month and between 0 and 18 °C in the coldest month. Therefore, the
660 paleotemperature estimates for CLL1 based on FCT variables for the hottest month (26.7 °C)
661 and the coldest month (24.4 °C) indicate a tropical climate, consistent with the two biome
662 attributions favored by the multivariate analyses. On the other hand, paleobotanical evidence
663 from other localities and nearby basins suggests that the plant community from CLL1 would
664 not be representative of the zonal vegetation, which would have been characterized by a higher
665 proportion of mega-mesothermal taxa and deciduous elements, overall denoting subtropical to
666 warm-temperate (rather than tropical) climate conditions in the Vallès-Penedès Basin around
667 the transition between the early and late Vallesian (Marmi et al., 2012, and references therein).

668 It is thus reasonable to assume that, far from the wetlands, more open woodlands would have
669 been present by this time (Alba et al., 2011a, 2011b; Marmi et al., 2012), and that
670 paleotemperature estimates for CLL1 based on FCT variables might be biased to some extent
671 toward higher temperatures than were actually present in the area by that time.

672 As stressed by Marmi et al. (2012) and Andrews (2015), the faunal composition of CLL1
673 further supports the presence of a marshy depositional environment, given the presence of
674 beavers and otters (Marmi et al., 2012; Andrews, 2015), the bovid *M. pannoniae* (which
675 displays adaptations to wet environments; Köhler, 1993), and the tragulid *D. nauii* (which shows
676 many similarities with the extant water chevrotian, a forest-dwelling frugivorous animal with
677 aquaphilous preferences; Alba et al., 2011c, and references therein). The presence of large
678 browsing herbivores (*C. goldfussi*, *M. aff. flourensianus*, *A. anocerus*, *T. priscus*, *Aceratherium*
679 *incisivum*, and *Alicornops simorreense*), in turn, is indicative of a densely forested environment
680 (Marmi et al., 2012), which is further supported by a diverse assemblage of flying squirrels and
681 tree dormice, which are quite diverse albeit not particularly abundant (Casanovas-Vilar and
682 Agustí, 2007; Marmi et al., 2012; Casanovas-Vilar et al., 2015). Flying squirrels are remarkably
683 diverse, including up to five different species representing both large (*Miopetaurista crusafonti*,
684 *Miopetaurista neogrivensis*, *Albanensia* aff. *grimmi*) and small (*Blackia miocaenica*, cf.
685 *Plioperaturista* sp.) species. Such diversity of flying squirrels is currently only recorded in the
686 tropical and subtropical forests of southeastern Asia, which show a complex and stratified
687 canopy (Jackson 2012, Lu et al. 2013). This is further consistent with the presence of a large-
688 bodied ape such as *H. laietanus*, particularly given the previous locomotor inferences based on
689 its partial skeleton, indicating that it possessed an orthograde body plan with suspensory
690 adaptations, even if displaying a higher degree of above-branch quadrupedalism than extant
691 apes (Moyà-Solà and Köhler, 1996; Almécija et al., 2007; Alba et al., 2010, 2012b; Pina et al.,
692 2012; Tallman et al., 2013; Susanna et al., 2014). On the other hand, the presence of a giraffid

693 (Köhler, 1993) and rodents such as the cricetid *Hispanomys* and ground squirrels (Casanovas-
694 Vilar and Agustí, 2007) hint at the presence of more open woodlands nearby (Marmi et al.,
695 2012).

696 Unlike other artiodactyls, suids have not been previously considered when making
697 paleoenvironmental inferences for CLL1, even though they can provide interesting insights. The
698 taxonomic revision of the large herbivorous mammals from CLL1 performed in this work has
699 confirmed the presence of a diverse suid assemblage, clearly dominated by the small
700 tetraconodontine *Pa. crusafonti*, but further including (in order of decreasing abundance) *P.*
701 *palaeochoerus*, *L. splendens*, and *Pa. valentini*. The dietary ecology of *L. splendens* has been
702 thoroughly discussed, as these suids stand out by its lophodont morphology and the lack of
703 adaptations for the rooting feeding behaviors characteristic of most suids (Fortelius et al.,
704 1996a; Van der Made et al., 2014, 2022), allowing them to survive when other types of food
705 are scarce. The occlusal morphology of *L. splendens* was originally interpreted as an adaptation
706 for a mainly folivorous diet (Van der Made, 1996) and microwear analyses supported that this
707 species was mainly a browser (Hunter and Fortelius, 1994). This has been confirmed by isotopic
708 analyses, which further suggest a considerable consumption of fruits and maybe some grass
709 (Aiglstorfer et al., 2014). Van der Made et al. (2014) hypothesized that *L. splendens* would have
710 inhabited relatively open or mosaic environments, but most recently Van der Made et al. (2022)
711 favored the view that, given the lack of rooting adaptations, *Listriodon* would have been more
712 limited than other suids to environments where nutritious leaves and fruits were available
713 throughout the year. Based on dental morphology, it has been inferred that *P. palaeochoerus*
714 would have been even better adapted for rooting behaviors than medium to large-sized
715 tetraconodontines of the genera *Parachleuastochoerus* and *Versoporcus* (Van der Made, 2010;
716 Van der Made et al., 2014). However, isotopic data indicate that these tetraconodontines also
717 consumed underground resources (Aiglstorfer et al., 2014), and indeed isotopic data and trace

718 elements from Rudabánya (Hungary)—a hominoid-bearing site roughly coeval to CLL1—
719 indicate that tetraconodontines might have feed on such resources more frequently than
720 *Propotamochoerus* (Eastham et al., 2016, 2017; Iannucci and Begun, 2022). This suggests a
721 more varied omnivorous diet for *Propotamochoerus*, in agreement with the greater
722 development of secondary cusps typical of suines (Fortelius et al., 1996a).

723 These dietary inferences for suids recorded at CLL1 are relevant for interpreting the
724 extinction of *H. laietanus* because some parallelism can be established with the diet of *H.*
725 *laietanus* and also because the extinction of *L. splendens* has been related to the
726 paleoenvironmental changes during the early/late Vallesian transition, which are generally
727 considered the trigger of the Vallesian Crisis (Van der Made et al., 2022). The latter is a regional
728 turnover event, originally identified in the Vallès-Penedès Basin, that allegedly implied the
729 extinction of mammals adapted to warm and humid forested environments and their
730 replacement by taxa adapted to more open and drier environments (Agustí and Moyà-Solà,
731 1990; Moyà-Solà and Agustí, 1990). The extension of the Vallesian Crisis to a continental scale
732 (e.g., Fortelius et al., 1996b; Agustí et al., 1999) has been questioned (Casanovas-Vilar et al.,
733 2005, 2010), being alternatively attributable to sampling biases (Casanovas-Vilar et al., 2014,
734 2016a). This has been conclusively shown based on micromammals from the Vallès-Penedès
735 Basin (Casanovas-Vilar et al., 2014), where the correction of such biases indicates that the
736 purported Vallesian Crisis was a protracted faunal turnover rather than an abrupt extinction
737 event. Although this remains to be ascertained for large mammals, it has been convincingly
738 argued that changes in vegetation structure led to the extinction of multiple forest-adapted
739 frugivorous taxa, particularly primates (Agustí et al., 2003; Marmi et al., 2012; Casanovas-
740 Vilar et al., 2016a) and some suids (Van der Made et al., 2022).

741 Dental microwear analyses indicate that *H. laietanus* displayed a frugivorous diet (Ungar,
742 1996; DeMiguel et al., 2014), probably emphasizing soft ripe fruits but also including hard

743 fruits as fallback fruits on a seasonal basis (DeMiguel et al., 2014). This would have allowed
744 this species to survive in the face of marked environmental instability around the early/late
745 Vallesian transition. This is supported by the presence of abundant enamel hypoplasias (Skinner
746 et al., 1995; Eastham et al., 2009), which indicate repeated episodes of malnutrition due to
747 seasonal resource abundance fluctuations, suggesting that *H. laietanus* probably feed on hard
748 foods during the unfavorable season (DeMiguel et al., 2014). Although there are no
749 paleodietary data for *Pa. crusafonti*, small suids are generally interpreted as forest-adapted
750 forms (Fortelius et al., 1996a), in agreement with the abundance in this taxon at CLL1. This
751 suggests that *Pa. crusafonti* might have displayed on the ground a similar feeding strategy to
752 that of *H. laietanus* in an arboreal niche, i.e., predominantly based on fruits and recouring to
753 other resources during the most unfavorable months of the year (maybe thanks to rooting
754 behaviors). The moderately abundant *P. palaeochoerus*, like the scarce *Pa. valentini*, could
755 have exploited other trophic resources and preferentially inhabited the more open areas far from
756 the wetland. In contrast, this explanation is more unclear in the case of *L. splendens*, whose
757 scarcity at CLL1 might be related to the lack of a continuous fruit supply during the unfavorable
758 season, given its lack of rooting adaptations.

759 With regard to the biome classification of CLL1 as a tropical rainforest or a tropical seasonal
760 forest/savanna biome, the analyses of mammalian community structure performed by Andrews
761 (1996) using different methods reconstructed both CLL1 and Rudabánya as subtropical
762 seasonal forests, thus supporting a classification of the former as a tropical seasonal forest rather
763 than as a tropical rainforest (note that an alternate classification of CLL1 as a temperate rain or
764 seasonal forest biome is discounted by the results of our analyses). Similarly, based on
765 multivariate analyses of faunal composition, Hernández Fernández et al. (2003) classified
766 CLL1 as a deciduous tropical forest with a posterior probability of 99.5%—the second option
767 (savanna) and other remaining possibilities (rainforest and laurel forest) being non-significant.

768 Despite being based on a much less sophisticated approach, the results of Hernández Fernández
769 et al. (2003) are also broadly consistent with those derived in this work, supporting that CLL1
770 is more readily interpreted as a tropical seasonal forest/savanna biome than as a tropical
771 rainforest. In contrast, Costeur's (2005) cenogram analyses concluded that CLL1 displayed
772 more closed and humid conditions than Rudabánya, attributing the former to a tropical forest
773 and the latter to a subtropical forest/savanna mosaic. Additional support to the classification of
774 CLL1 as a tropical seasonal forest/savanna instead of a tropical rainforest comes from
775 preliminary isotope analyses performed on muroid rodents from the Vallès-Penedès Basin
776 (Casanovas-Vilar et al., 2019, 2020). These confirm that hominoid-bearing sites are more
777 humid on average than those where primates are not recorded, with most of the former being in
778 the range of tropical deciduous forests to evergreen warm mixed forests. For CLL1,
779 paleoprecipitation estimates derived from muroid stable isotopes result in MAP well above
780 1000 mm while paleotemperature estimate is comparable to that derived in this work (I.
781 Casanovas-Vilar, pers. comm. of unpublished data). Nevertheless, the value derived from
782 isotopes is much lower than the one that would be expected for a tropical rainforest, confirming
783 that CLL1 does not correspond to this type of biome. Unpublished isotope analyses based on
784 the equid *Hip. catalaunicum* from CLL1 indicate a diet entirely based on C₃ vegetation (Misas
785 Alcàntara, 2022). Following the methods by Kohn (2010) these can be used to infer
786 paleoprecipitation, although ideally a broader taxonomic sample should be considered for the
787 calculations. Tooth enamel $\delta^{13}\text{C}$ ranges from -10.7‰ to -12.5‰ (Misas Alcàntara, 2022), which
788 results in a MAP estimation of ~700–1000 mm, thus consistent with the results yielded by the
789 multivariate analyses of FCT variables. Misas Alcàntara (2022) noted that, if *Hip. catalaunicum*
790 had inhabited and fed in the locally humid environment next to the depositional environment,
791 this would have resulted in more negative isotopic values—in further agreement with the
792 greater abundance of *Hippotherium* remains in the channel deposits than in the primate-bearing

793 levels of CLL1. Therefore, the values reported are taken as an indication of less humid, and
794 presumably more open, environments nearby.

795 It has been hypothesized that *H. laietanus* would have preferred the humid forested
796 environments close to permanent water due to the availability of ripe, soft fruit supplies on a
797 year-round basis (Alba et al., 2011a, 2011b; Marmi et al., 2012), or at least during part of the
798 year (DeMiguel et al., 2014), despite the fact that warm-temperate mixed forests, composed
799 mainly of deciduous taxa, would have probably been present far from these wetlands (Alba et
800 al., 2011a, 2011b; Marmi et al., 2012). Similarly, the roughly coeval *Rudapithecus hungaricus*
801 from Rudabánya (Hungary) is associated with a subtropical swamp forest dominated by swamp
802 cypress (*Taxodium*; Andrews and Cameron, 2010; Andrews, 2015). Tooth enamel stable
803 isotope analyses of the large mammal assemblage of Rudabánya indicate a mosaic of
804 environments and ecological niche partitioning (Eastham et al., 2016). Some taxa, such as *D.*
805 *nauyi* and *C. goldfussi*, would have fed in closed canopy environments, while others such as
806 *Hippotherium intrans* would have preferred more open habitats. Therefore, the environment
807 associated with *R. hungaricus* in Rudábanyá has strong similarities with that associated with *H.*
808 *laietanus* in CLL1, the two corresponding to local wetlands. However, there are also some
809 differences because the riparian forest composition (as evidenced from paleobotanical data) is
810 clearly different and woodlands away from the wetlands appear to have been more humid and
811 warm-temperate in Rudabánya (Andrews, 2015).

812 Within such environments, Late Miocene dryopithecines occupied a mainly arboreal and
813 frugivorous niche. Although these environments might have been quite common in the Vallès-
814 Penedès Basin during the early Vallesian (Alba et al., 2011b; Marmi et al., 2012), from the late
815 Vallesian onwards, tropical and subtropical taxa (such as palm and fig trees) would have
816 progressively disappeared as temperatures dropped (Sanz de Siria Catalán, 1994), while
817 deciduous trees (such as poplars or willows) became dominant in forested areas and wetlands

818 (Agustí et al., 2003; Alba et al., 2011a, 2011b; Marmi et al., 2012). As a result, these new
819 environments would not have provided the necessary resources to sustain a population of *H.*
820 *laietanus* (and other taxa dependent on forest trophic resources, such as probably *Pa. crusafonti*
821 and *L. splendens*) throughout the year, especially during the cold season, leading to their
822 progressive demise and eventual extinction in the Vallès-Penedès Basin and other areas of
823 Western Europe (Agustí et al., 2003; Casanovas-Vilar et al., 2005, 2010; Alba et al., 2011a,
824 2011b; Marmi et al., 2012). In this regard, it is noteworthy that the record of *L. splendens* from
825 CLL1 represents the latest well-dated occurrence of this taxon in Europe, whereas *Pa.*
826 *crusafonti* is last recorded slightly later at La Tarumba 1 (Van der Made, 1990, 1997; Van der
827 Made et al., 2022) at ~9.6 Ma (Casanovas-Vilar et al., 2016b), coinciding with the last record
828 of *H. laietanus* (Casanovas-Vilar et al., 2011; Alba et al., 2018). The extinction of hominoids
829 in other areas of Western mainland Europe would have followed a similar, although
830 diachronous, pattern (Agustí et al., 2003; Casanovas-Vilar et al., 2010, 2011; Merceron et al.,
831 2010; DeMiguel et al., 2014).

832

833 **5. Conclusions**

834 This study for the first time applied a full FCT scheme to analyze a Miocene fossil site. The
835 results of this work indicate that FCT variables in combination with regional predictive models
836 calibrated on Kenyan national parks as well as case-based reasoning over a selection of present-
837 day biomes are not very powerful for providing unambiguous biome classifications for CLL1.
838 Paleoprecipitation values appear potentially more biased than paleotemperature estimates,
839 which show a greater agreement with isotopic data and both plant and faunal composition.
840 Canonical variate analyses, in turn, failed to distinguish some particular biomes. Nevertheless,
841 when both approaches based on FCT variables are combined, the results are in broad agreement
842 with previous inferences based on other sources of data, suggesting that FCT variables are a

843 useful complementary approach to make ecometric comparisons among multiple sites with
844 limited associated cost, thus being potentially useful to refine inferences based on other, more
845 traditional methods of paleoecological inference.

846 Regarding CLL1, the multivariate analyses based on FCT support a biome classification as
847 tropical rainforest or tropical seasonal forest/savanna, but paleotemperature and
848 paleoprecipitation estimates, particularly considering the amplitude of rainfall seasonality, are
849 in better agreement with the latter. These results are in further accordance with previous
850 inferences derived from fossil plants and mammals, as well as preliminary isotopic data. Based
851 on these other sources of evidence, it is concluded that the inability of the multivariate analysis
852 to unambiguously classify CLL1 as a tropical seasonal forest is due to the fact that the fossil
853 assemblage mixes forest-adapted taxa (such as *H. laietanus* and *Pa. crusafonti*), likely restricted
854 to the closed forest environment surrounding the marshy depositional area, with other taxa that
855 likely inhabited more open woodland environments far from the wetland (such as
856 *Propotamochoerus* and *Hippotherium*). In other words, the CLL1 local paleoenvironment to
857 which *H. laietanus* was adapted, in isolation, would not be representative of the biome at a
858 more regional scale, characterized by a mosaic of dense forests around the wetlands and more
859 open vegetation between these areas. Overall, our results are consistent with previous studies
860 that related the extinction of frugivorous hominoids in Western mainland Europe with that of
861 other forest-adapted taxa—the so-called Vallesian Crisis. Even though paleobiodiversity
862 analyses of micromammals suggest that this was a more protracted event rather than an abrupt
863 crisis, it remains to be determined if the same applies to large mammals or whether some
864 important paleoenvironmental threshold (such as the complete replacement of tropical seasonal
865 forest patches by deciduous tropical forests) was surpassed at ~9.5 Ma, at least in the Vallès-
866 Penedès Basin. Future studies based on FCT variables in other well-sampled Vallesian localities
867 of this basin, preceding (e.g., Castell de Barberà, Creu de Conill, Can Poncic) or postdating

868 (e.g., La Tarumba, Torrent de Febulines) CLL1, might provide further precision in assessing
869 the causes of the extinction of Miocene apes in Europe.

870

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1315

1316 **Figure captions**

1317

1318 **Figure 1.** Simplified geological map of the Vallès-Penedès Basin showing the location of Can
1319 Llobateres 1 (CLL1) and location of the basin within the Iberian Peninsula (inset). Modified
1320 from Casanovas-Vilar et al. (2016a: Fig. 1).

1321

1322 **Figure 2.** Whittaker's diagram with biome classification for Can Llobateres 1 (blue star) based
1323 on estimated paleotemperature and paleoprecipitation (Table 5), along with the nine extant
1324 localities from Kenyan national parks based on actual temperature and precipitation data
1325 (Žliobaitė et al., 2016).

1326

1327 **Figure 3.** Results of a principal component analysis based on the seven functional crown type
1328 (FCT) variables of 13 extant localities from Kenyan national parks from four different biomes
1329 and Can Llobateres 1 (blue star), as depicted by a bivariate plot of PC2 vs. PC1. The percentage
1330 of variance summarized by each axis is indicated within parentheses. Vectors represent the
1331 loadings of the seven FCT variables (average values) on each axis. Each locality is color-coded
1332 according to Whittaker biome classification (see legend). Abbreviations: PC = principal
1333 component; HYP = hypsodonty; HOD = horizodonty; AL = acute lophs; OL = obtuse lophs;
1334 SF = structural fortification; OT = occlusal topography; CM = coronal cementum.

1335

1336 **Figure 4.** Results of a canonical variate analysis based on the seven functional crown type
1337 (FCT) variables of 18,671 extant localities from five different Whittaker biomes, as depicted
1338 by a bivariate plot of CV2 vs. CV1. The percentage of variance summarized by each axis is
1339 indicated within parentheses. Vectors represent the loadings of the seven FCT variables
1340 (average values) on each axis. Each locality is color-coded according to Whittaker biome
1341 classification (see legend). Ellipses represent the 95% confidence interval of each group
1342 included a priori. The nine localities from Kenyan national parks classified by this analysis,
1343 together with CLL1 (blue star), are also depicted. Kenyan localities: 1 = Shimba Hills; 2 =
1344 Kakamega; 3 = Aberdares; 4 = Mt Kenya; 5 = Masaai Mara; 6 = Tsavo; 7 = Nairobi; 8 =
1345 Naivasha; 9 = Elgon. Abbreviations: CV = canonical variate; HYP = hypsodonty; HOD =
1346 horizodonty; AL = acute lophs; OL = obtuse lophs; SF = structural fortification; OT = occlusal
1347 topography; CM = coronal cementum.

1348

1349 **Figure 5.** Schematic vegetation profile for Can Llobateres 1 based on macrofloral remains
1350 recovered from the site. Vegetation zones as well as names of characteristic plants are also
1351 indicated. Bold font indicates taxa that have not been recovered at Can Llobateres 1 but occur

1352 in other sites of the same basin. A marshy environment populated by reeds (*Phragmites* and
1353 *Typha*) is depicted to the left, bordered by a dense riparian evergreen forest with palms (*Sabal*),
1354 figtrees (*Ficus*), and laurels (*Cinnamomum*) that would have represented a favorable habitat for
1355 hominoids. A more arid, open, and seasonal environment, including areas dominated by
1356 leguminous trees, shrubs, and herbaceous plants, is depicted to the right far from the wetlands.
1357 Artwork by Roc Olivé.