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# Palaeoenvironmental reconstruction of the late Miocene macroflora of La Bisbal d'Empordà (Catalonia, Spain). Comparison with small mammals

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## Abstract

The late Miocene flora from La Bisbal d'Empordà (Catalonia, Spain) provides significant data for characterising the coastal vegetation from the north-eastern Iberian Peninsula during a key period in Neogene climatic evolution. To this end, a historical leaf collection from La Bisbal d'Empordà was re-examined, analysed from a palaeoenvironmental viewpoint and compared with data provided by the associated small mammal fauna. This flora dates from 9.6-9.7 Ma in age (early Tortonian) according to small mammal biostratigraphy.

The fossil-bearing beds were deposited in the floodplain of a meandering river system.

Three palaeoecological assemblages were recognized: 1) Helophytic plant stems related to a wetland community. 2) Torn leaves of *Fraxinus* sp., *Ulmus* sp., *Zelkova* sp.,

24 *Cedrelospermum* sp. *Populus balsamoides*, *Alnus gaudinii*, *Carpinus* sp., *Platanus* sp.,  
25 *Acer tricuspidatum*, *Daphnogene* sp. and, *Laurophyllum* sp. which would have  
26 belonged to a riparian forest located beyond the wetland community, with *Fraxinus*  
27 being the plant growing in closest proximity; 3) Isolated complete *Paliurus* seeds,  
28 interpreted as mainly wind-transported, which provide evidence of an open and more  
29 arid landscape situated distally from the floodplain. The small mammal assemblages  
30 associated with this flora are consistent with this palaeoenvironmental interpretation.  
31 The paucity of small arboreal mammal taxa and insectivores suggests limited forested  
32 vegetation areas, while the more common terrestrial species indicate better developed  
33 open landscapes. Our results show a more heterogeneous environment than previously  
34 thought and that the riverine processes impinged the flora, somewhat limiting the  
35 climatic conclusions that might be derived from leaf physiognomic analyses such as  
36 CLAMP.

37

38 **Keywords:** Neogene, riverine vegetation, taphonomy, paleoecology, micromammals,  
39 South Europe

40

## 41 **1. Introduction**

42 The global cooling event at the middle Miocene climate transition (Westerhold et al.,  
43 2020) triggered a floristic reorganisation and increase of regionalism during the late  
44 Miocene (Zachos et al., 2001; Utescher et al.; 2007a, Pound et al.; 2012). In Central  
45 Europe and the Western Paratethys zonal deciduous forests dominated, locally  
46 containing broadleaved evergreen elements (Erdei et al., 2007; Utescher et al., 2007a;  
47 Ivanov et al., 2011). In contrast, in Southern Europe, broadleaved evergreen

48 dicotyledonous plants prevailed together with thermophilous conifers and, in lower  
49 proportions, sclerophyllous plants (Utescher et al., 2007a,b).

50 During most of the Tortonian (partly equivalent to the Vallesian European land  
51 mammal age), the Iberian Peninsula had a particular regional vegetation gradient which  
52 would have been climatically controlled impinging on the more general European  
53 latitudinal pattern during this time span (Fauquette et al., 2007; Jiménez-Moreno et al.,  
54 2010; Barrón et al., 2016). According to the latter three studies, three vegetation belts  
55 can be distinguished based on pollen analyses. (1) The southern belt, which would  
56 comprise the region of Andalusia, was dominated by an open savannah-like woodland  
57 mainly constituted by herbs and shrubs (2) The second belt, which would correspond to  
58 the central part of the Iberian Peninsula, was characterised as belonging to the plant  
59 locality of Zaratán (Valladolid province). This vegetation belt was mainly composed of  
60 a mixed evergreen assemblage made of *Quercus* and *Pinus*, associated with Cistaceae,  
61 Cupressaceae and Ericaceae. This plant locality is situated at the same latitude as the  
62 coeval palaeobotanical site of La Bisbal d'Empordà, which is studied here, and  
63 Terrassa, both near the Miocene coastline to the east. However, the plant assemblage  
64 from Terrassa is relatively richer in thermophilous plants than La Bisbal d'Empordà,  
65 e.g., *Celastrus*, *Parrotia* or *Myrsine* (Sanz de Siria Catalán, 1997; Agustí et al., 2003);  
66 (3) The third belt is located in the northern part of the Iberian Peninsula corresponding  
67 to the Pyrenees and Cantabrian mountains. It was mainly characterised by arboreal  
68 deciduous dicotyledonous angiosperms, conifers, a few palaeotropical elements such as  
69 *Daphnogene*, *Mahonia* or *Cassia* and a few herbaceous taxa.

70 A comprehensive study of the plant palaeoecology of late Miocene macroflora of the  
71 north-eastern Iberian Peninsula has not yet been conducted. Only the upland flora of La  
72 Cerdanya has been studied in detail (Barrón, 1992, 1996a, 1996b, 1996c; Barrón and

73 Diéguez, 1994; Martín-Closas et al., 2005, 2006; Barrón et al., 2014, Tosal et al., 2021),  
74 with little attention to the lowland plant communities from this area. The historical leaf  
75 collection from La Bisbal d'Empordà was gathered by Sanz de Siria Catalán (1981,  
76 1985) and Sanz (1988) and is a palaeobotanical collection that has yet to be re-examined  
77 using modern taxonomic, taphonomic and palaeoecological criteria. Sanz de Siria  
78 Catalán (1981) reported 27 species, interpreted as forming two distinct floral  
79 associations. The first, and the most significant, belonging to humid environments that  
80 included *Equisetum parviflorum* Heer *Poacites* sp. and *Typha latissima* Brongniart  
81 characteristic of the lake and riverbanks. The second was interpreted as a closed forest  
82 growing in the lowlands and hills around the depositional setting and included taxa such  
83 as *Cinnamomum polymorphum* Heer (25% of the plant assemblage), *Pterocarya*  
84 *fraxinifolia* Spach. (30% of the plant assemblage), *Quercus drymeja* Unger, *Quercus*  
85 aff. *ilex*, *Quercus* sp., *Ulmus braunii* Heer, *Ulmus* sp., *Acer trilobatum* (Sternb.) A.  
86 Braun *Acer* sp., *Fraxinus delecta* Heer, and *Sapindus bilinicus* Ettingsh. This  
87 combination of elements which are more characteristic of temperate forests, such as  
88 *Pterocarya fraxinifolia*, alongside with others more typical of subtropical forests, such  
89 as *Cinnamomum polymorphum*, was interpreted by Sanz de Siria Catalán (1981) as  
90 representing the climatic transition from a warmer stage in the middle Miocene to the  
91 milder temperate climates of the late Miocene. Furthermore, the relatively low latitude  
92 of the basin and its proximity to the coastline would have allowed, according to this  
93 author, for the longer persistence of subtropical species in comparison with  
94 contemporaneous floras from higher latitudes in central Europe, which were richer in  
95 more temperate (Arctotertiary) species (Uhl et al., 2007). These conclusions have  
96 subsequently been assumed in several palaeobotanical syntheses of European and

97 Iberian basins, e.g., Barrón (2003), Kovar-Eder (2003) and Barrón et al. (2010), but new  
98 data have not been added to the original description and interpretation of the collection.

99 Plant remains occur in the same facies that have also yielded small mammals and in the  
100 vicinity of layers where a small number of larger mammal remains have also been  
101 found. Villalta (1958) and Crusafont (1962) first reported some isolated large mammal  
102 finds in various clay beds near or within the quarries of this area, including  
103 proboscideans (*Deinotherium*, *Tetralophodon*), several artiodactyls (*Miotragocerus*,  
104 *Micromeryx*, *Dorcatherium*, *Euprox*, *Conohyus*, *Hyotherium*) and the three-toed equid  
105 *Hippotherium*. The composite large mammal fauna (for an updated faunal list see Rufí-  
106 Casals et al., 2017) is indicative of a Vallesian age. Later fieldwork mostly focused on  
107 the recovery of small mammals in order to constraint the age of the different fossil sites  
108 (Gibert et al., 1979, 1980; Llenas et al., 2002; Casanovas-Vilar et al., 2010).

109 Gibert et al. (1979, 1980) reported two small-mammal-bearing sites (La Bisbal 1 and La  
110 Bisbal 2) each of which yielded relatively few remains. Knowledge of the small  
111 mammal fauna increased significantly with the addition of new sites after the work  
112 carried out by Llenas et al. (2002) and Casanovas-Vilar et al. (2010), so that currently  
113 seven different fossiliferous levels are known (although some may be roughly  
114 equivalent) and the recovered collection includes about 150 identifiable micromammal  
115 specimens in total. Most of the micromammal fauna is described in Gibert et al. (1980),  
116 Agustí (1981) and Casanovas-Vilar et al. (2010). As to present knowledge, the small  
117 mammal fauna of AVM4 includes the cricetids (hamster relatives) *Megacricetodon* cf.  
118 *minutus* (Plate I.1), *Megacricetodon ibericus* (Plate I.2–3), and *Hispanomys dispectus*  
119 (Plate I.14–16), the glirid (dormouse) *Miodyromys hamadryas* (Plate I.8) and the  
120 ochotonid lagomorph (pikas) *Prolagus* sp. The same taxa are also present at Can  
121 Colomer 1 and La Bisbal 1 and 2. In contrast, AVM10 and AVM11 includes two

122 species of ground squirrel (*Heteroxerus rubricati*, *Spermophilinus bredai*), the  
123 ochotonid *Prolagus*, the glirid *M. hamadryas*, four species of cricetid (*Democricetodon*  
124 cf. *nemoralis* [Plate I.4], *Neocricetodon ambarrensis* [misidentified as *Cricetulodon*  
125 *hartenbergeri* in Casanovas-Vilar et al., 2010; Plate I.9–11], *Rotundomys* cf. *freirensis*  
126 [Plate I.5–7] and *Hispanomys* sp.) and three distinct insectivores.

127 Here an in-depth physiognomic study of the fossil plant remains of the La Bisbal  
128 d'Empordà palaeobotanical site is presented and its sedimentary and taphonomic  
129 constraints analysed. The palaeobotanical results of this study are compared with the  
130 data provided by the associated small mammal fauna to provide a more holistic view of  
131 the palaeoenvironment of the La Bisbal d'Empordà fossil site.

132

133 -----Insert Plate I near here-----

134

## 135 **2. Material and methods**

136 The studied material was originally collected by Sanz de Siria Catalán (1981) from the  
137 outcrops called La Bisbal-1 and La Bisbal-2, which at the time corresponded at the time  
138 to an active clay pit in La Bisbal d'Empordà. The 72 specimens in the collection are  
139 stored at the Institut Català de Paleontologia Miquel Crusafont (ICP) at Sabadell  
140 (Catalonia, Spain) with catalogue numbers IPS109701 to IPS109772.

141 Approximately 50% of the fossil plant specimens from La Bisbal d'Empordà are  
142 sufficiently well preserved for a detailed description using the leaf architecture  
143 terminology of Ellis et al. (2009). The most representative specimen(s) of each  
144 morphotype were selected and photographed. Between 20–40 images of each specimen

145 were taken using a Nikon 5300 camera and focus stacked using Helicon Focus 5.3  
146 ([www.heliconsoft.com](http://www.heliconsoft.com)). Leaf measurements were taken using the SketchandCalc  
147 software ([www.sketchandcalc.com](http://www.sketchandcalc.com)).

148 The original leaf-bearing beds are no longer accessible due to subsequent works in the  
149 clay pit. However, the approximate stratigraphic position of these beds is reported in  
150 Casanovas-Vilar et al. (2010) and Rufí-Casals et al. (2017). Stratigraphically equivalent  
151 beds allowed for a facies analysis to compare the sedimentological data with the  
152 taphonomic features observed in the leaf collection. In this regard, five sections were  
153 studied, which are, from base to top of the succession: (1) the active quarry called Can  
154 Colomer, located at Avinguda del Puntuí, (41°96'16"N, 3°02'08"E), (2) the  
155 abandoned, and now flooded quarry Estanyol Cordat (41°97'10"N, 3°02'16"E), (3) the  
156 succession, opposite to the previous locality, to the north of the factory "Argiles Bisbal  
157 SL" (41°97'11"N, 3°02'17"E), (4) the exposure near the farm Can Fuertes  
158 (41°96'91"N, 3°01'82"E), and (5) the stratigraphic succession bordering the  
159 Vacamorta landfill (41°96'53"N, 3°01'72"E).

160 Small mammal remains were recovered after sediment screen-washing in successive  
161 field campaigns in the early 2000s (Llenas et al., 2002; Casanovas-Vilar et al., 2010).  
162 The area surveyed mostly corresponds to the Can Colomer clay pit which since 2005  
163 has been occupied by the Vacamorta landfill. Before the landfill was built, two samples  
164 (named Can Colomer 1 and Can Colomer 2) were collected from this area. After screen-  
165 washing, a limited collection consisting of about 70 identifiable small mammal remains  
166 were recovered. A preliminary faunal list is given in Llenas et al. (2002), while some  
167 specimens are described in Casanovas-Vilar et al. (2010). During the preparatory works  
168 for the Vacamorta landfill palaeontologists surveyed the area and collected 12  
169 additional samples from several lutite beds in the search for microvertebrate fossils.

170 Three of these samples (AVM4, AVM10, AVM11) were positive and allow for a  
171 comparison with the plant-bearing beds studied here, which are laterally equivalent.  
172 About 20 identifiable micromammal teeth were recovered in each case. The material is  
173 described in Casanovas-Vilar et al. (2010)

174

### 175 **3. Geological setting and biostratigraphy**

176 The La Bisbal d'Empordà outcrops are located within the Neogene of the L'Empordà  
177 Basin (Fig. 1), which is situated in the northeastern part of the Iberian Peninsula, in  
178 Catalonia (Spain). The basin was formed as part of a rifting process that affected the  
179 western Mediterranean throughout the Neogene and Quaternary periods (Saula et al.,  
180 1996). In the Iberian Peninsula, this rifting produced a system of NE-SW orientated  
181 normal faults broadly parallel to the present-day coastline and resulted in the formation  
182 of several sedimentary basins including the L'Empordà Basin (Picart et al., 1996; Saula  
183 et al., 1996). The basin is geologically limited by the Palaeozoic outcrops of the  
184 L'Albera ranges to the north, Eocene rocks of La Garrotxa to the west, the metamorphic  
185 and igneous rocks of the Les Gavarres ranges to the south and by the Mediterranean Sea  
186 to the east (Picart et al., 1996).

187 From a stratigraphic viewpoint, the localities studied belong to the eastern part of an  
188 upper Miocene alluvial-fluvial fan system, particularly the so-called Les Gavarres fan  
189 system (Saula et al., 1996). The accumulated thickness of the Les Gavarres fan system  
190 deposits is up to 100 m. These are formed by a succession of greenish-grey and red  
191 mottled clays interbedded with conglomerates, gravels and sandstones of varying  
192 thickness (Picart et al., 1996; Casanovas-Vilar et al., 2010). The lithologies of the clasts  
193 within the conglomeratic beds are variable. The most frequent are quartz, mottled

194 schists and altered granites of Palaeozoic age, which originated from the Les Gavarres  
195 ranges; Eocene sandstones originating from the western margin of the basin, and  
196 Neogene basalts corresponding to the volcanism associated with the basin origin.

197 The age of the studied flora from La Bisbal d'Empordà is based on mammal  
198 biostratigraphy. Crusafont (1962) had already assigned the La Bisbal d'Empordà  
199 outcrops to the Vallesian European land mammal age (earliest late Miocene, 11.2–8.9  
200 Ma) due to the presence of the three-toed equid *Hippotherium*. Later, Gibert et al.  
201 (1979, 1980) found two micromammal fossil sites in La Bisbal d'Empordà i.e., La  
202 Bisbal 1 and 2 which indicated a correlation with the early Vallesian, i.e., European  
203 mammal Neogene zone MN9 (currently ranging from 11.2 to 9.9 Ma). Some years later,  
204 Llenas (2002) found two additional small mammal sites at the clay pit of Can Colomer.  
205 This author also named them La Bisbal 1 and 2 but these beds are distinct from those  
206 previously reported by Gibert et al. (1979, 1980). To avoid confusion, Casanovas-Vilar  
207 et al. (2010) renamed the mammal beds of Llenas (2002) Can Colomer 1 and Can  
208 Colomer 2 for La Bisbal 1 and 2 respectively. They also correlated Can Colomer 1 and  
209 2 with the fossiliferous beds at the Vacamorta landfill. Level AVM4 was considered  
210 approximately equivalent to Can Colomer 1 and to La Bisbal 1 and 2 of Gibert et al.  
211 (1979, 1980), and was further correlated with the first half of the MN9. The small  
212 mammal assemblage of Can Colomer 2 was correlated to AVM10 and AVM11, which  
213 are stratigraphically equivalent to the beds that provided the fossil macroflora from La  
214 Bisbal d'Empordà. Casanovas-Vilar et al. (2010) initially correlated these beds with the  
215 late MN9, although noting apparent incongruences. Recent biostratigraphic works  
216 carried out by Casanovas-Vilar et al. (2016a, 2016b) in the Vallesian type area, at the  
217 nearby Vallès-Penedès Basin (Barcelona, Catalonia), allows constraining the age of La  
218 Bisbal fossil sites. AVM4, Can Colomer 1 and La Bisbal 1 and 2 would correlate with

219 the earliest Vallesian *Hippotrium* – *Cricetulodon hartenbergeri* Interval Subzone of  
220 the Vallès-Penedès Basin, thus resulting in an estimated age of 11.2–10.3 Ma for these  
221 sites. On the other hand, AVM10, AVM11 and Can Colomer 2 are correlated with the  
222 short-lasting *Cricetulodon sabadellensis* + *Progonomys hispanicus* Concurrent Range  
223 Subzone of the Vallès-Penedès Basin, corresponding to the earliest late Vallesian (early  
224 MN10) and yielding an age of 9.73–9.65 Ma. This estimate differs from that given in  
225 Casanovas-Vilar et al. (2010), who suggested an MN9 (early Vallesian) age for these  
226 sites after mistaking *Neocricetodon ambarrensis* for *Cricetulodon hartenbergeri*. The  
227 diagnostic elements for the *C. sabadellensis* + *P. hispanicus* subzone have not been  
228 found. However, *Rotundomys freirensis*, which occurs at AVM10 and AVM11, is only  
229 known from this subzone in the Vallès-Penedès, thus supporting this interpretation.  
230 Furthermore, *N. ambarrensis* is also a typical late Vallesian element.

231 -----Insert Figure 1 near here-----

232

## 233 **4. Results**

234 *4.1. Stratigraphy and sedimentology*

235 *4.1.1. Description and interpretation of facies*

236 A 130-m-thick composite stratigraphic section was obtained after lithostratigraphic  
237 correlation of five detailed stratigraphic logs from the Neogene of La Bisbal d'Empordà  
238 (Figs. 2, 3). The localities Can Colomer, Estanyol Cordat and Can Fuertes, allow  
239 characterisation of the lower part of the succession, the central part of which is well  
240 exposed at Argiles Bisbal SL, while the last 30 m of the succession are accessible at the  
241 Vacamorta landfill. Five intervals were recognised and are described below (Fig. 3).

242

243 -----Insert Figure 2 near here-----

244 -

245

246 **Interval 1**

247 *Description.* This interval is best exposed at the still active quarry of Can Colomer and  
248 is 10 m thick. It is composed of greenish-grey, brownish and red clays and siltstones  
249 with calcareous nodules of up to 1 cm in diameter (Plate II.1). These facies include  
250 micromammal remains (locality AVM4) and poorly-preserved fragmented plant  
251 remains. Intercalations of fine-grained tabular and lenticular, beds of sandstones up to  
252 0.5 m thick are visible.

253 *Interpretation.* This succession is attributed to sedimentation of overbank deposits in a  
254 fluvial floodplain. Based on the sedimentary models of Boggs (2006), clays and  
255 siltstones represent the sediments formed by decantation of suspended load after a  
256 flooding event, while sandstone beds represent overbank lobes. According to the  
257 observations of Kraus and Aslan (1999) in Bighorn Basin (Wyoming, USA), the  
258 different coloured lutites show different degrees of subaerial exposure with a grey-  
259 greenish colour indicating longer periods in subaquatic environment while red clays  
260 show increased subaerial oxidation. These features, along with the occurrence of  
261 calcareous nodules suggest that hydromorphic soils developed in this setting.

262

263 -----Insert Figure 3 near here-----

264

265    **Interval 2**

266    *Description.* Interval 2 crops out at Estanyol Cordat is separated from the previous  
267    outcrop by 66 m of covered deposits. The total thickness of this interval is 17 m, and it  
268    is mainly represented by grey, red and ochre clays sometimes mottled, intercalated with  
269    ochre coarse-grained tabular to lenticular sandstones up to 1m thick with erosive bases  
270    and epsilon-cross bedding (Plate II.2).

271    *Interpretation.* The succession at the Estanyol Cordat section represents sedimentation  
272    in a river floodplain with better drainage than in the previous outcrop. Based on the  
273    studies of Allen (1970, 1974), tabular to lenticular sandstones with accretional features  
274    represent the lateral migration of meandering river channels, while mottled variegated  
275    clays indicate changes in the Eh due to water table oscillation in the floodplain (Kraus  
276    and Aslan, 1999).

277

278

279    **Interval 3**

280    *Description.* This interval is 13 m thick and is well-exposed at the Argiles Bisbal SL  
281    factory section and the lower part of the Can Fuertes section. It is characterised by  
282    ochre, mottled greenish-grey clays with rootlet marks (Plate II.3), interbedded with up  
283    to 4 m thick tabular or lenticular sandstone or conglomerate bodies. Commonly,  
284    conglomerates show a marked erosive base and are supported by rounded clasts, up to  
285    30 cm across, of whitish quartz, granitoids, mottled schists, and trachyte (Plate II.4; Fig.  
286    4). These bodies are followed by cross-bedded and multistorey sandstones forming  
287    finning upward sequences. Another type of body is represented by 2–3 m thick tabular  
288    conglomerates with a matrix-supported fabrics, formed by poorly-selected lutite and

289 coarse sandstone. The clast composition and sizes are identical to those in the  
290 conglomerates of the sandstone beds.

291 *Interpretation.* The succession of interval 3 corresponds to a more proximal setting  
292 within an alluvial-fluvial fan system than previous intervals, based on the sedimentary  
293 models provided by Nichols (2009). Multistorey sandstone beds with cross-bedded  
294 stratification represents the infilling sequence of braided-river channels, based on  
295 Miall's (1977) models, while mottled lutites with rootlet marks represent sedimentation  
296 in vegetated floodplains. Tabular conglomerates with matrix-supported fabrics would  
297 correspond to sedimentation of debris flows in a medial alluvial-fan setting.

298

299 -----Insert Plate II near here-----

300

301 **Interval 4**

302 *Description.* This interval is ca. 25 m thick and corresponds to the upper part of the Can  
303 Fuertes section and the basal part of the Vacamorta landfill section. It is mainly  
304 composed of alternating red, mottled greyish-ochre and locally white clays, with rootlet  
305 marks and is rich in plant and micromammal remains. These fossiliferous beds would  
306 be equivalent to those where Sanz de Siria Catalán (1981) collected the leaf flora  
307 studied herein while the micromammal-bearing beds correspond to AVM9–AVM12 of  
308 Casanovas-Vilar et al. (2010). At Can Fuertes, sandstone beds with undulating bases  
309 and epsilon cross-bedding occur at the top of the interval (Plate II.5).

310 *Interpretation.* The succession of interval 4 represents a meandering fluvial system that  
311 developed in the more distal areas of an alluvial-fluvial fan. Sandstones with internal

312 epsilon cross-bedding from the Can Fuertes outcrop indicate meandering river channels,  
313 based on the sedimentary models of Miall (2016). The variegated clay colours and  
314 rootlet marks represent deposition in flooded areas where the development of  
315 hydromorphic soils was important. In contrast, red clays resulted from the deposition of  
316 overbank deposits under oxidized conditions by subaerial exposition.

317

318 -----Insert Fig. 4 near here-----

319

320 **Interval 5**

321 *Description.* This interval, up to 10 m thick, corresponds to the upper part of the  
322 Vacamorta section. It is composed of lenticular cross-bedded conglomerates forming  
323 two thick, overlapping bodies separated by laminated red clay and siltstone beds.  
324 Conglomerate clasts are sub-rounded, up to 20 cm in diameter and composed of altered  
325 granite, mottled schist, acidic volcanic rocks (trachyte) and sandstone (Plate II.6).

326 *Interpretation.* The succession of this interval would correspond to a more proximal  
327 setting within an alluvial-fluvial fan than the previous interval. Conglomerates with  
328 cross-bedding would indicate a constant high flow energy consistent with that of  
329 braided rivers (Nichols, 2009). Laminated red clays and siltstones represent the  
330 corresponding over bank deposits.

331

332 *4.1.2. Depositional model*

333 The late Miocene section that crops out at La Bisbal d'Empordà corresponds mainly to  
334 a fluvial belt, formed by braided river channels grading distally to meandering river

335 channels and their associated floodplain facies. More rarely, proximal to medial alluvial  
336 fan facies (debris flow facies) are associated with previous deposits.

337 From intervals 1 to 3, a progradation trend of the alluvial-fluvial fan is apparent, from  
338 floodplain deposits that represent distal fluvial facies in interval 1 to meandering river  
339 facies in interval 2, and finally to braided river and debris-flow facies in interval 3.

340 Interval 4 represents a retrogradation of the alluvial-fluvial fan system, which resulted  
341 in an extension of the meandering river belt facies over the braided river facies of  
342 interval 3. The studied leaf-bearing beds were deposited in this retrogradation context.

343 Finally, interval 5 again shows more proximal facies in the system with a development  
344 of thick braided river facies on top of the section.

345 The whole section is dominated by fluvial processes from distal parts of the alluvial-  
346 fluvial fan i.e., channel-fill and over bank deposits, with local evidence of unconfined-  
347 flow processes that would be more characteristic of proximal alluvial settings. This  
348 expands the facies range reported in a previous study by Picart et al. (1996), who  
349 associated the sedimentation in La Bisbal d'Empordà strictly with an alluvial context.

350 Fluvial floodplain facies are especially interesting for this study since they contain the  
351 fossiliferous beds where the La Bisbal d'Empordà flora and micromammals were  
352 collected. The combination of greenish and reddish clays, calcareous nodules, mottling  
353 and vertically oriented rooting structures, suggest the formation of an alfisol, which is  
354 typical of stable floodplain, including forested environments. The sediment associated  
355 with the palaeobotanical material studied here includes pale greyish to ochre silts and  
356 some more yellowish, fine sands. This material shows some mottling and presents fine,  
357 millimetre-scale plane parallel lamination, which is consistent with the sedimentary  
358 features of the distal floodplain facies.

359

360 4.2. *Systematic palaeobotany*

361 The purpose of this section is to describe the dicotyledonous specimens from La Bisbal  
362 d'Empordà using the definitions of Ellis et al. (2009) to provide new details about the  
363 leaf features, such as the venation pattern and the teeth shape. Many of the plant  
364 remains studied here were significantly damaged during the biostratinomic phase,  
365 making it difficult to provide a precise taxonomic determination.

366

367 Order LAURALES Berchtold et Presl

368 Family LAURACEAE Jussieu

369 Genus **Daphnogene** Unger

370 *Daphnogene* sp.

371 (Plate III.1)

372 **Material:** IPS109714, an almost complete blade. Some other fragments miss the left  
373 half of the lamina and the apex (IPS109718 and IPS109754).

374 **Description:** The leaf is elliptic, petiolate and the margin is entire. It measures up to 4.4  
375 cm long and 1.7 cm wide. The base is cuneate and displays basal width asymmetry  
376 while the apex is straight.

377 The primary venation is suprabasal actinodromous. The lateral veins emerge at 30°–40°  
378 from the central vein. The lateral primary veins reach the apical part of the leaf where  
379 they are topped with the first pair of secondary veins. The secondary venation pattern is  
380 brochidodromous. These veins rise from the central primary vein with angles of 60°–

381 70°. The exterior secondary veins are looped. The intercostal tertiary venation fabric  
382 follows a straight path and arises perpendicularly from the secondary veins. The  
383 quaternary vein fabrics are irregularly reticulate with moderate areolation development.

384 **Remarks:** This leaf was first attributed to *Cinnamomum polymorphum* by Sanz de Siria  
385 Catalán (1981). It is attributed here to *Daphnogene* sp. since the identification of the  
386 extant genus *Cinnamomum* is problematic when the cuticle is not preserved (Kvaček  
387 1971; Kvaček and Walther 1998, 2004).

388

389 Genus **Laurophyllum** Goeppert

390 *Laurophyllum* sp.

391 (Plate III.2; Fig.5.1)

392 **Material:** IPS109721, IPS109739, IPS109749, IPS109756, IPS109768, including 2  
393 complete blades.

394 **Description:** The leaf is elliptic, petiolate and measures up to 3.5 cm in length and 1 cm  
395 in width. The margin is entire, the apex is straight and the base convex-rounded.  
396 The primary vein is pinnate. The major secondary framework is simple  
397 brochidodromous and the secondary vein spacing is irregular. These veins rise from the  
398 midvein at 45°–60° and the attachment to the midvein is decurrent.

399 **Remarks:** This specimen was attributed to *Sapindus bilinicus* by Sanz de Siria Catalán  
400 (1981) in his Figure 12. A further specimen illustrated by Sanz de Siria Catalán (1981,  
401 Pl. I, Fig. 9) and named as *Laurophyllum princeps*, would be equivalent to this  
402 morphotype. A species-specific affinity was not assigned due to the high morphological  
403 variability of the Lauraceae and the limited material available. Based on Mihajlovič and

404 Ljubotenski (1994) and Teodoridis (2003) cuticular preservation would be necessary to  
405 refine the attribution provided ).

406

407 Order PROTEALES Berchtold et Presl

408 Family Platanaceae Lestibudois

409 Genus **Platanus** Linnæus

410 *Platanus* sp.

411

412 (Plate III.3)

413 **Material:** IPS109709 is a proximal fragment of a blade with a strongly-marked  
414 venation pattern.

415 **Description:** The portion of the leaf blade available is 3.25 cm long and 4.5 cm wide.

416 The base has a concave form. The margin is toothed with only one acute tooth preserved  
417 (concave shape in both flanks).

418 The primary vein framework is palmate and suprabasal actinododromous, with just one  
419 basal vein. This forms a distinct, forked shape with the two exterior primaries leaving  
420 the midvein at angles of 25°. The gauge width of the primaries is at least twice that of  
421 the major secondaries. There are minor secondary veins arising from the lateral  
422 primaries to the margin. They form loops close to the margin with a vein arising from  
423 the loop to the tooth apex. The intercostal tertiary vein fabric is irregular reticulated.  
424 The tertiaries intersecting the primary veins are reticulate and the exterior tertiary vein  
425 course forms loops close to the margin.

426 **Remarks:** The asymmetric blade shape and tooth margin together with the distinctive  
427 course of the primary veins resemble that of *Platanus intermedia* described by Tschan  
428 et al. (2008). However, the only fragment available does not provide enough  
429 information to assign it to a species.

430

431 Order MALPIGHIALES Martius

432 Family SALICACEAE Mirbel

433 Genus **Populus** Linnæus

434 *Populus balsamoides* Goepert, 1855

435 (Plate III.4; Fig. 5.2)

436 1855 *Populus balsamoides* Goepert, 23; pl. 15 F

437 1856 *Populus melanaria* Heer, vol. II, 16; pl. 54, fig. 7a; pl. 57, fig.1

438 1979 *Populus gaudini* Fisher, Fernández-Marrón et al., 8; pl. 8, fig.1

439 **Material:** IPS109715, IPS109729 and IPS109766 are an almost complete blade, but  
440 with poor preservation of the leaf margin and the lower order veins.

441 **Description:** The leaf blade is up to 12 cm in length and 2.95 cm in width. The base is  
442 obtuse in angle with a round shape. The apex angle is acute and acuminate in shape,  
443 with drip tip. The margin probably is entire.

444 The primary vein network is pinnate with one basal sympodial vein. The major  
445 secondary veins rise from the midveins with irregular spacing and uniform angles of  
446 40°–50°. The attachment of the major secondaries to the midvein is decurrent and  
447 deflects the midvein. The first pair of secondary basal veins are thinner in width than

448 other secondaries and at a greater angle to the midvein ( $70^\circ$ ) but are also  
449 brochidodromous.

450 **Remarks:** IPS 109715 had already been attributed to *Populus balsamoides* by Sanz de  
451 Siria Catalán (1981), according to his hand-drawing in Figure 16. However, the  
452 specimens IPS109729 and IPS109766 were attributed to *Carya bilinica* Unger by Sanz  
453 de Siria Catalán (1981). The specimens studied show similar physiognomic characters,  
454 including the venation pattern, to *Populus balsamoides* described by Barrón (1999)  
455 from Izarra (Álava, Spain) and by Barrón and Postigo-Mijarra (2011) in the lower  
456 Miocene from Ribesalbes (Castelló, Spain).

457

458 Order ROSALES Perleb

459 Family RHAMNACEAE Durande

460 Genus **Paliurus** Miller

461 *Paliurus* sp.

462 (Plate III.5)

463      **Material:** IPS 109703, IPS 109718, IPS 109760 whole or slightly-damaged winged  
464      seeds.

465 **Description:** Indehiscent, winged drupe up to 1.9 cm across, showing an endocarp, 4  
466 mm in diameter. The wing is thin, circular in shape, and displays dichotomizing and  
467 anastomosing venation.

468 **Remarks:** These specimens were also attributed to *Paliurus* sp. by Sanz de Siria  
469 Catalán (1981). Based on Burge and Manchester (2008) the receptacle shape allows for

470 a distinction between two organ-species of Cenozoic *Paliurus* seeds. Unfortunately, this  
471 character is missing in the specimens studied.

472

473 -----Insert near here Plate III-----

474

475 Rosaceae gen. et sp. indet.

476 (Plate III.6; Fig. 5.3)

477 **Material:** IPS109745 is an almost complete blade missing the proximal-most part of the  
478 base. Further incomplete specimens of the same morphotype are IPS109701 and  
479 IPS109732.

480 **Description:** The lamina measures 3.85 cm in length and 3.1 cm in width. The margin  
481 is poorly preserved. The shape of the lamina is obovate with medial symmetry. The  
482 apex shape might be rounded or emarginate.

483 The primary vein framework is pinnate with one basal vein. The major secondaries are  
484 brochidodromous and are placed somewhat irregularly, but the distances between major  
485 secondary veins decreases distally. The angle of the major secondaries with the midvein  
486 is uniform at 60°–70°, but they curve upwards towards the margins, before forming a  
487 loop with the adjacent secondary. The attachment of the major secondaries is excurrent.  
488 The intercostal tertiary fabric is straight to slightly sinuous, rising at 70° from the  
489 secondary veins.

490 **Remarks:** This specimen was attributed to *Alnus stenophylla* (Saporta et Marion) by  
491 Sanz de Siria Catalán (1981) due to what he interpreted as an emarginate apex. Here this  
492 feature is regarded as damage to the apex and therefore not considered. The few leaf

493 features preserved, i.e. the blade shape and the brochidodromous venation pattern,  
494 suggest that it belongs to family Rosaceae. However, the poor preservation of the  
495 specimens does not permit a more precise taxonomic assignation.

496

497 Order FAGALES Engler

498 Family BETULACEAE Gray

## 499 Genus **Alnus** Miller

500 *Alnus gaudinii* (Heer, 1859) Knobloch et Kvaček, 1976

501 1859 *Rhamnus gaudinii* Heer, 79; pl. 124, figs. 4–15, pl. 125, figs. 1, 7, 13.

502 1961 ?*Pterocarya* aff. *denticulata* (Göppert) Schlech-Tendal; Knobloch, 264; pl. 11, fig.  
503 10.

504 1961 cf. *Alnus kefersteinii* (Göppert) Unger; Knobloch, 267; pl. 2, figs. 9, 11.

505 1976 *Alnus gaudinii* (Heer); Knobloch et Kvaček, 33; pl. 6, figs. 1, 3, pl. 7, figs. 1, 5, pl.  
506 13, fig. 4, pl. 15, figs. 1–4, 7–8, 10–11, 15, 17, pl. 16, figs. 1–5, pl. 19, fig. 15, pl. 20,  
507 figs. 10–12.

508 1998 *Alnus gaudinii* (Heer) Knobloch et Kvaček; Kvaček and Walther, 7; pl. 3, figs 51–  
509 3, text-figs 13.4–5.

510 2004 *Alnus gaudinii* (Heer) Knobloch et Kvaček; Kvaček and Walther, 18; pl. 2, figs 5–  
511 7, text-fig. 11.6.

512

513 (Plate III.7; Fig. 5.4)

514 **Material:** IPS109707, IPS109722, IPS109726, IPS109738, IPS109759 and IPS109761

515 are incomplete blades and all of them lack the apex.

516 **Description:** The laminar attachment is marginal and the laminar size is estimated at  
517 around 11 cm in length by 8.5 cm in width. The laminar shape is ovate with both basal  
518 and medial symmetry. The base probably had a cordate form. The poor preservation of  
519 the margin makes it difficult to ascertain if it is toothed or entire.

520 The primary vein framework is pinnate with one basal vein. The major secondary  
521 framework is brochidodromous with regular spacing and angles that increase  
522 proximally. The attachment of the major secondaries to the midvein is strongly  
523 decurrent. The first pair of secondary veins arises from the base forming an angle of 80°  
524 with the midvein and they soon display a perpendicular course to the midvein. The  
525 intercostal tertiary venation fabric is sinuous, with angles generally decreasing towards  
526 the margins in relation to the midvein. The quaternary venation fabric is mixed  
527 percurrent, and the quintenary is irregular reticulated. The areolation is moderate to  
528 good. Free ending veinlets usually have one branch and a simple termination.

529 **Remarks:** The ovate blade shape and the secondary brochidodromous venation pattern,  
530 which shows an angle increasing from 80° at the base to 40° at the apex, are common  
531 leaf features of *A. gaudinii*, according to Knobloch and Kvaček (1976).

532

533 Genus **Carpinus** Linnæus

534 *Carpinus* sp.

535 (Plate III.8)

536 **Material:** IPS109744 displays the apical two thirds of a blade, with poor preservation  
537 detail of the margin and lower order veins. The same leaf morphotype is also  
538 represented by a fragment that preserves the base (IPS109747).

539 **Description:** The leaf is 2.8 cm in length and 1.67 cm wide, elliptical in shape and  
540 symmetric. The apex is attenuate and the base rounded. The margin is damaged.

541 The primary vein network is pinnate with one basal vein. The secondary vein  
542 framework is possibly craspedodromous with regular spacing. The attachment of the  
543 major secondaries to the midvein is excurrent with uniform angles of 30°.

544 **Remarks:** The blade shape and the venation pattern of the specimen seems to be  
545 consistent with *Carpinus*. Unfortunately, the preservation is not good enough to assign  
546 these specimens to a lower taxonomic rank, nor does this morphotype seem comparable  
547 to any description or illustration by Sanz de Siria Catalán (1981).

548

549 Order SAPINDALES Dumortier

550 Family SAPINDACEAE Jussieu

551 Genus **Acer** Linnaeus

552 *Acer tricuspidatum* Brøn, 1838

553 (Plate III.9)

554 1823 *Phyllites trilobatus* Sternberg, 37; pl. 50, fig. 2.

555 ? 1838 *Acer tricuspidatum* Brøn, 865; pl. 35, figs 10a, b – missing holotype.

556 ? 1845 *Acer trilobatum* Al. Braun, 172.

557 ? 1855 *Acer tricuspidatum* Al. Braun; Heer, 14; pl. 2, fig. 3.

558 1870 *Acer trilobatum* Al. Braun; Engelhardt, 28; pl. 8, figs 1–2.

559 1963 *Acer trilobatum* (Sternberg) Al. Braun; Mai, 79; pl. 11, fig. 2.

560 1964 *Acer trilobatum* (Sternberg) Al. Braun; Walther, 59; pl. 21, pl. 22, figs 1–6, pl. 23,

561 figs 2, 5, 8.

562 ? 1968 *Acer tricuspidatum* Brönn; Walther, 363; pl. 2, fig. 1 – neotype.

563 1972 *Acer tricuspidatum* Brönn; Walther, 78; pl. 15, figs. 1–12, pl. 45, figs. 2–10.

564 1996 *Acer tricuspidatum* Brönn; Walther, 14; fig. 3.28.

565 **Material:** IPS109741 is an almost complete blade lacking some detail of the margin and  
566 the apex.

567 **Description:** The specimen studied is 4.1 cm long and 3.2 cm wide. The shape of the  
568 lamina is elliptical and symmetric. The apex is not preserved and the base is cordate.  
569 The margin is lobulated, composed of three lobes, and toothed. The teeth are closely  
570 and regularly spaced, convex or straight in the proximal flank and straight in the distal  
571 flank. The teeth sinuses are angular.

572 The primary vein network is basally actinodromous with five basal veins, three of  
573 which are primary veins, while the exterior two are secondaries. Principal primary veins  
574 terminate at the lobe apex. Simple veins run between the exterior primary veins and the  
575 margin (agrophic veins). These veins are craspedodromous and end at the tooth tip. The  
576 major secondary framework is craspedodromous and the spacing increases proximally  
577 while the angle between the central primary vein and the secondaries is uniform (40°–  
578 60°). The attachment of the major secondaries to the midvein is excurrent. The  
579 intersecondaries run a course that is parallel to the subjacent major secondaries and  
580 occur at a rate of <1 per intercostal area. They are <50% the length of major

581 secondaries. The intercostal tertiary fabric is mixed percurrent, dominated by opposite  
582 percurrent veins at the proximal-most intercostal areas with consistent angles.  
583 Occasionally, some intercostal tertiary veins reach the apex of the tooth.

584 **Remarks:** Sanz de Siria Catalán (1981) attributed this species to *Acer trilobatum*  
585 Sternberg, which was reassigned to *A. tricuspidatum* by Walther (1972).

586

587 Order URTICALES Jussieu et Presl

588 Family ULMACEAE Mirbel

589 *Ulmus* sp.

590 (Plate IV.1)

591 **Material:** IPS109772 is a portion of the blade missing the lower half.

592 **Description:** The leaf measures 1.75 cm in length and 1.25 cm in width acute apex. The  
593 margin is toothed with compound teeth. The main teeth display convex flanks and they  
594 are closely and regularly spaced. Secondary teeth occur on the basal flank of the main  
595 teeth. The tooth sinus is angular.

596 The primary vein framework is pinnate with one basal vein. The major secondary  
597 framework is semicraspedodromous with the principal veins terminating marginally at  
598 the tooth apices. The major secondary spacing is irregular at angles that are uniform at  
599 40°–55°. The attachment of the major secondaries to the midvein is excurrent. The  
600 intercostal tertiary vein fabric is sinuous, however, the tertiaries that intersect the  
601 midvein form chevrons. The quaternary vein fabric is reticulate.

602 **Remarks:** This specimen could correspond to the leaf drawing of Sanz de Siria Catalán  
603 (1981, Plate 1, fig. 7) that he attributed to *Zelkova*. However, the compound teeth of  
604 IPS109772 are unusual for this genus and are instead common in genera *Hemiptelea*  
605 and *Ulmus* (Denk and Grimm, 2005). Attribution to the latter genus appears more  
606 probable based on secondary veins pattern.

607

608 Genus **Zelkova** Spach

609 *Zelkova* sp.

610 (Plate IV.2)

611 **Material:** IPS109703 is almost a complete leaf. IPS 109706 is a highly distorted  
612 specimen. IPS109736 and IPS109743 are respectively part and counter-part specimens  
613 of an incomplete blade that lacks the apical part.

614 **Description:** The leaf measures 1.75–3.4 cm in length and 1.25–2.1 cm in width with  
615 an elliptical shape. It shows medial and basal symmetry and the apex is missing. The  
616 base is acute. The margin is damaged but toothed with simple teeth. Teeth display  
617 convex flanks and they are closely and regularly spaced with 8 teeth per cm. The tooth  
618 sinus is angular.

619 The primary vein framework is pinnate with one basal vein. The major secondary  
620 framework is semicraspedodromous with the principal veins terminating marginally at  
621 the tooth apices. The major secondary spacing is irregular at angles that are uniform at  
622 40°–55°. The attachment of the major secondaries to the midvein is excurrent. The  
623 intercostal tertiary vein fabric is sinuous, however, the tertiaries that intersect the  
624 midvein form chevrons. The quaternary vein fabric is reticulate.

625 **Remarks:** Sanz de Siria Catalán (1981) noted the presence of *Zelkova* within the  
626 collection, attributing one specimen to *Zelkova ungeri* Ettingshausen. We identified five  
627 specimens belonging to this genus in the collection, two being the part and counter-part  
628 of the same leaf and assigned them to *Zelkova* sp., based on the semicraspedodromous  
629 venation pattern that distinguishes it from other Ulmaceae (Wang et al., 2001).  
630 However, without more complete preservation, a more precise taxonomic attribution  
631 would be problematic.

632

633 **Genus *Cedrelospermum***

634 *Cedrelospermum* sp.

635 (Plate IV.3)

636 **Material:** IPS109740 shows an almost complete blade. IPS109742 and IPS109767 are  
637 fragmentary specimens.

638 **Description:** The position of the laminar attachment is marginal and the size of the  
639 complete blade is at least 3.23 cm long, lacking the very tip of the apex, and 0.85 cm  
640 wide. The laminar shape is elliptical with both medial and basal symmetry. The base  
641 might be cordate and the apex was likely acute but is not complete. The margin is  
642 toothed with regularly and closely spaced teeth, showing a convex shape along both  
643 flanks.

644 The primary vein framework is pinnate. The major secondaries are craspedodromous  
645 and end at the apex of the teeth. They are regularly spaced (7 veins per cm) and arise at  
646 angles of 45°–80° from the midvein. The angle between the midvein and the secondary  
647 vein decreases towards the apex. The secondary vein attachment is excurrent. The

648 intersecondaries appear to be parallel to the major secondaries but this is only seen in  
649 the distal third of the specimen. There is one intersecondary vein per intercostal area.  
650 The intercostal tertiary vein fabric is reticulate.

651 **Remarks:** This leaf was probably attributed to *Salix lavateri* (Braun) by Sanz de Siria  
652 Catalán (1981), as deduced by comparison of IPS109740 with his hand drawings.  
653 However, according to Fernández-Marrón (1971) the first pair of secondary veins of *S.*  
654 *lavateri* rises from the midvein with acute angles, while in the specimen studied from  
655 La Bisbal d'Empordà it forms a 70°–80° angle with the midvein. The secondary and  
656 tertiary venation pattern and the blade shape of *Cedrelospermum* sp. from Shuanghu  
657 County (Tibet, China) described by (Jia et al., 2018) matches the leaf features from the  
658 specimen from La Bisbal d'Empordà, suggesting ascription to this genus.

659

660 Order LAMIALES Bromhead

661 Family OLEACEAE Hoffmanns et Link

662 Genus **Fraxinus** Tourn. ex Linnæus

663 *Fraxinus* sp.

664 (Plate IV.4)

665 **Material:** Blades with excellent preservation of the venation but partial preservation of  
666 margins, apex or base in IPS109701, IPS109711, IPS109716, IPS109730, IPS109731,  
667 IPS109733, IPS109753, IPS109575, IPS109758, IPS109765 and IPS109766. Specimen  
668 IPS109753 appears to be a compound leaf, with anatomically connected leaflets.

669 **Description:** Compound leaf comprising at least five leaflets. Leaflets arrangement is  
670 opposite or subopposite. The leaflets measure up to 3.2 cm in length and 1 cm in width

671 and have a petiolule. The shape of the leaflet lamina is elliptic with both basal and  
672 medial symmetry. Usually, the apex and base of leaflets are acute, but they vary to  
673 rounded in some specimens. The margin is toothed. The tooth shape is straight at the  
674 proximal and distal flanks and the sinuses are angular. The teeth are regularly spaced,  
675 with up to 8 teeth per cm.

676 In leaflets, the primary vein framework is pinnate. The major secondary framework is  
677 brochidodromous with irregular spacing and angles, which generally increase  
678 proximally but irregularly. The secondary veins rise from the midvein at 60°–70° and  
679 the attachment to the midvein is excurrent. The intersecondaries run parallel to the  
680 subjacent major secondary vein and usually there is one intersecondary vein per  
681 intercostal area. The tertiary venation fabric is mixed percurrent with angles that  
682 decrease in relation to the midvein as they approach the margins. The epimedial  
683 tertiaries are reticulate and the exterior tertiaries form loops. The quaternary fabric is  
684 mixed percurrent and the quintenary fabric is reticulating to form irregular polygons.  
685 The areolation is paxillate and with good development.

686 **Remarks:** These leaves were attributed by Sanz de Siria Catalán (1981) to *Pterocarya*  
687 *fraxinifolia* (Spach). Nevertheless, *Pterocarya* leaves are compound with sessile leaflets  
688 displaying asymmetrical bases, instead of the petiolulate symmetrical leaflets found in  
689 the fossils studied from la Bisbal. The base shape varies in both flanks of the leaflet.  
690 The proximal flank is rounded while the distal flank is straight. This contrasts with  
691 *Fraxinus* leaflets which shows straight shape in both flanks. In addition, extant *P.*  
692 *fraxinifolia* leaflets are oblong rather than elliptic in shape. As regards venation, the  
693 secondary veins of *P. fraxinifolia* rise from the midvein in 40° which contrasts with the  
694 60°–70° of the fossil specimens from La Bisbal d'Empordà. In turn, the tertiary venation

695 framework of *P. fraxinifolia* is regular reticulate while the fossils species studied here  
696 shows a mixed tertiary venation pattern.

697 Otherwise, sample IPS109753 is most likely a compound leaf with subopposite leaflets  
698 that rules out affinities with other genera that may show similar leaf/leaflet margin  
699 features, such as *Salix*, but do not bear composite leaves.

700

701 -----Insert Plate IV near here-----

702 -

703

704 Incertae sedis

705 Undetermined magnoliopsid 1

706 (Plate V.1)

707 **Material:** IPS109718, a distal half of a blade with some damage to the apex and  
708 margin.

709 **Description:** Blade measuring at least 2.75 cm in length and 3.16 cm in width. There is  
710 medial symmetry. The margin is toothed. The tooth shape is straight or slightly convex  
711 at the proximal and distal flanks and the sinuses are angular.

712 The primary vein is pinnate and sympodial. The major secondary vein framework is  
713 brochidodromous.. The attachment of the major secondaries to the midveins is decurrent  
714 and form angles of 45°–60°.. The intersecondaries run at a greater angle than the major  
715 secondaries. The intercostal tertiary vein fabric is straight, forming 45° with the  
716 midvein.. The exterior tertiaries terminate at the tooth apex or form loops.

717 **Remarks:** The limited material available and its poor preservation is considered  
718 insufficient to know its taxonomic attribution.

719.

720

721 Undetermined magnoliopsid 2

722 (Plate V.2; Fig. 5.5)

723 **Material:** IPS109734 is an incomplete proximal part of a blade. Another leaf fragment  
724 is glued to the same specimen and this piece was recognised here as a counterpart piece  
725 of the specimen apex.

726 **Description:** The only specimen available is 3.45 cm in long and 6.35 cm wide, and  
727 lacks the leaf margin. The shape of the blade is ovate and symmetric. The base is  
728 cordate.

729 The primary vein framework is palmate with three actinodromous basal veins. Interior  
730 secondaries display a sinuous course. The secondary veins arise from the primary veins  
731 at  $45^{\circ}$ – $110^{\circ}$  and their spacing along the blade is irregular. The attachment of the major  
732 secondaries to the midvein is decurrent. The intercostal tertiary fabric is sinuous.

733 **Remarks:** The preservation is not good enough to assign IPS109734 to a lower  
734 taxonomic rank, nor does this morphotype seem comparable to any description or  
735 illustration by Sanz de Siria Catalán (1981). For these reasons, it has been kept as an  
736 undetermined magnoliopsid.

737

738 Undetermined magnoliopsid 3

739

(Plate V.3; Fig. 5.6)

740 **Material:** IPS109729 and IPS109766 are two incomplete blades, both missing the base.

741 **Description:** The leaf is ovate and symmetric. The laminar size is estimated at 12 cm in  
742 length. The position of the laminar attachment is marginal

743 The primary venation pattern is pinnate. The major secondary framework is  
744 brochidodromous with irregular spacing and angles that increase proximally. The  
745 attachment to the midvein is decurrent. The intersecondary veins have a proximal  
746 course rising parallel to the subjacent major secondary but distally they are curved  
747 towards the base to join the adjacent major secondary. The intersecondaries are 50% the  
748 length of the major secondaries. The intercostal tertiary fabric is percurrent convex with  
749 angles that increase towards the margins in relation to the midvein. The exterior  
750 tertiaries are looped. The quaternary vein fabric is regular reticulated.

751 **Remarks:** These specimens were attributed to *Carya bilinica* Unger by Sanz de Siria  
752 Catalán (1981), who illustrated one of them in his hand-drawing of Figure 16, however  
753 here the limited material available and its poor preservation is considered insufficient to  
754 confirm his attribution.

755

756 -----Insert Fig.5 near here-----

757

758 Undetermined magnoliopsid 4

759

(Plate V.4; Fig. 5.7)

760 **Material:** IPS109767 is a deformed and incomplete blade. The apical and the basal  
761 part, some interior fragments and the right margin are damaged. Possible fragmentary  
762 material is also found in IPS109762.

763 **Description:** The specimen IPS109767 is at least 2.7 cm long and 2.35 cm wide. The  
764 base, apex and margin shape is unknown.

765 The primary vein is pinnate with one basal vein. The major secondary framework rises  
766 from the midvein at 30°–40°. The major secondary spacing abruptly decreases distally  
767 with angles that increase proximally. The attachment of the major secondaries to the  
768 midvein is excurrent. The intercostal tertiary fabric is percurrent forming chevrons. The  
769 quaternary and quintenary fabrics are reticulate forming irregular polygons. The  
770 areolation is well-developed.

771 **Remarks:** This specimen was attributed to *Viburnum* sp. by Sanz de Siria Catalán  
772 (1981) due to an observed similarity with the extant *Viburnum opulus*. It is also similar  
773 to *Beringiaphyllum cupanioides* Manchester from the Paleocene of Montana and  
774 Wyoming (U.S.A.), on the basis of (1) the distinct secondary venation with few major  
775 secondaries, which have a greater angle closer to the base of the lamina and form the  
776 principal veins of the teeth, and (2) the percurrent tertiaries. However, the preservation  
777 of a long petiole would be necessary to be more certain of the specimens' affinities to  
778 *Beringiaphyllum cupanioides* (Manchester et al., 1999).

779

780 Undetermined magnoliopsid 5

781 (Plate V.5)

782 **Material:** IPS109710 is a complete blade, lacking some details of the margin.

783 **Description:** The specimen studied measures 1 cm in length and 0.65 cm in width and  
784 the lamina has an elliptical shape. There is both medial and possible basal symmetry.  
785 The base is convex and the apex is straight, with an obtuse angle. The margin is toothed.  
786 The tooth shape is convex in the proximal and distal flank. They are closely and  
787 regularly spaced. The sinuses are acute.

788 The primary vein framework is pinnate with one basal vein. The major secondary vein  
789 framework is craspedodromous forming the principal vein termination at the apex of the  
790 teeth. The spacing of the major secondaries is regular and they have uniform angles of  
791 50–60°. The attachment of the major secondaries to the midvein is decurrent. The  
792 intercostal tertiary vein framework is reticulate forming irregular polygons.

793 **Remarks:** According to drawings in Sanz de Siria Catalán (1981) this specimen was  
794 assigned to the genus *Ulmus* however, since the base is not asymmetric this attribution  
795 has not been maintained and IPS109710 is provisionally regarded as an undetermined  
796 magnoliopsid herein.

797

798

799 Undetermined magnoliopsid 6

800 (Plate V.6)

801 **Material:** IPS109708 is an incomplete basal part of a blade, with damaged margins.

802 **Description:** The laminar attachment is marginal. The size of the specimen is 4.1 cm in  
803 length and 5.3 cm in width. There is medial symmetry and the base is straight and  
804 slightly decurrent. The margin is possibly trilobed but too damaged to provide further  
805 details.

806 The primary vein network is palmate and palinactinodromous with three basal-  
807 suprabasal veins. The exterior primaries are concave to the midvein in the basal-most  
808 part, and form angles of 45°. Then they follow a straight course. The major secondaries  
809 have irregular spacing and the attachment with the primary veins is excurrent. The  
810 secondary venation pattern is unknown. The intersecondaries arise at a greater angle  
811 than the major secondaries and occur infrequently. The intercostal tertiary vein fabric  
812 forms irregular polygons. The lower order venation fabrics also seems reticulate and  
813 with good areolation development.

814 **Remarks:** Based on the venation pattern and the preserved parts of the margin, the  
815 specimen may correspond to the genus *Acer*. However, the primary veins of IPS109708  
816 diverge in a series of branches rather than from a single point as shown in *Acer* sp. from  
817 La Bisbal d'Empordà (IPS109741). The limited and fragmentary material available is  
818 considered insufficient to confirm this attribution.

819 Undetermined magnoliopsid 7

820 (Plate V.7)

821 **Material:** IPS109771 is a complete blade with a preserved petiole but with poorly  
822 preserved veins.

823 **Description:** The leaf blade is 1.93 cm long and 0.9 cm wide and has an elliptical  
824 shape. There is medial symmetry and possible basal asymmetry. The base is acute and  
825 the apex is missing. The margin is toothed. The teeth are acute with a straight edge on  
826 both sides, regularly and distantly spaced with angular sinuses.

827 The primary vein network is pinnate with one basal vein. The major secondary venation  
828 framework is craspedodromous with veins showing a regular spacing and uniform  
829 angles of 50°–55°. The attachment of the major secondaries to the midvein is excurrent.

830 The principal secondary veins terminate at the apices of teeth. The intercostal tertiary  
831 venation fabric is percurrent to reticulating.

832 **Remarks:** Sanz de Siria Catalán (1981) also considered this specimen as belonging to  
833 *Ulmus*, however, the base is not clearly asymmetric therefore a lower taxonomic rank  
834 attribution was not attempted here.

835

836 Undetermined magnoliopsid 8

837 (Plate V.8)

838 **Material:** IPS109728 is a damaged blade missing clear detail of the apex and basal  
839 parts of the lamina and with eroded margins.

840 **Description:** The blade measures 1.9 cm in length and 0.9 cm in width. The shape of  
841 the lamina is obovate and symmetric. The margin is unlobed and possibly toothed. The  
842 base shape is acute.

843 The primary vein framework is pinnate with just one basal vein. The major secondary  
844 venation framework is craspedodromous although the termination of the principal veins  
845 is not clear. The spacing of the major secondaries is irregular and the angles with  
846 respect to the primary vein increase proximally. The attachment of the major  
847 secondaries is decurrent. The intersecondaries have a course which is parallel to the  
848 major secondaries but then reticulates towards the margin. Intersecondaries occur  
849 infrequently between the major secondaries, and display a length that represents less  
850 than half of the length of the major secondaries.

851 **Remarks:** The preservation is not good enough to assign it to a lower taxonomic rank,  
852 nor does this morphotype seem comparable to any description or illustration by Sanz de  
853 Siria Catalán (1981).

854

855 -----Insert Plate V near here-----

856 *4.3 Plant taphonomy and palaeoecology*

857 The taphonomic analysis of the plant remains from La Bisbal d'Empordà allows to  
858 elucidate the palaeoenvironment in which the plants grew, as well as the possible biases  
859 that were introduced during the formation of the deposits which yielded them.

860 *Description.* The preservation quality of the assemblage is poor. The assemblage  
861 consists of 72 specimens, some containing multiple blades or fragments, 45% of which  
862 have the tertiary or lower order venation present. However, only 13% of the plant  
863 remains have a complete blade and just 3% of them also have the tertiary or lower  
864 order venation preserved. Over 50% of the samples have evidence of leaf tearing and  
865 more than 45% have extensively fragmented lamina that are completely undiscernible  
866 and lack any defining features. Identifiable leaf remains correspond to *Daphnogene* sp.,  
867 *Laurophyllum* sp., *Platanus* sp., *Alnus gaudinii*, *Carpinus* sp., *Acer tricuspidatum*,  
868 *Fraxinus* sp., *Zelkova* sp., *Populus balsamoides*, *Ulmus* sp. and *Cedrelospermum* sp.  
869 These specimens bear evidence of leaf tearing, many presenting a polygonal tearing  
870 pattern that follows the primary and secondary venation (Plate VI.1). Of those which  
871 present a reasonably complete lamina, at least half of the assemblage has eroded or  
872 damaged leaf margins.

873 Less than 20% of the samples bear helophytic plant stems, likened to reeds, and  
874 sometimes multiple stem portions occur in a given sample (Plate VI.2). These plant

875 portions are 3–4 cm long and 1–2 cm wide. Furthermore, about 10% of the specimens  
876 are orbicular winged *Paliurus* seeds. Most of them are complete but a few show a small  
877 amount damage to the wing (Plate VI.3). *Fraxinus* leaflets are commonly isolated as  
878 seen in Plate III.4, with just a single occurrence of a compound leaf, thought to belong  
879 to this genus (Plate VI.4).

880

881 -----Insert Plate VI near here-----

882

883 *Interpretation:* The taphonomic evidence is consistent with the sedimentological  
884 interpretation provided in section 4.1., suggesting that most of the leaf-assemblage  
885 underwent significant water transport in tractive fluvial flows (e.g., in fluvial channels)  
886 before its deposition on the floodplain. The high percentage of fragmented remains,  
887 mainly corresponding to *Daphnogene* sp., *Laurophyllum* sp., *Acer tricuspidatum*,  
888 *Zelkova* sp., *Populus balsamoides*, *Platanus* sp., *Alnus gaudinii* and *Carpinus* sp., with  
889 angular breaks and tearing along the axis of the primary and secondary veins, is typical  
890 of damage incurred by traction in the water column (Spicer, 1981; Ferguson, 1985;  
891 Martín-Closas and Gomez, 2004). In particular, the evidence of breakage along the  
892 primary veins is indicative of a relatively high energy environment and turbulent flow  
893 (Spicer, 1981; Ferguson, 1985). Therefore, these plant remains would constitute an  
894 allochthonous assemblage.

895 The relatively abundant and almost intact winged seeds of *Paliurus* together with the  
896 absence of other organs of this plant such as leaves, indicate a clear plant organ  
897 selection. These taphonomic data are consistent with aerial transport. Based on the  
898 observations carried out by Ridley (1930), ripe winged seeds such as *Paliurus* are

899 known to be aerodynamic and thus easily transported by the wind before being  
900 sedimented in the depositional setting. Some *Paliurus* fossil seeds from La Bisbal  
901 d'Empordà would have also undergone a short and gentle transport somewhat damaging  
902 the wing. In both cases, these plant remains would also constitute an allochthonous  
903 assemblage.

904 The presence of just one articulated compound leaf of *Fraxinus* suggests that the  
905 organ's abscission, transportation and its final introduction into the depositional  
906 environment was most likely the result of a traumatic event such as a storm (Ferguson,  
907 1985). This suggests the reasonable proximity of living *Fraxinus* sp. to the depositional  
908 environment indicating paraautochthony.

909 The helophytic plant portions (stems of reeds), which may sometimes be abundant,  
910 were transported to the floodplain after physiological abscission and more or less  
911 prolonged flotation period, probably within the same depositional setting. Therefore,  
912 they define a paraautochthonous assemblage.

913 **5. Discussion**

914 The taxonomic description of the La Bisbal d'Empordà fossil leaf collection together  
915 with the sedimentological and taphonomic results are significant for the  
916 characterisation of the Vallesian lowland vegetation of this locality in the northeast of  
917 the Iberian Peninsula. Associated small mammal fossils provide an independent and  
918 complementary source of information for palaeoenvironmental reconstruction.

919

920 *5.1. Vallesian plant composition of La Bisbal d'Empordà*

921 The taxonomic results for the La Bisbal d'Empordà fossil leaf collection presented  
922 herein considerably improve previous knowledge by including the details of the  
923 venation pattern and foliar polymorphism. These prompt reconsideration of the species  
924 composition and abundance reported by Sanz de Siria Catalán (1981). As a matter of  
925 fact, many of the leaf morphotypes he distinguished are only represented by one or a  
926 few specimens, which in some cases are of dubious taxonomic attribution. For example,  
927 the specimens within the assemblage identified here as *Daphnogene* sp., equivalent to  
928 *Cinnamomum polymorpha* in Sanz de Siria Catalán (1981), comprise just three  
929 individual leaves in stark contrast to the 25% abundance reported by this author. Also,  
930 morphotypes attributed by this author to genus *Quercus*, have been reassigned here to  
931 genera *Zelkova* and *Cedrelospermum*. These differences are partly due to the careful  
932 description of the venation pattern, which is considered to provide more diagnostic  
933 characters for species identification in contrast to the general leaf morphology and leaf  
934 margin features considered in previous work. A single notable morphotype represented  
935 by multiple specimens, sometimes with leaflets in anatomical connection, is *Fraxinus*  
936 sp., equivalent to *Pterocayra fraxinifolia* in Sanz de Siria Catalán (1981). This taxon  
937 accounts for 30% of the assemblage, equivalent to the abundance of his *P. fraxinifolia*,  
938 suggesting both its importance in the community and, most likely its proximity to the  
939 environment of deposition.

940 Sanz de Siria Catalán (1997) in his study of the macroflora of Terrassa (Vallès-Penedès  
941 Basin), also of late Vallesian age (MN10, 9.3 Ma; see Agustí et al., 2003), found certain  
942 similarities in plant composition with La Bisbal d'Empordà, but highlighted a clear  
943 dominance of five species in the latter collection (*P. fraxinifolia*, *Cinnamomum*  
944 *polymorpha*, *Platanus aceroides*, *Populus balsamoides* and *Acer trilobatum*) whereas  
945 the Terrassa assemblage is more balanced. However, our re-examination of the La

946 Bisbal d'Empordà assemblage suggests that aside from the high abundance of *Fraxinus*  
947 sp., its composition is indeed more similar sharing many genera including, *Acer*, *Ulmus*,  
948 *Carpinus*, *Populus*, *Zelkova*, *Daphnogene* (“*Cinnamomum*”) and *Laurophyllum*.

949

950 *5.2. Reconstruction of the Vallesian plant communities from La Bisbal d'Empordà*

951 The sedimentary deposits exposed at La Bisbal d'Empordà and the surrounding  
952 outcrops of the L'Empordà Basin were originally interpreted as a lake margin  
953 environment (Sanz de Siria Catalán, 1981) and later as part of a strictly alluvial system  
954 (Picart et al., 1996). Casanovas-Vilar et al. (2010) also interpreted these facies as  
955 belonging to a distal part of an alluvial fan with the fossil-bearing clays being deposited  
956 in low energy settings. As discussed herein, the sedimentology strongly suggests that  
957 there was an active fluvial influence within this alluvial-fluvial system, in contrast to  
958 previous interpretations. A tractive flow with sufficient energy is needed to produce the  
959 observed sedimentary structures of the cross-bedded channel lenses (Nichols, 2009) as  
960 well as the characteristic leaf tearing seen in a high percentage of the specimens. In the  
961 more proximal parts of the streams there was possibly some precipitation seasonality, as  
962 this is required to form braided channels (Miall, 1992). Although there is certainly some  
963 evidence of alluvial systems (i.e., a single debris-flow deposit seen in the Can Fuertes  
964 section from the present study), these are by no means the dominant facies.

965

966 The combined results of the sedimentology together with the taphonomic analysis of the  
967 Vallesian flora from La Bisbal d'Empordà provide significant new palaeoecological  
968 data compared to previous studies and suggest that the plant remains studied here  
969 belong to three plant palaeocommunities (Fig. 6):

970 - Helophytic plant belt: This was mainly composed of reed plants, that were locally  
971 abundant. *Equisetum parlatorii* described and figured by Sanz de Siria Catalan (1981),  
972 could also be assigned to this plant community, but wasnot found in the studied  
973 collection here. This suggests that there were stable water tables capable of supporting a  
974 wetland community. This community is consistent with the edaphic features of the  
975 strata. However, this community is usually related to hydromorphic soils (Retallack,  
976 2008), which is in contrast with the dominance of alfisols recognised in the field.

977 -Riparian vegetation: It would have consisted of *Fraxinus* sp., *Ulmus* sp., *Zelkova* sp.,  
978 *Cedrelosperrum* sp. *Populus balsamoides*, *Alnus gaudinii*, *Carpinus* sp., *Platanus* sp.,  
979 *Acer tricuspidatum*, *Daphnogene* sp. and, *Laurophylum* sp. Most of the leaves from  
980 these genera and species are significantly damaged following the venation pattern.  
981 These taphonomic features indicate that they were transported by traction flows from an  
982 area located not far from the floodplain. However, the abundance of leaflets and the  
983 exceptional articulation of one leaf suggest that *Fraxinus* grew nearby the floodplain  
984 water table.

985 - Open landscape vegetation: This would be the biotope of *Paliurus*, from which only  
986 the orbicular winged seeds were found. This organ selection would indicate a wind  
987 transport of these seeds from a site beyond previous communities, without excluding a  
988 later transport by water or floatation until reaching the floodplain water table. Therefore,  
989 this plant would be the sole representative of the assemblage forming an open  
990 community beyond the riverine vegetation that entered the fossil record.

991

992 -----Insert Figure 6 near here-----

993 The results of the taphonomic analysis conform with that of the sedimentology in that  
994 most of the leaf assemblage corresponds to a riparian forest. Sanz de Siria Catalán  
995 (1981) inferred the presence of similar vegetation belts, yet our taphonomic analyses  
996 indicate that the riparian forest would have been limited to humid zones close to the  
997 floodplain, rather than defining an extensive forest as previously suggested.

998 Azonal riparian vegetation may share little similarities with the overall vegetation  
999 (Ferguson, 1985). Most of the species from azonal vegetation display toothed margins  
1000 and thus provide a more humid and cooler climatic signal when methods based on leaf  
1001 physiognomy such CLAMP (Climate Leaf Analysis Multivariate Program) or LMA  
1002 (Leaf Margin Analysis) are used to infer paleoclimate (Royer and Wilf, 2006). In  
1003 contrast, the occurrence of *Paliurus* seeds in the assemblage from La Bisbal d'Empordà,  
1004 which we interpret as a zonal element of the Vallesian at L'Empordà Basin, would be a  
1005 reliable climatic indicator. Some extant *Paliurus* species such as *P. ramosissimus* and *P.*  
1006 *hirsutus* are restricted to riparian and coastal environments, while one species, *P. spina-*  
1007 *christi*, inhabits more arid environments where it forms part of the open landscape  
1008 vegetation. Based on taphonomic evidence, Vallesian *Paliurus* from La Bisbal  
1009 d'Empordà would prefer open and relatively more arid environments than those from  
1010 the floodplain and surrounding riverine vegetation.

1011

1012 *5.3. Comparison with the associated small mammal fauna*

1013 The mammal fauna found at the La Bisbal d'Empordà sites provides additional  
1014 information on the palaeoenvironment. The exact provenance of the large mammal  
1015 remains is uncertain. Although Villalta (1958) stated that the large mammal remains  
1016 from this locality were found 1 km west of La Bisbal d'Empordà village, and thus near

1017 the Can Colomer clay pit, the exact bed is unknown and are not taken into consideration  
1018 for palaeoenvironmental reconstruction herein.

1019 The small mammal assemblages from La Bisbal d'Empordà are dominated by cricetids  
1020 (hamsters and relatives) and ochotonid lagomorphs and include a few insectivores  
1021 (Eulipotyphla) and arboreal taxa. The glirid *Muscardinus hispanicus*, which belongs to  
1022 the same genus as the extant hazel dormouse (*Muscardinus avellanarius*), is the only  
1023 presumably arboreal form in the whole assemblage and is only represented by 2  
1024 specimens (out of 56) in Can Colomer 2. Same as arboreal mammals, insectivorous  
1025 mammals (mainly belonging to the order Eulipotyphla) are more taxonomically diverse  
1026 in more humid and forested habitats (Van Dam, 2006; Van Dam and Utescher, 2016).

1027 Not surprisingly, these are rare at the La Bisbal d'Empordà sites, only being represented  
1028 by an undetermined soricid (shrew), an erinaceid (hedgehog) and the dimylid  
1029 *Plesiodymylus* sp. at Can Colomer 2. Although the studied samples are limited, the  
1030 rarity of such taxa indicates somewhat arid conditions. The presence of solely terrestrial  
1031 squirrels (*Heteroxerus*, *Spermophilinus*) and none of the arboreal or gliding forms that  
1032 are common at Miocene sites, reinforces this conclusion, together with the occurrence  
1033 of the dormouse *Myodyromys hamadryas*, which is also believed to have favoured open  
1034 environments (see Van der Meulen and De Bruijn, 1982). Finally, the moderately high-  
1035 crowned molars of the cricetids *Hispanomys dispectus* and *Rotundomys freirensis*,  
1036 which are common at the sites, are indicative of a diet that includes abrasive plants such  
1037 as the grasses characteristic of open, relatively arid, landscapes (Van Dam and Weltje,  
1038 1999; Casanovas-Vilar and Agustí, 2007).

1039 The composition of the Vallesian rodent faunas from the L'Empordà Basin contrasts  
1040 with that of the nearby the Vallès-Penedès Basin situated 90 km to the southwest. The  
1041 Vallès-Penedès sites often include a higher diversity of arboreal dormice and

1042 insectivores than La Bisbal d'Empordà, with the addition of flying squirrels which are  
1043 absent at the latter (Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2016a).  
1044 These differences might be due in part to the limited sample size of the La Bisbal  
1045 d'Empordà sites or reflect taphonomic biases. Indeed, a remarkable proportion of  
1046 specimens show taphonomical alterations produced by predators, such as partial  
1047 dissolution of enamel and dentine by gastric acids (see Plate I.3, I.15–16). The degree of  
1048 digestion ranges from moderate to heavy, as characteristic of certain aerial raptors (see  
1049 digestion categories in Fernández-Jalvo and Andrews, 2016). The hunting range for  
1050 aerial predators is generally broad, and these may have hunted in various habitats far  
1051 from humid areas. Subsequently raptor pellets with undigested bones would have been  
1052 regurgitated and ended up in the depositional site. Therefore, the small mammal  
1053 assemblage would not only include taxa living near the depositional environment but  
1054 also others that would have likely dwelled in the more open areas away from it. In  
1055 summary, small mammal evidence from the Vallesian deposits from La Bisbal  
1056 d'Empordà is congruent with the palaeobotanical reconstruction based on the plant  
1057 collection, showing a mixture of taxa that inhabited humid and forested landscapes with  
1058 others that likely preferred more open country. Taphonomic biases may partly account  
1059 for the underrepresentation of the former.

1060

## 1061 **6. Conclusions**

1062 Sedimentological and taphonomic evidence presented here challenges former  
1063 interpretations of the depositional environment of the La Bisbal d'Empordà  
1064 palaeobotanical site. Previously thought to correspond to a lake margin or to be of

1065 strictly alluvial fan facies, we now show that fluvial processes were dominant in the  
1066 section, thus accounting for the preservation and composition of the plant assemblage.

1067 Three plant palaeocommunities are recognized for the Vallesian deposits of La Bisbal  
1068 d'Empordà: 1) Helophytic plants grew in the floodplain facies forming a wetland  
1069 vegetation. 2) *Fraxinus* sp., *Ulmus* sp., *Zelkova* sp., *Cedrelospermum* sp. *Populus*  
1070 *balsamoides*, *Alnus gaudinii*, *Carpinus* sp., *Platanus* sp., *Acer tricuspidatum*,  
1071 *Daphnogene* sp and, *Laurophyllum* sp. would have constituted a riparian forest that  
1072 grew behind the helophytic belt. 3) Open landscape vegetation, about which only very  
1073 limited information is available. Only winged seeds of *Paliurus* sp. are represented and  
1074 are thought to have mainly been wind transported, thus indicating that this plant grew  
1075 away from previous belts in relatively less humid areas. Future palynological studies of  
1076 the Vallesian La Bisbal d'Empordà sites will probably provide much more information  
1077 on this plant community than do the plant mega-remains.

1078 The associated small mammal fauna coeval to the plant remains studied here is  
1079 consistent with this environmental interpretation. The bulk of the micromammal fauna  
1080 is defined by terrestrial species linked to open landscapes, while arboreal species, such  
1081 as *Muscardinus hispanicus* or insectivores associated with humid and forested  
1082 environments, are rare in the assemblage. The apparent overrepresentation of open-  
1083 landscape taxa may be explained by taphonomic factors.

1084 The prevalence of riparian elements in the La Bisbal d'Empordà floral assemblage  
1085 should be carefully considered in palaeoclimatic reconstructions based on leaf margin  
1086 analysis such as CLAMP or LMA. The dominant riparian elements would certainly  
1087 distort the results of this type of analyses by showing exaggerated humidity and low  
1088 temperature ranges.

1089 Finally, our results illustrate the value of combined taxonomic and sedimentological-  
1090 taphonomic analyses for palaeoenvironmental reconstruction. Similar studies should be  
1091 conducted in other coeval macrofloral assemblages from neighbouring basins, such as  
1092 in the Vallès-Penedès Basin (Terrassa assemblage) to better characterise the late  
1093 Miocene lowland vegetation of NE Iberia and to compare it to other parts of Southern  
1094 Europe.

1095

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1112

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1360

1361 **Figure captions**

1362 **Figure 1:** Geological setting of the L'Empordà Basin with location of the study area  
1363 (square), modified from Picart et al. (1996).

1364 **Figure 2:** Map with the location of the sections studied. Modified from ICGC  
1365 (<http://www.icc.cat>).

1366 **Figure 3:** Stratigraphic section studied in the Vallesian from La Bisbal with the  
1367 estimated position of the plant bed studied.

1368 **Figure 4:** Argiles Bisbal SL outcrop (interval 3) and facies interpretation, showing  
1369 fluvial features such as clast-supported conglomerates, cross-bedding and marked  
1370 erosive bases.

1371 **Figure 5:** Line drawing of some leaves from the Vallesian deposits of La Bisbal  
1372 d'Empordà showing the characteristic foliar characters. 1: *Laurophyllum* sp. displaying  
1373 the brochidodromous secondary veins (IPS109721). 2: *Populus balsamoides* with  
1374 brochidodromous secondary veins (IPS109715). 3: Rosaceae gen. et sp. indet showing  
1375 the straight path of the tertiary veins (IPS109745). 4: *Alnus gaudinii* displaying the first  
1376 pair of secondary veins forming almost a perpendicular angle with the midvein and the  
1377 sinuous path of the tertiary venation pattern (IPS109761). 5: Undetermined  
1378 magnoliopsid 2 with sinuous tertiary veins (IPS109734). 6: Undetermined magnoliopsid  
1379 3 showing sinuous tertiary veins and quaternary vein fabric reticulate (IPS109729).  
1380 .7: Undetermined magnoliopsid 4 with sinuous tertiary veins (IPS109767).. Scale bar 1  
1381 cm.

1382 .

1383 **Figure 6:** Palaeoenvironmental reconstruction of the Vallesian from La Bisbal  
1384 d'Empordà flora.

1385 **Plate I:** Fossil rodents from the Vallesian sites from La Bisbal d'Empordà. 1:  
1386 *Megacricetodon* cf. *minutus*, left lower first molar (IPS29925) from AVM4. 2:  
1387 *Megacricetodon ibericus* left lower first molar (IPS29922) from AVM4. 3:  
1388 *Megacricetodon ibericus* right upper first molar (IPS29921, reversed) from AVM4  
1389 showing partial digestion of enamel and dentine in the labial cusps (arrows) that have  
1390 altered the morphology in this area. 4: *Democricetodon* cf. *nemoralis*, left upper first  
1391 molar (IPS29938) from AVM10. 5: *Rotundomys* cf. *freirensis*, right upper first molar  
1392 (IPS1992, reversed) from Can Colomer 2. 6: *Rotundomys* cf. *freirensis*, same specimen  
1393 (IPS1992) in lingual view, note the semi-hypsodont crown and flat wear surface  
1394 (compare with Plate I.10). 7: *Rotundomys* cf. *freirensis*, left lower first molar  
1395 (IPS29940) from AVM10. 8: *Miodyromys hamadryas*, right upper second molar  
1396 (IPS29936, reversed) from AVM4. 9: *Neocricetodon ambarrensis*, left upper first  
1397 molar (IPS29938) from AVM10. 10: *Neocricetodon ambarrensis*, same specimen  
1398 (IPS29938) in lingual view showing the low-crowned, bunodont pattern. 11:  
1399 *Neocricetodon ambarrensis*, left lower first molar (IPS29941) from AVM10. 12:  
1400 *Muscardinus hispanicus*, left upper third molar (IPS120016) from Can Colomer 2. 13:  
1401 *Heteroxerus* sp., left upper first or second molar (IPS120070) from La Bisbal 2. 14:  
1402 *Hispanomys dispectus*, right lower first molar (IPS29929, reversed) from AVM4. 15:  
1403 *Hispanomys dispectus*, right upper first molar (IPS29933, reversed) from AVM4  
1404 showing partial digestion of the enamel in the lingual cusps, particularly the hypocone  
1405 (arrows). 16: *Hispanomys dispectus*, detail of the hypocone of the same specimen  
1406 (IPS29933, reversed) highlighting the digested area. Scale bar is 1 mm in all figures  
1407 except in Figure 16, in which it is 500 µm.  
1408 **Plate II:** Lithofacies from the Vallesian of La Bisbal d'Empordà. 1: Red clays and  
1409 siltstones with intercalations of fine-grained sandstones of interval 1 from Can Colomer

1410 section. 2: Intercalations of sandstones and siltstones of interval 2 from Estanyol Cordat  
1411 section. 3: Red clays with root marks of interval 3 from Can Fuertes section. 4: Clast-  
1412 supported conglomerates from interval 3 at Can Fuertes. 5: Sandstone beds with cross-  
1413 bedding and undulated, erosive beds at interval 4 from Can Fuertes. 6: Lenticular  
1414 conglomerate beds with intercalations of sandstones from interval 5 of Vacamorta  
1415 section.

1416 **Plate III:** Fossil plant taxa from the Vallesian plant collection from La Bisbal  
1417 d'Empordà. 1: *Daphnogene* sp. (IPS109714) 2: *Laurophyllum* sp. (IPS109721). 3:  
1418 *Platanus* sp. (IPS109709). 4: *Populus balsamoides* (IPS109715). 5: *Paliurus* sp.  
1419 (IPS109760). 6: Rosaceae gen. et sp. indet (IPS109745). 7: *Alnus gaudinii* (IPS109722).  
1420 8: *Carpinus* sp. (IPS109744). 9: *Acer tricuspidatum* (IPS 109741). Scale bar 1 cm.

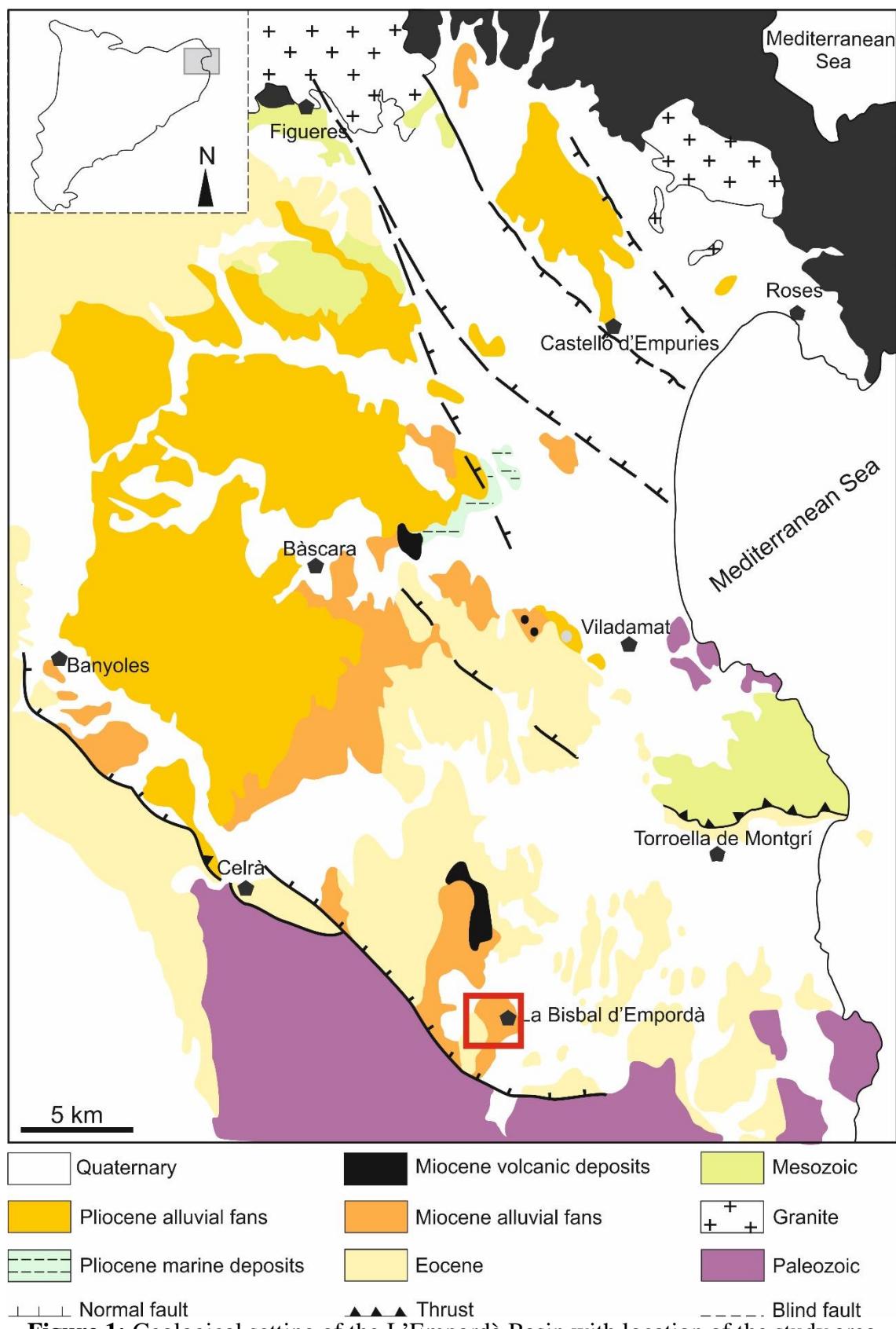
1421 **Plate IV:** Fossil plant taxa from the Vallesian plant collection from La Bisbal  
1422 d'Empordà (continued). 1: *Ulmus* sp. (IPS109772). 2: *Zelkova* sp. (IPS109703). 3:  
1423 *Cedrelospermum* sp. (IPS109740). 4: *Fraxinus* sp. (IPS109765). Scale bar 1 cm.

1424 **Plate V:** Incertae sedis from the Vallesian deposits of La Bisbal d'Empordà  
1425 (continued). 1: Undetermined magnoliopsid 1 (IPS109708). 2: Undetermined  
1426 magnoliopsid 2 (IPS109734). 3: Undetermined magnoliopsid 3 (IPS109729). 4:  
1427 Undetermined magnoliopsid 4 (IPS109767). 5: Undetermined magnoliopsid 5  
1428 (IPS109710). 6: Undetermined magnoliopsid 6 (IPS109708). 7: Undetermined  
1429 magnoliopsid 7 (IPS109728). 8: Undetermined magnoliopsid 8 (IPS109765). Scale bar  
1430 1 cm.

1431 **Plate VI:** Taphonomic plant features from the Vallesian deposits of La Bisbal  
1432 d'Empordà. 1: Torn leaf (IPS109740). 2: Helophytic plant portions forming a

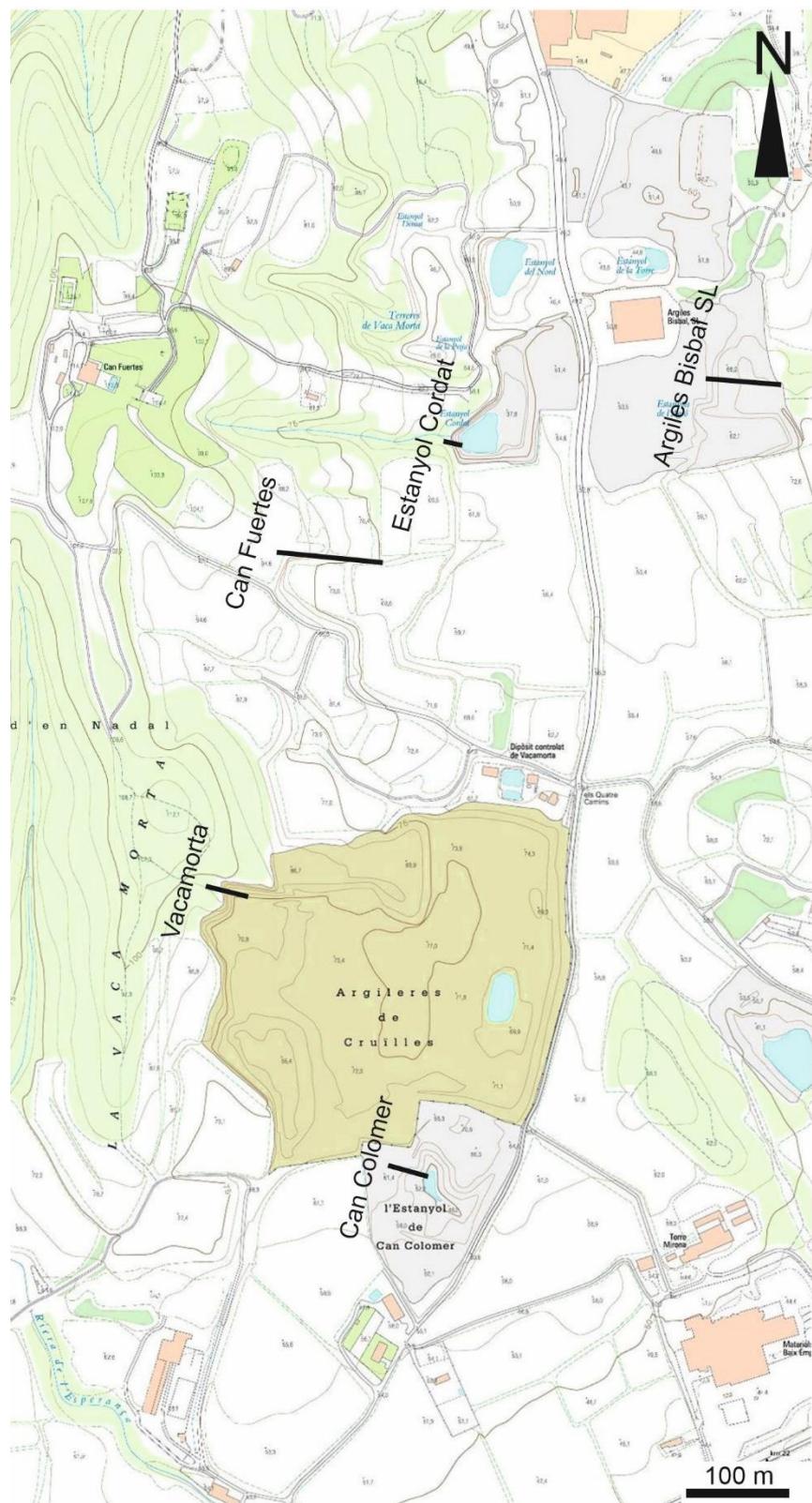
1433 monospecific assemblage (IPS109769). 3: Almost intact *Paliurus* seed (IPS109718). 4:

1434 Leaf with anatomically connected leaflets of *Fraxinus* sp. (IPS109753). Scale bar 1 cm.

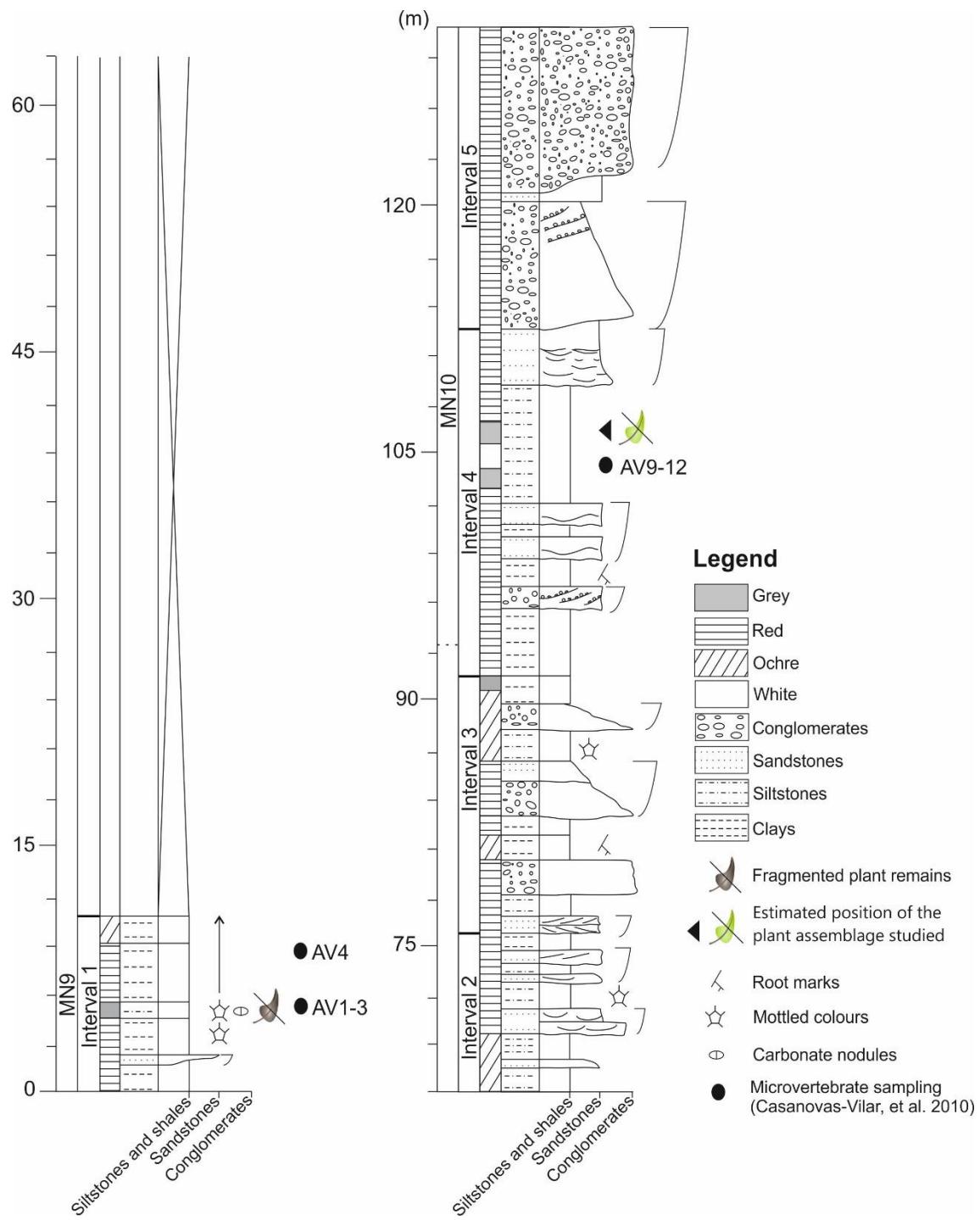


**Figure 1:** Geological setting of the L'Empordà Basin with location of the study area

(square), modified from Picart et al. (1996).



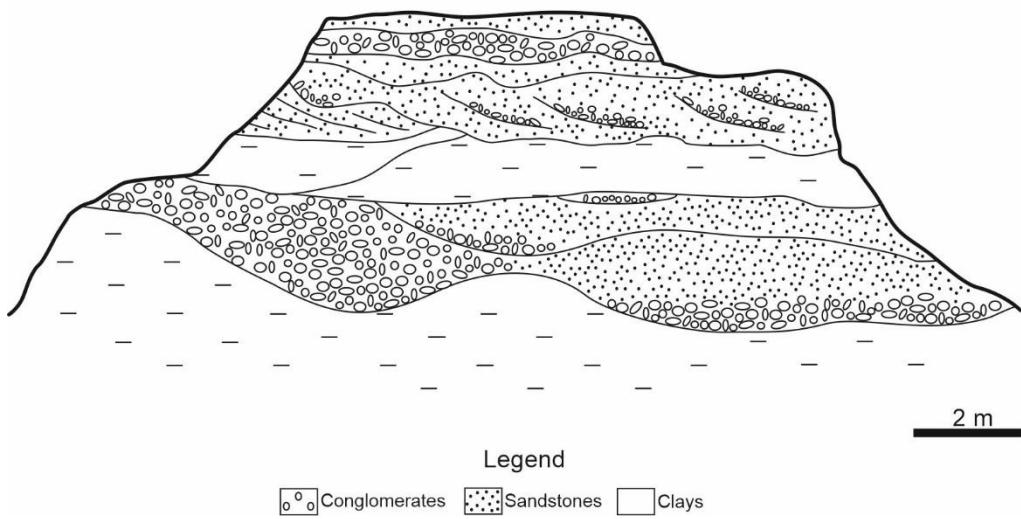
**Figure 2:** Map with the location of the sections studied. Modified from ICGC (<http://www.icc.cat>).



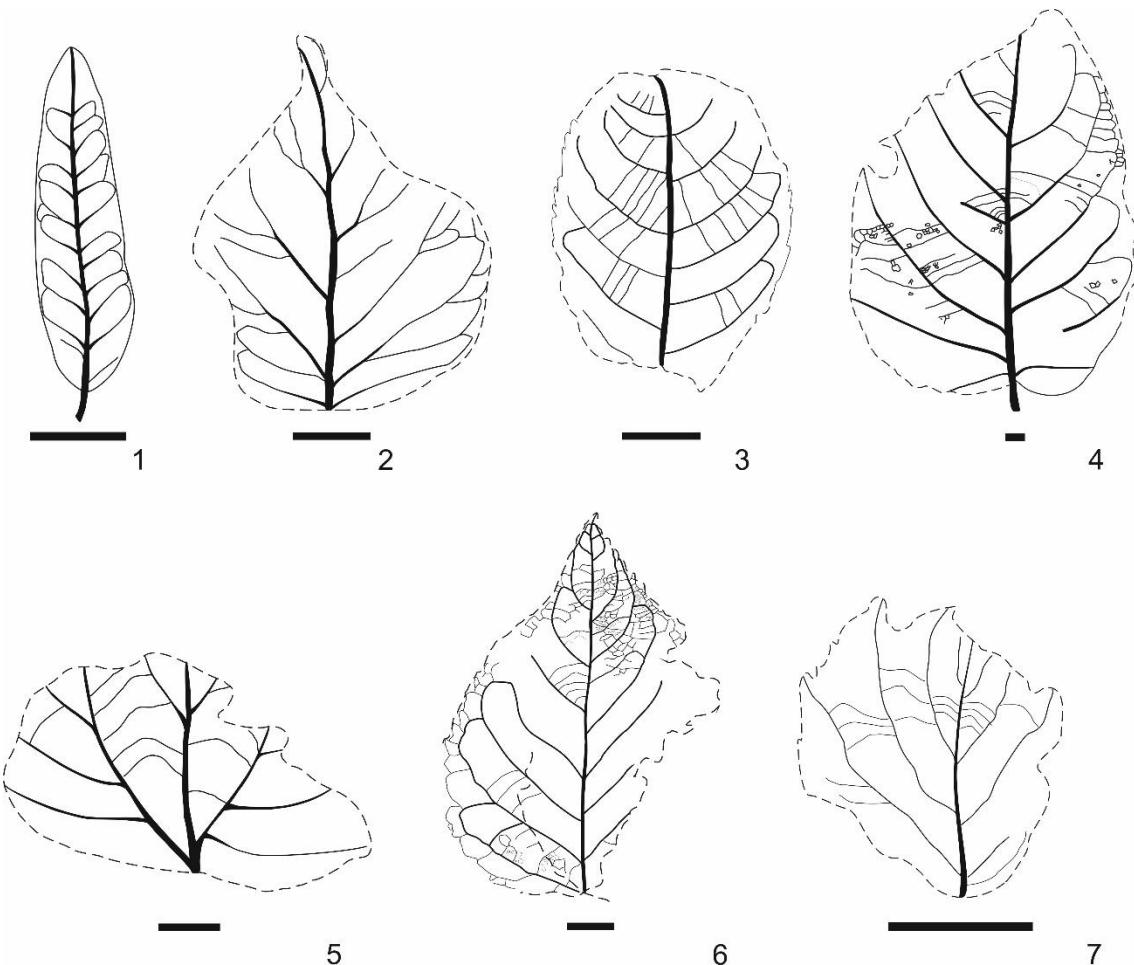
**Figure 3:** Stratigraphic section studied in the Vallesian from La Bisbal with the estimated position of the plant bed studied.



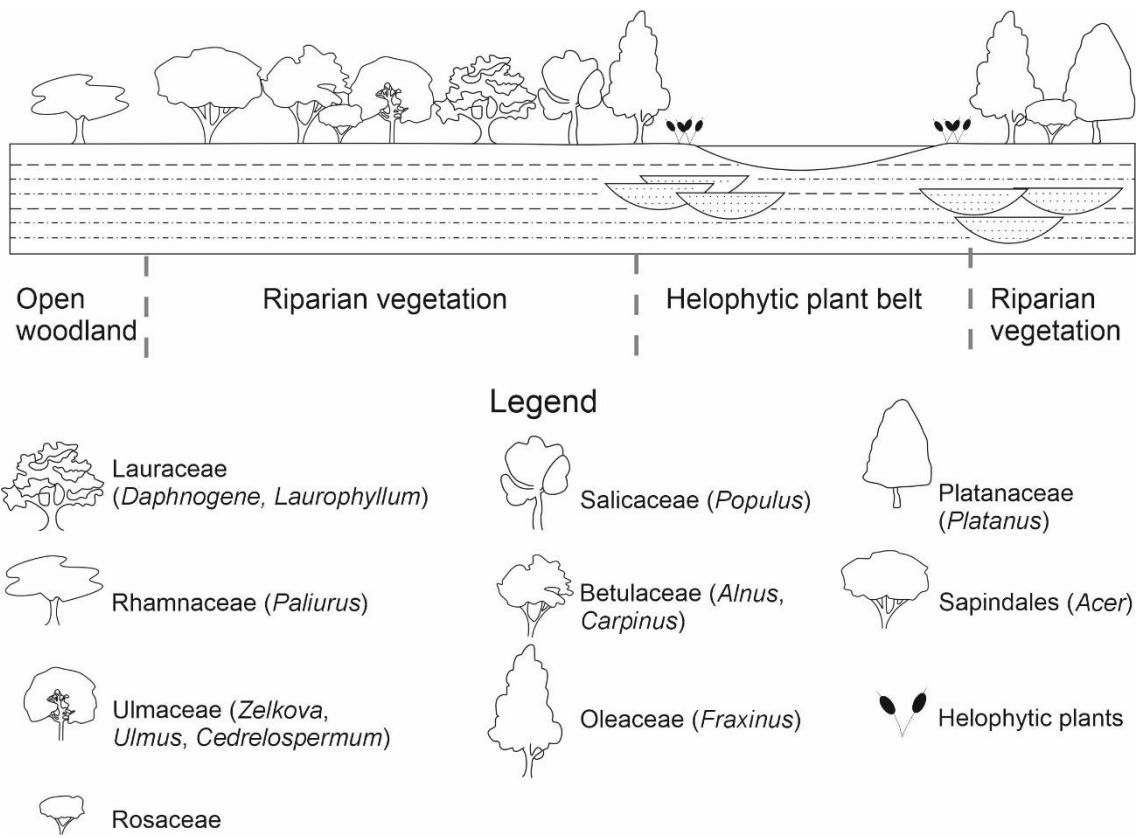
W-E



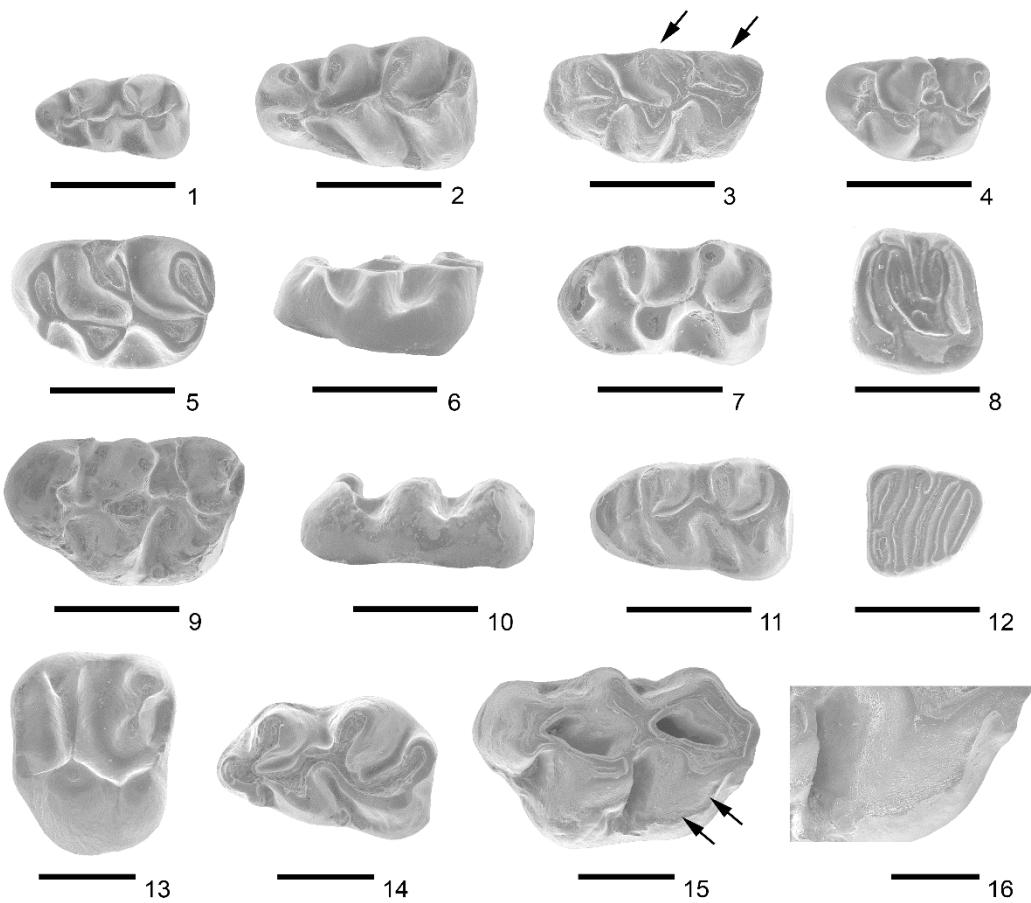
**Figure 4:** Argiles Bisbal SL outcrop (interval 3) and facies interpretation, showing fluvial features such as clast-supported conglomerates, cross-bedding and marked erosive bases.



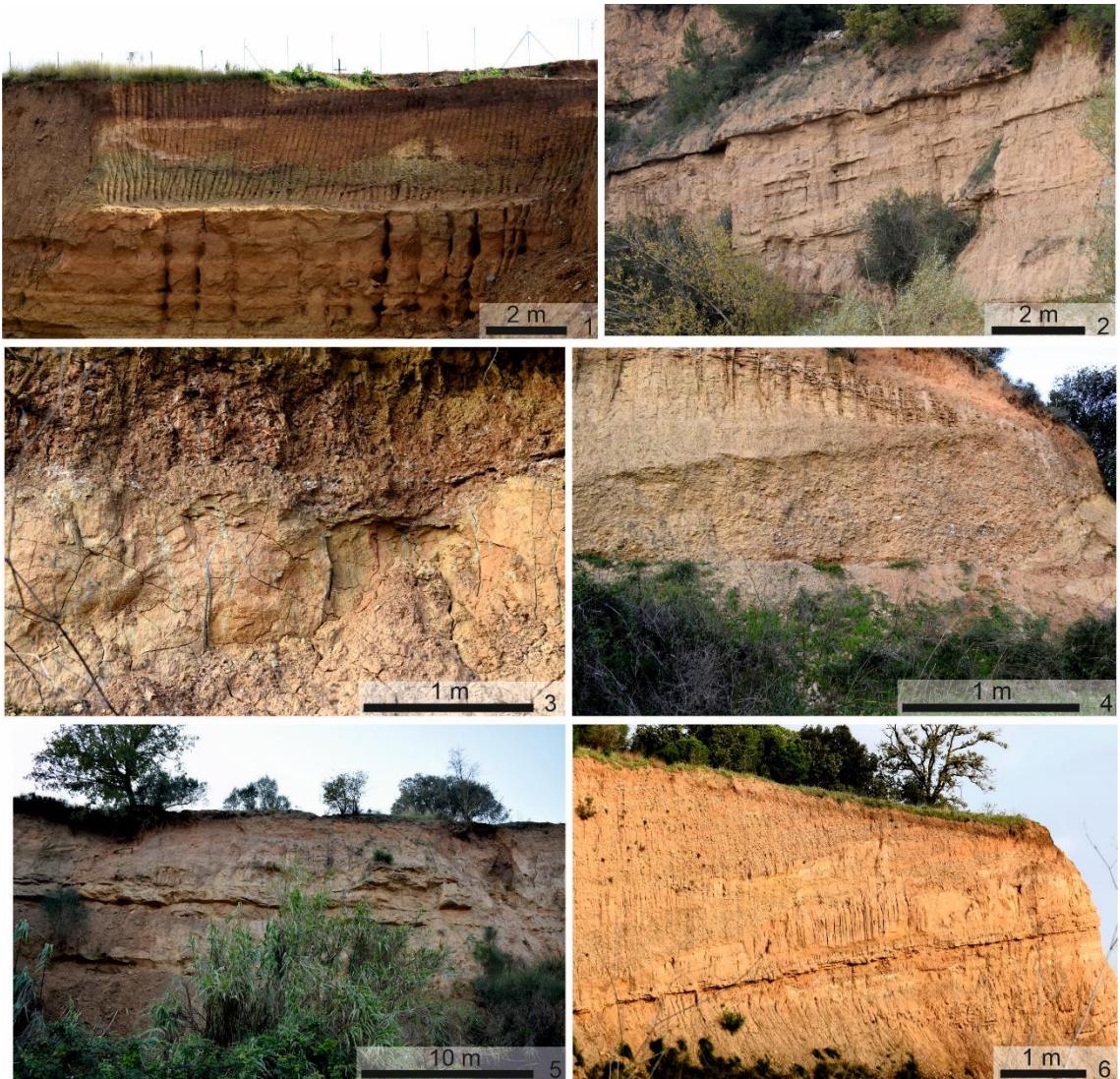
**Figure 5:** Line drawing of some leaves from the Vallesian deposits of La Bisbal d'Empordà showing the characteristic foliar characters. 1: *Laurophyllum* sp. displaying the brochidodromous secondary veins (IPS109721). 2: *Populus balsamoides* with brochidodromous secondary veins (IPS109715). 3: Rosaceae gen. et sp. indet showing the straight path of the tertiary veins (IPS109745). 4: *Alnus gaudinii* displaying the first pair of secondary veins forming almost a perpendicular angle with the midvein and the sinuous path of the tertiary venation pattern (IPS109761). 5: Undetermined magnoliopsid 2 with sinuous tertiary veins (IPS109734). 6: Undetermined magnoliopsid 3 showing sinuous tertiary veins and quaternary vein fabric reticulate (IPS109729). 7: Undetermined magnoliopsid 4 with sinuous tertiary veins (IPS109767). Scale bar 1 cm



**Figure 6:** Palaeoenvironmental reconstruction of the Vallesian from La Bisbal d'Empordà flora.



**Plate I:** Fossil rodents from the Vallesian sites from La Bisbal d'Empordà. 1: *Megacricetodon* cf. *minutus*, left lower first molar (IPS29925) from AVM4. 2: *Megacricetodon ibericus* left lower first molar (IPS29922) from AVM4. 3: *Megacricetodon ibericus* right upper first molar (IPS29921, reversed) from AVM4 showing partial digestion of enamel and dentine in the labial cusps (arrows) that have altered the morphology in this area. 4: *Democricetodon* cf. *nemoralis*, left upper first molar (IPS29938) from AVM10. 5: *Rotundomys* cf. *freirensis*, right upper first molar (IPS1992, reversed) from Can Colomer 2. 6: *Rotundomys* cf. *freirensis*, same specimen (IPS1992) in lingual view, note the semi-hypsodont crown and flat wear surface (compare with Plate I.10). 7: *Rotundomys* cf. *freirensis*, left lower first molar (IPS29940) from AVM10. 8: *Miodyromys hamadryas*, right upper second molar (IPS29936, reversed) from AVM4. 9: *Neocricetodon ambarrensis*, left upper first molar (IPS29938) from AVM10. 10: *Neocricetodon ambarrensis*, same specimen (IPS29938) in lingual view showing the low-crowned, bunodont pattern. 11: *Neocricetodon ambarrensis*, left lower first molar (IPS29941) from AVM10. 12: *Muscardinus hispanicus*, left upper third molar (IPS120016) from Can Colomer 2. 13: *Heteroxerus* sp., left upper first or second molar (IPS120070) from La Bisbal 2. 14: *Hispanomys dispectus*, right lower first molar (IPS29929, reversed) from AVM4. 15: *Hispanomys dispectus*, right upper first molar (IPS29933, reversed) from AVM4 showing partial digestion of the enamel in the lingual cusps, particularly the hypocone (arrows). 16: *Hispanomys dispectus*, detail of the hypocone of the same specimen (IPS29933, reversed) highlighting the digested area. Scale bar is 1 mm in all figures except in Figure 16, in which it is 500 µm.



**Plate II:** Lithofacies from the Vallesian of La Bisbal d'Empordà. 1: Red clays and siltstones with intercalations of fine-grained sandstones of interval 1 from Can Colomer section. 2: Intercalations of sandstones and siltstones of interval 2 from Estanyol Cordat section. 3: Red clays with root marks of interval 3 from Can Fuertes section. 4: Clast-supported conglomerates from interval 3 at Can Fuertes. 5: Sandstone beds with cross-bedding and undulated, erosive beds at interval 4 from Can Fuertes. 6: Lenticular conglomerate beds with intercalations of sandstones from interval 5 of Vacamorta section.

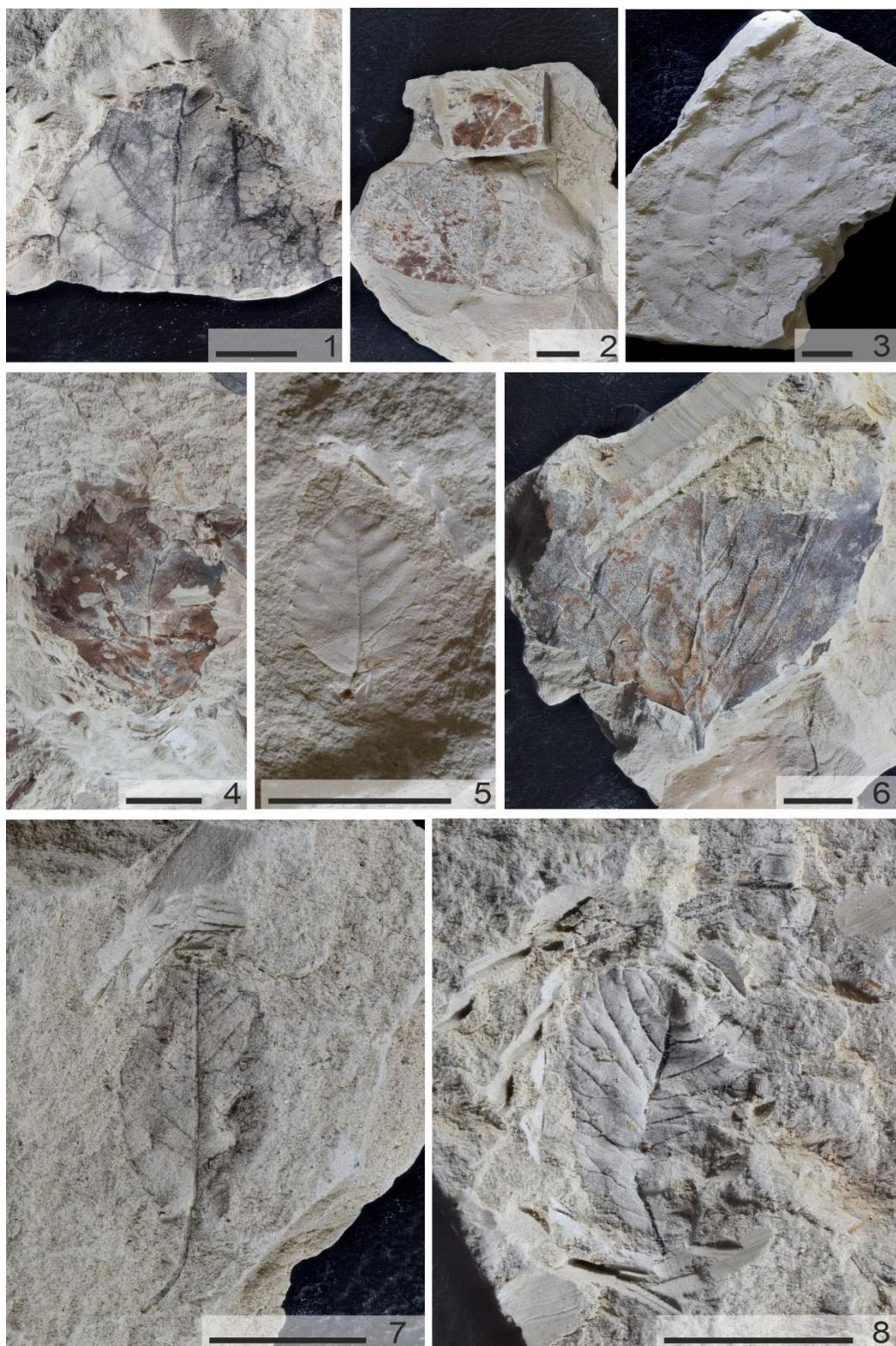


**Plate III:** Fossil plant taxa from the Vallesian plant collection from La Bisbal d'Empordà.

1: *Daphnogene* sp. (IPS109714) 2: *Laurophyllum* sp. (IPS109721). 3: *Platanus* sp. (IPS109709). 4: *Populus balsamoides* (IPS109715). 5: *Paliurus* sp. (IPS109760). 6: Rosaceae gen. et sp. indet (IPS109745). 7: *Alnus gaudinii* (IPS109722). 8: *Carpinus* sp. (IPS109744). 9: *Acer tricuspidatum* (IPS 109741). Scale bar 1 cm.



**Plate IV:** Fossil plant taxa from the Vallesian plant collection from La Bisbal d'Empordà (continued). 1: *Ulmus* sp. (IPS109772). 2: *Zelkova* sp. (IPS109703). 3: *Cedrelospermum* sp. (IPS109740). 4: *Fraxinus* sp. (IPS109765). Scale bar 1 cm.



**Plate V:** Incertae sedis from the Vallesian deposits of La Bisbal d'Empordà (continued).  
 1: Undetermined magnoliopsid 1 (IPS109708). 2: Undetermined magnoliopsid 2 (IPS109734). 3: Undetermined magnoliopsid 3 (IPS109729). 4: Undetermined magnoliopsid 4 (IPS109767). 5: Undetermined magnoliopsid 5 (IPS109710). 6: Undetermined magnoliopsid 6 (IPS109708). 7: Undetermined magnoliopsid 7 (IPS109728). 8: Undetermined magnoliopsid 8 (IPS109765). Scale bar 1 cm.



**Plate VI:** Taphonomic plant features from the Vallesian deposits of La Bisbal d'Empordà. 1: Torn leaf (IPS109740). 2: Helophytic plant portions forming a monospecific assemblage (IPS109769). 3: Almost intact *Paliurus* seed (IPS109718). 4: Leaf with anatomically connected leaflets of *Fraxinus* sp. (IPS109753). Scale bar 1 cm.