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

Aixa Tosal [a,*], Sophie Roselyn Coward [a], Isaac Casanovas-Vilar [b], Carles Martín-Closas [a]

[a] Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona-UB, 08028 Barcelona, Catalonia, Spain
[b] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Barcelona, Spain

A B S T R A C T

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

1. Introduction

The global cooling event at the middle Miocene climate transition (Westerhold et al., 2020) triggered a floristic reorganisation and increase of regionalism during the late Miocene (Zachos et al., 2001; Utescher et al., 2007a; Pound et al., 2012). In Central Europe and the Western Paratethys zonal deciduous forests dominated, locally containing broadleaved evergreen elements (Erdei et al., 2007; Utescher et al., 2007a; Ivanov et al., 2011). In contrast, in Southern Europe, broadleaved evergreen dicotyledonous plants prevailed together with thermophilous conifers and, in lower proportions, sclerophyllous plants (Utescher et al., 2007a, 2007b).

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

---

* Corresponding author.
E-mail addresses: atosal@ub.edu (A. Tosal), sophie.coward@myport.ac.uk (S.R. Coward), isaac.casanovas@icp.cat (I. Casanovas-Vilar), cmartinclosas@ub.edu (C. Martín-Closas).

palaeotropical elements such as *Daphnogene, Mahonia* or *Cassia* and a few herbaceous taxa.

A comprehensive study of the plant palaeoecology of late Miocene macroflora of the north-eastern Iberian Peninsula has not yet been conducted. Only the upland flora of La Cerdanya has been studied in detail (Barrón, 1992, 1996a, 1996b, 1996c; Barrón and Diéguez, 1994; Martín-Closas et al., 2005, 2006; Barrón et al., 2014; Tosal et al., 2021), with little attention to the lowland plant communities from this area. The historical leaf collection from La Bisbal d'Empordà was gathered by Sanz de Siria Catalán (1981, 1985) and Sanz (1988) and is a palaeobotanical collection that has yet to be re-examined using modern taxonomic, taphonomic and palaeoecological criteria. Sanz de Siria Catalán (1981) reported 27 species, interpreted as forming two distinct floral associations. The first, and the most significant, belonging to humid environments that included *Equisetum parlatorii* Heer *Poacites* sp. and *Typha latissima* Brongniart characteristic of the lake and riverbanks. The second was interpreted as a closed forest growing in the lowlands and hills around the depositional setting and included taxa such as *Cinnamomum polymorphum* Heer (25% of the plant assemblage), *Pterocarya fraxinifolia* Spach. (30% of the plant assemblage), *Quercus drymeja* Unger, *Quercus* aff. *ilex, Quercus* sp., *Ulmus braunii* Heer, *Ulmus* sp., *Acer trilobatum* (Sternb.) A. Braun *Acer* sp., *Fraxinus delecta* Heer, and *Sapindus bilinicus* Ettingsh. This combination of elements which are more characteristic of temperate forests, such as *Pterocarya fraxinifolia*, alongside with others more typical of subtropical forests, such as *Cinnamomum polymorphum*, was interpreted by Sanz de Siria Catalán (1981) as representing the climatic transition from a warmer stage in the middle Miocene to the milder temperate climates of the late Miocene. Furthermore, the relatively low latitude of the basin and its proximity to the coastline would have allowed, according to this author, for the longer persistence of subtropical species in comparison with contemporaneous floras from higher latitudes in central Europe, which were richer in more temperate (Arctotertiary) species (Uhl et al., 2007). These conclusions have subsequently been assumed in several palaeobotanical syntheses of European and Iberian basins, e.g., Barrón (2003), Kovar-Eder (2003) and Barrón et al. (2010), but new data have not been added to the original description and interpretation of the collection.

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

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

contrast, AVM10 and AVM11 includes two species of ground squirrel (*Heteroxerus rubricati, Spermophilinus bredai*), the ochotonid *Prolagus*, the glirid *M. hamadryas*, four species of cricetid (*Democricetodon* cf. *nemoralis* [Plate I.4], *Neocricetodon ambarrensis* [misidentified as *Cricetulodon hartenbergeri* in Casanovas-Vilar et al., 2010; Plate I.9–11], *Rotundomys* cf. *freirensis* [Plate I.5–7] and *Hispanomys* sp.) and three distinct insectivores.

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

2. Material and methods

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

Approximately 50% of the fossil plant specimens from La Bisbal d'Empordà are sufficiently well preserved for a detailed description using the leaf architecture terminology of Ellis et al. (2009). The most representative specimen(s) of each morphotype were selected and photographed. Between 20 and 40 images of each specimen were taken using a Nikon 5300 camera and focus stacked using Helicon Focus 5.3 (www.heliconsoft.com). Leaf measurements were taken using the SketchandCalc software (www.sketchandcalc.com).

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

Small mammal remains were recovered after sediment screen-washing in successive field campaigns in the early 2000s (Llenas et al., 2002; Casanovas-Vilar et al., 2010). The area surveyed mostly corresponds to the Can Colomer clay pit which since 2005 has been occupied by the Vacamorta landfill. Before the landfill was built, two samples (named Can Colomer 1 and Can Colomer 2) were collected from this area. After screen-washing, a limited collection consisting of about 70 identifiable small mammal remains were recovered. A preliminary faunal list is given in Llenas et al. (2002), while some specimens are described in Casanovas-Vilar et al. (2010). During the preparatory works for the Vacamorta landfill palaeontologists surveyed the area and collected 12 additional samples from several lutite beds in the search for microvertebrate fossils. Three of these samples (AVM4, AVM10, AVM11) were positive and allow for a comparison with the plant-bearing beds studied here, which are laterally equivalent. About 20 identifiable micromammal teeth were recovered in each case. The material is described in Casanovas-Vilar et al. (2010).

3. Geological setting and biostratigraphy

The La Bisbal d'Empordà outcrops are located within the Neogene of the L'Empordà Basin (Fig. 1), which is situated in the northeastern part
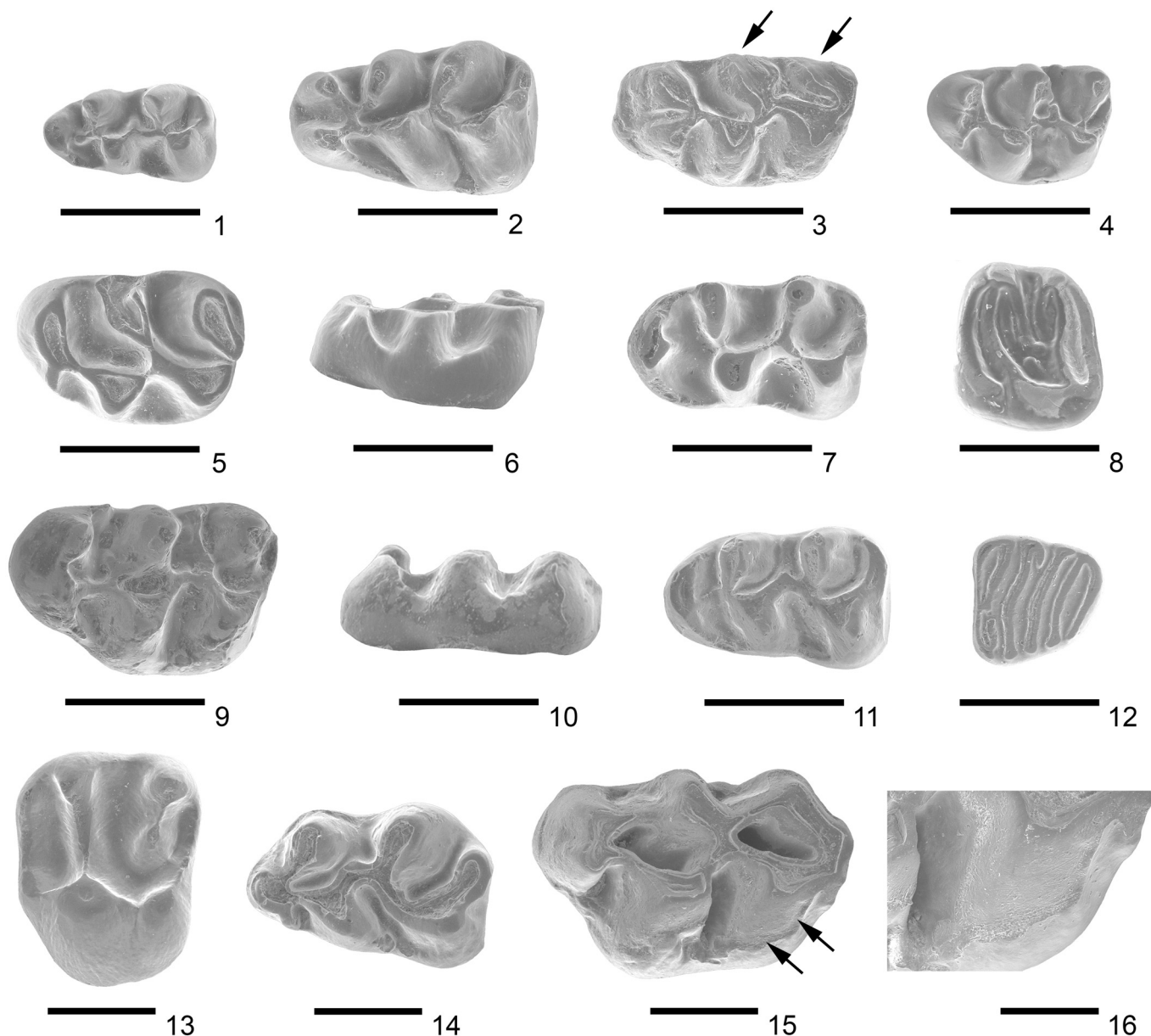
Plate I. Fossil rodents from the Vallesian sites from La Bisbal d'Empordà. 1: *Megacricetodon* cf. *minutus*, left lower first molar (IPS29925) from AVM4. 2: *Megacricetodon ibericus* left lower first molar (IPS29922) from AVM4. 3: *Megacricetodon ibericus* right upper first molar (IPS29921, reversed) 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 fig. 16, in which it is 500 μm.

of the Iberian Peninsula, in Catalonia (Spain). The basin was formed as part of a rifting process that affected the western Mediterranean throughout the Neogene and Quaternary periods (Saula et al., 1996). In the Iberian Peninsula, this rifting produced a system of NE–SW orientated normal faults broadly parallel to the present-day coastline and resulted in the formation of several sedimentary basins including the L'Empordà Basin (Picart et al., 1996; Saula et al., 1996). The basin is geologically limited by the Palaeozoic outcrops of the L'Albera ranges to the north, Eocene rocks of La Garrotxa to the west, the metamorphic and igneous rocks of the Les Gavarres ranges to the south and by the Mediterranean Sea to the east (Picart et al., 1996).

From a stratigraphic viewpoint, the localities studied belong to the eastern part of an upper Miocene alluvial-fluvial fan system, particularly the so-called Les Gavarres fan system (Saula et al., 1996). The accumulated thickness of the Les Gavarres fan system deposits is up to 100 m. These are formed by a succession of greenish-grey and red mottled clays interbedded with conglomerates, gravels and sandstones of varying thickness (Picart et al., 1996; Casanovas-Vilar et al., 2010). The lithologies of the clasts within the conglomeratic beds are variable. The most frequent are quartz, mottled schists and altered granites of Palaeozoic age, which originated from the Les Gavarres ranges; Eocene sandstones originating from the western margin of the basin, and
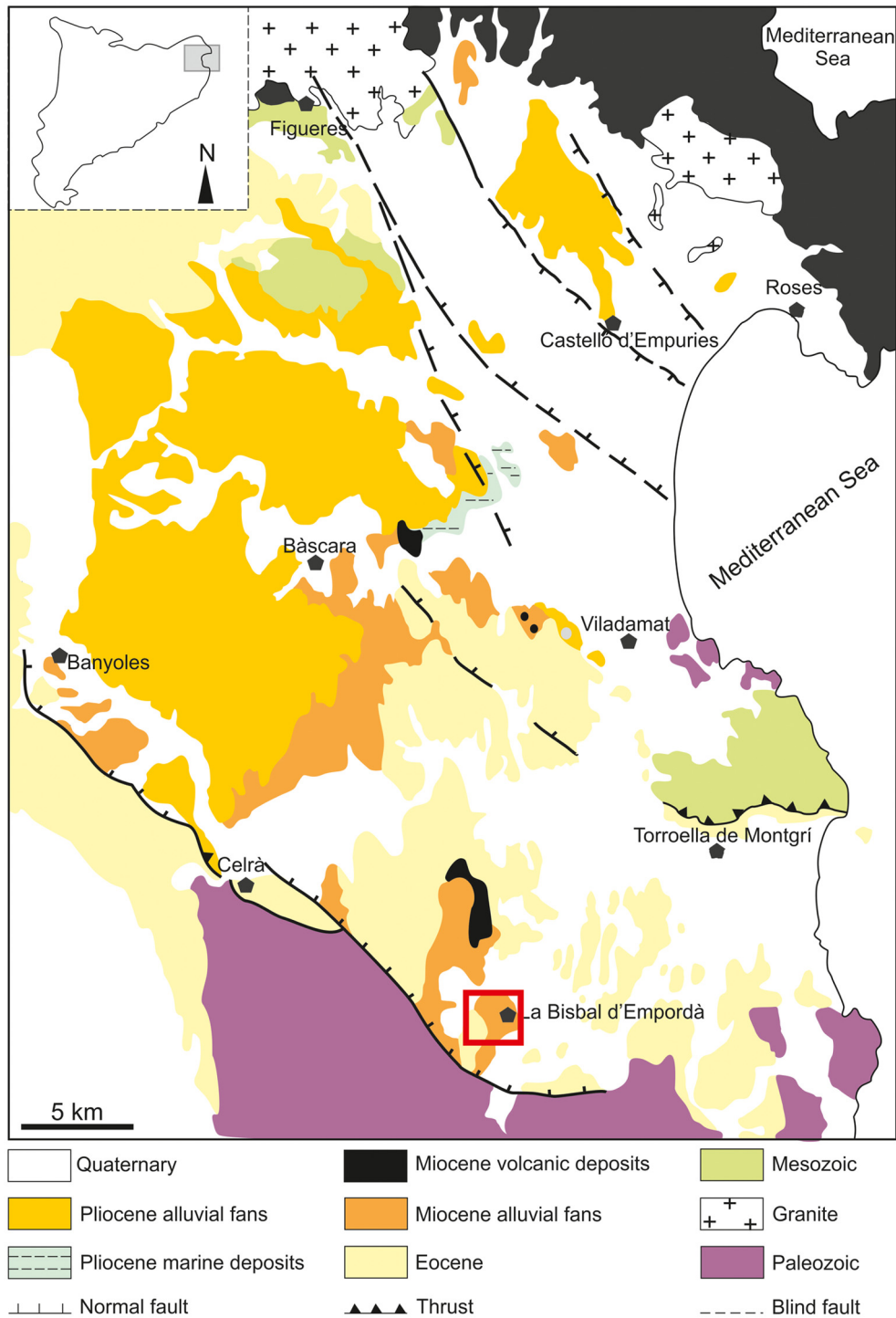
Fig. 1. Geological setting of the L'Empordà Basin with location of the study area (square), modified from Picart et al. (1996).

Neogene basalts corresponding to the volcanism associated with the basin origin.

The age of the studied flora from La Bisbal d'Empordà is based on mammal biostratigraphy. Crusafont (1962) had already assigned the La Bisbal d'Empordà outcrops to the Vallesian European land mammal age (earliest late Miocene, 11.2–8.9 Ma) due to the presence of the three-toed equid *Hippotherium*. Later, Gibert et al. (1979, 1980) found two micromammal fossil sites in La Bisbal d'Empordà i.e., La Bisbal 1 and 2 which indicated a correlation with the early Vallesian, i.e., European mammal Neogene zone MN9 (currently ranging from

11.2 to 9.9 Ma). Some years later, Llenas et al. (2002) found two additional small mammal sites at the clay pit of Can Colomer. This author also named them La Bisbal 1 and 2 but these beds are distinct from those previously reported by Gibert et al. (1979, 1980). To avoid confusion, Casanovas-Vilar et al. (2010) renamed the mammal beds of Llenas et al. (2002) Can Colomer 1 and Can Colomer 2 for La Bisbal 1 and 2 respectively. They also correlated Can Colomer 1 and 2 with the fossiliferous beds at the Vacamorta landfill. Level AVM4 was considered approximately equivalent to Can Colomer 1 and to La Bisbal 1 and 2 of Gibert et al. (1979, 1980), and was further correlated with the first

half of the MN9. The small mammal assemblage of Can Colomer 2 was correlated to AVM10 and AVM11, which are stratigraphically equivalent to the beds that provided the fossil macroflora from La Bisbal d'Empordà. Casanovas-Vilar et al. (2010) initially correlated these beds with the late MN9, although noting apparent incongruences. Recent biostratigraphic works carried out by Casanovas-Vilar et al. (2016a, 2016b) in the Vallesian type area, at the nearby Vallès-Penedès Basin (Barcelona, Catalonia), allows constraining the age of La Bisbal fossil sites. AVM4, Can Colomer 1 and La Bisbal 1 and 2 would correlate with the earliest Vallesian *Hippoterium – Cricetulodon hartenbergeri* Interval Subzone of the Vallès-Penedès Basin, thus resulting in an estimated age of 11.2–10.3 Ma for these sites. On the other hand, AVM10, AVM11 and Can Colomer 2 are correlated with the short-lasting *Cricetulodon sabadellensis + Progonomys hispanicus* Concurrent Range Subzone of the Vallès-Penedès Basin, corresponding to the earliest late Vallesian (early MN10) and yielding an age of 9.73–9.65 Ma. This estimate differs from that given in Casanovas-Vilar et al. (2010), who suggested an MN9 (early Vallesian) age for these sites after mistaking *Neocricetodon ambarrensis* for *Cricetulodon hartenbergeri*. The diagnostic elements for the *C. sabadellensis + P. hispanicus* subzone have not been found. However, *Rotundomys freirensis*, which occurs at AVM10 and AVM11, is only known from this subzone in the Vallès-Penedès, thus supporting this interpretation. Furthermore, *N. ambarrensis* is also a typical late Vallesian element.

4. Results

4.1. Stratigraphy and sedimentology

4.1.1. Description and interpretation of facies

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

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

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

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

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

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

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

4.1.1.4. Interval 4. Description: This interval is ca. 25 m thick and corresponds to the upper part of the Can Fuertes section and the basal part of the Vacamorta landfill section. It is mainly composed of alternating red, mottled greyish-ochre and locally white clays, with rootlet marks and is rich in plant and micromammal remains. These fossiliferous beds would be equivalent to those where Sanz de Siria Catalán (1981) collected the leaf flora studied herein while the micromammal-bearing beds correspond to AVM9–AVM12 of Casanovas-Vilar et al. (2010). At Can Fuertes, sandstone beds with undulating bases and epsilon cross-bedding occur at the top of the interval (Plate II.5).

Interpretation: The succession of interval 4 represents a meandering fluvial system that developed in the more distal areas of an alluvial-fluvial fan. Sandstones with internal epsilon cross-bedding from the Can Fuertes outcrop indicate meandering river channels, based on the sedimentary models of Miall (2016). The variegated clay colours and rootlet marks represent deposition in flooded areas where the development of hydromorphic soils was important. In contrast, red clays resulted from the deposition of overbank deposits under oxidized conditions by subaerial exposition.

4.1.1.5. Interval 5. Description: This interval, up to 10 m thick, corresponds to the upper part of the Vacamorta section. It is composed of lenticular cross-bedded conglomerates forming two thick, overlapping bodies separated by laminated red clay and siltstone beds. Conglomerate clasts are sub-rounded, up to 20 cm in diameter and composed of altered granite, mottled schist, acidic volcanic rocks (trachyte) and sandstone (Plate II.6).

Interpretation: The succession of this interval would correspond to a more proximal setting within an alluvial–fluvial fan than the previous interval. Conglomerates with cross-bedding would indicate a constant high flow energy consistent with that of braided rivers (Nichols, 2009). Laminated red clays and siltstones represent the corresponding over bank deposits.
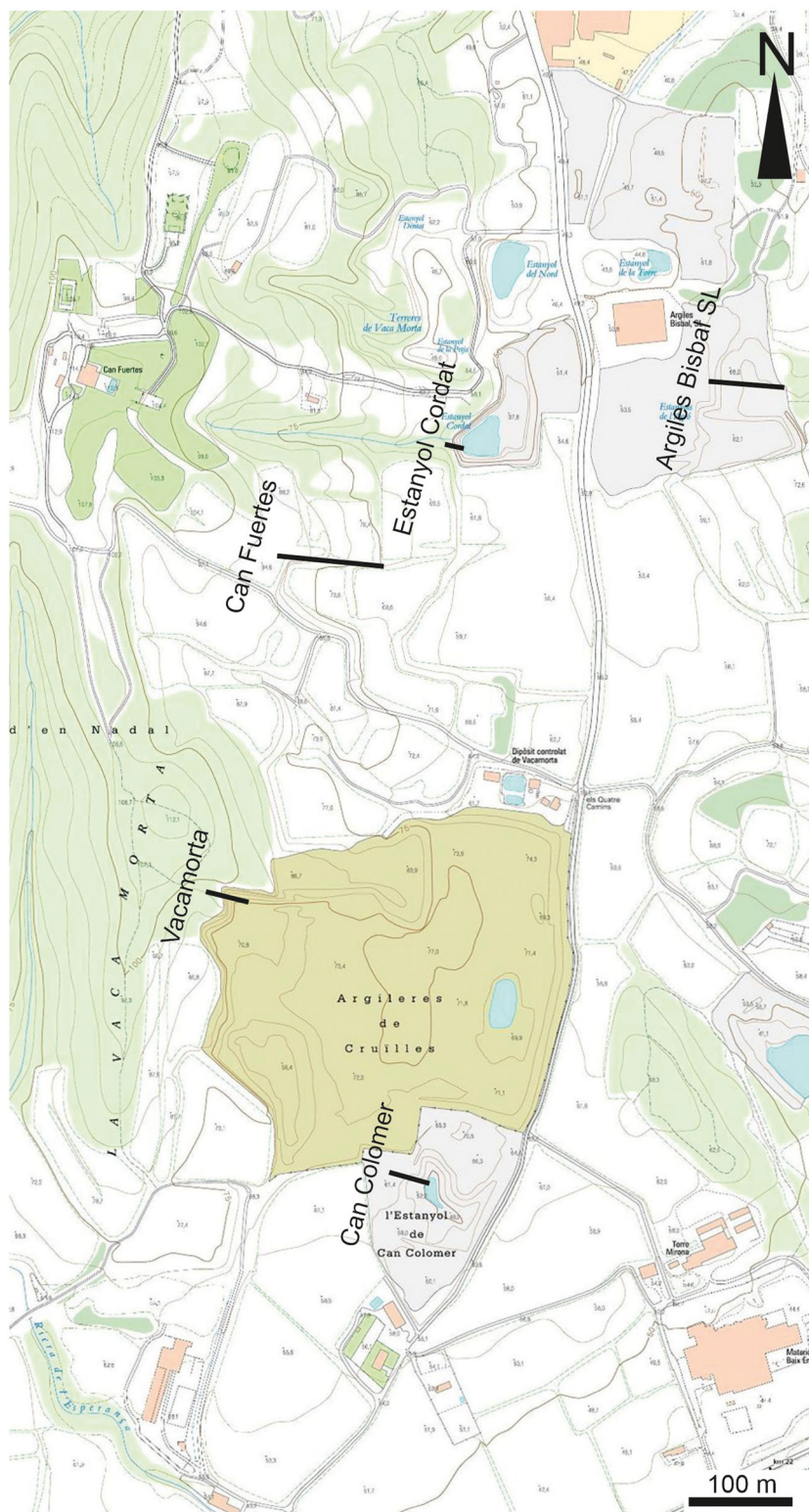
Fig. 2. Map with the location of the sections studied. Modified from ICGC (http://www.icc.cat).

4.1.2. Depositional model

The late Miocene section that crops out at La Bisbal d'Empordà corresponds mainly to a fluvial belt, formed by braided river channels grading distally to meandering river channels and their associated floodplain facies. More rarely, proximal to medial alluvial fan facies (debris flow facies) are associated with previous deposits.

From intervals 1 to 3, a progradation trend of the alluvial-fluvial fan is apparent, from floodplain deposits that represent distal fluvial facies in interval 1 to meandering river facies in interval 2, and finally to braided river and debris-flow facies in interval 3. Interval 4 represents a retrogradation of the alluvial-fluvial fan system, which resulted in an extension of the meandering river belt facies over the braided river
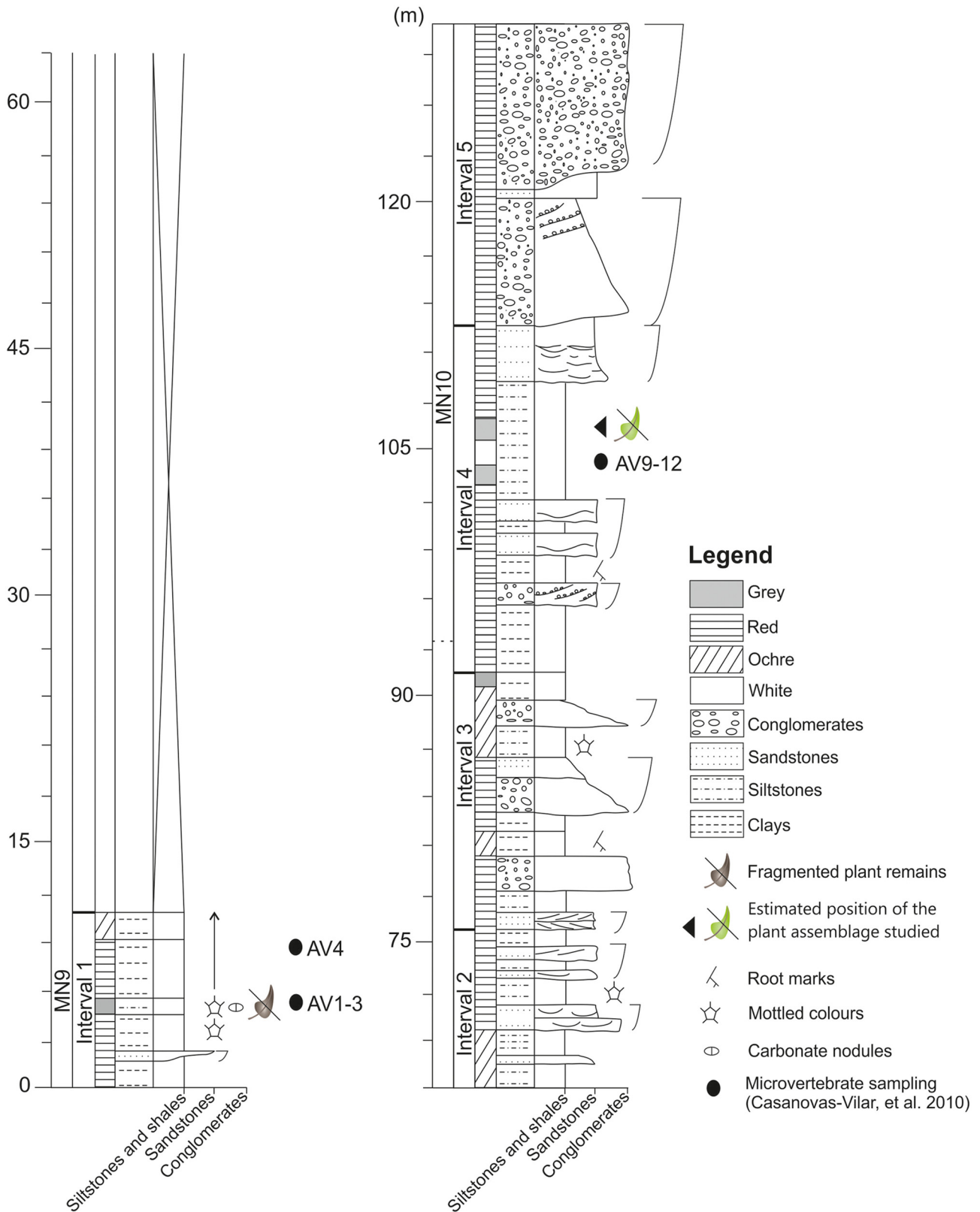
Fig. 3. Stratigraphic section studied in the Vallesian from La Bisbal with the estimated position of the plant bed studied.

facies of interval 3. The studied leaf-bearing beds were deposited in this retrogradation context. Finally, interval 5 again shows more proximal facies in the system with a development of thick braided river facies on top of the section.

The whole section is dominated by fluvial processes from distal parts of the alluvial-fluvial fan i.e., channel-fill and over bank deposits, with local evidence of unconfined-flow processes that would be more characteristic of proximal alluvial settings. This expands the facies
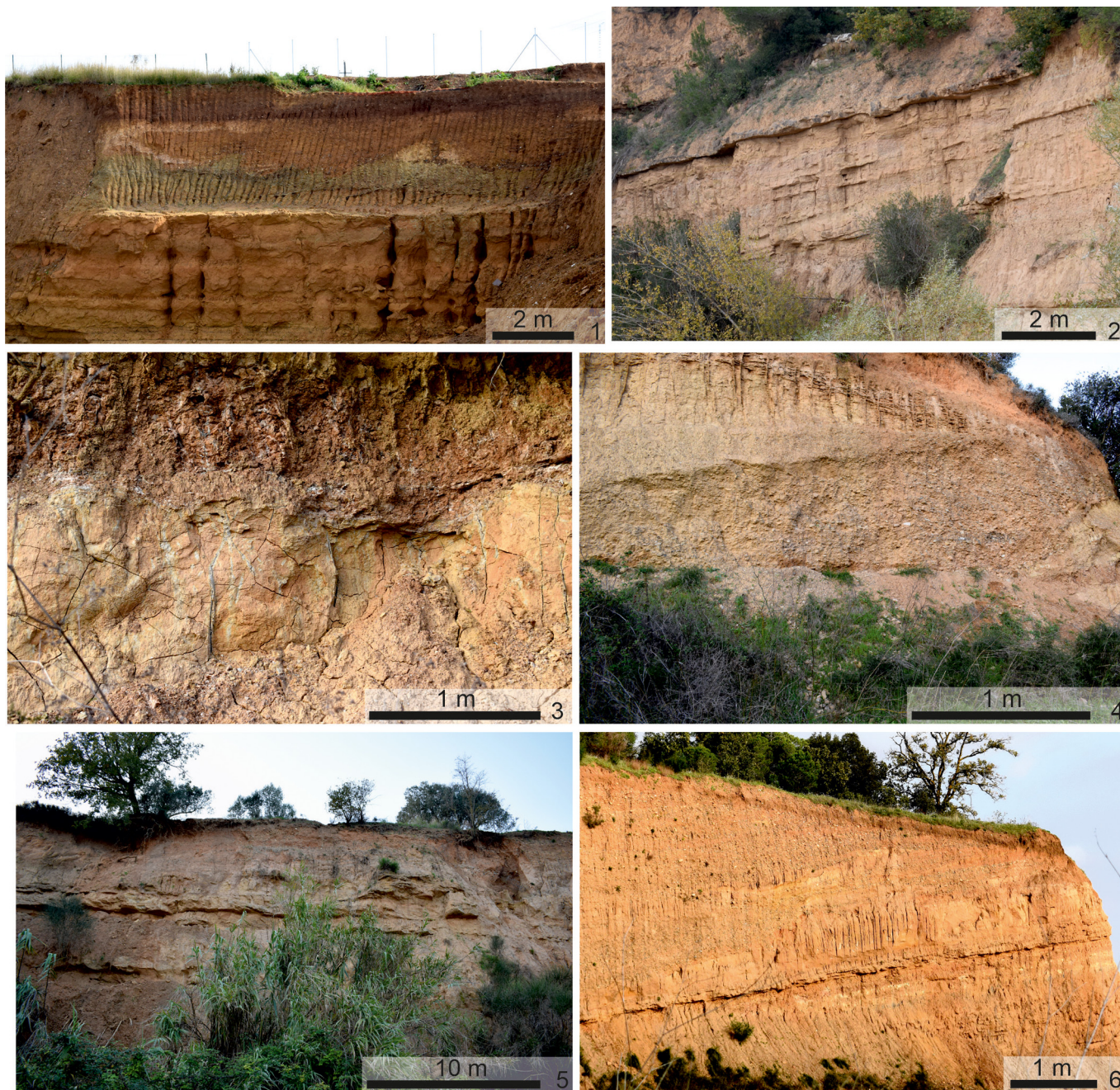
Plate II. Lithofacies from the Vallesian of La Bisbal d'Empordà. 1: Red clays and siltstones with intercalations of fine-grained sandstones of interval 1 from Can Colomer section. 2: Intercalations of sandstones and siltstones of interval 2 from Estanyol Cordat section. 3: Red clays with root marks of 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.

range reported in a previous study by Picart et al. (1996), who associated the sedimentation in La Bisbal d'Empordà strictly with an alluvial context.

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

4.2. Systematic palaeobotany

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

Order: Laurales Berchtold et Presl
Family: Lauraceae Jussieu
Genus: **Daphnogene** Unger
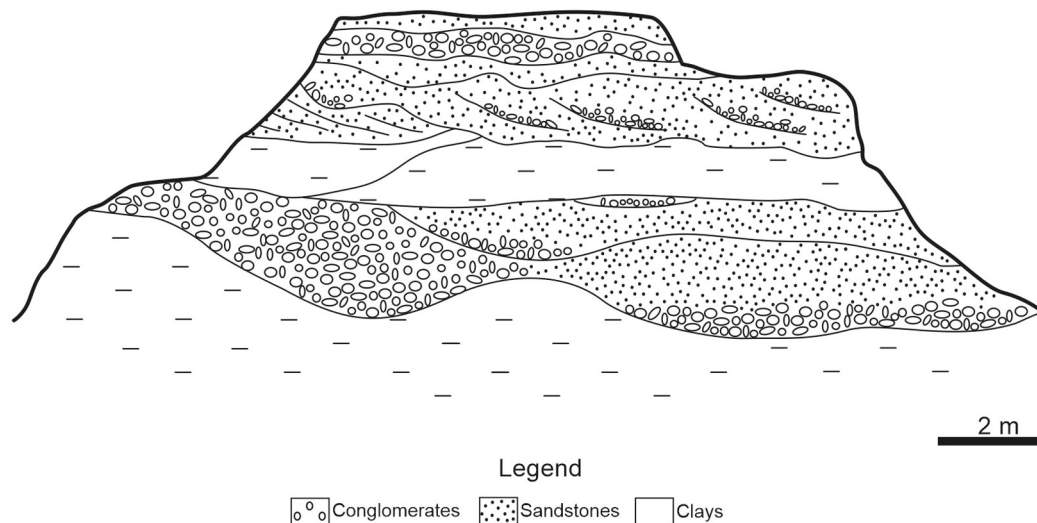*Daphnogene* sp.
(Plate III.1)

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

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

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

The primary venation is suprabasal actinodromous. The lateral veins emerge at 30°–40° from the central vein. The lateral primary veins reach the apical part of the leaf where they are topped with the first pair of secondary veins. The secondary venation pattern is brochidodromous. These veins rise from the central primary vein with angles of 60°–70°. The exterior secondary veins are looped. The intercostal tertiary venation fabric follows a straight path and arises perpendicularly from the secondary veins. The quaternary vein fabrics are irregularly reticulate with moderate areolation development.

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

Genus: **Laurophyllum** Goeppert
Laurophyllum sp.
(Plate III.2; Fig. 5.1)
Material: IPS109721, IPS109739, IPS109749, IPS109756, IPS109768, including 2 complete blades.

Description: The leaf is elliptic, petiolate and measures up to 3.5 cm in length and 1 cm in width. The margin is entire, the apex is straight and the base convex-rounded.

The primary vein is pinnate. The major secondary framework is simple brochidodromous and the secondary vein spacing is irregular. These

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.
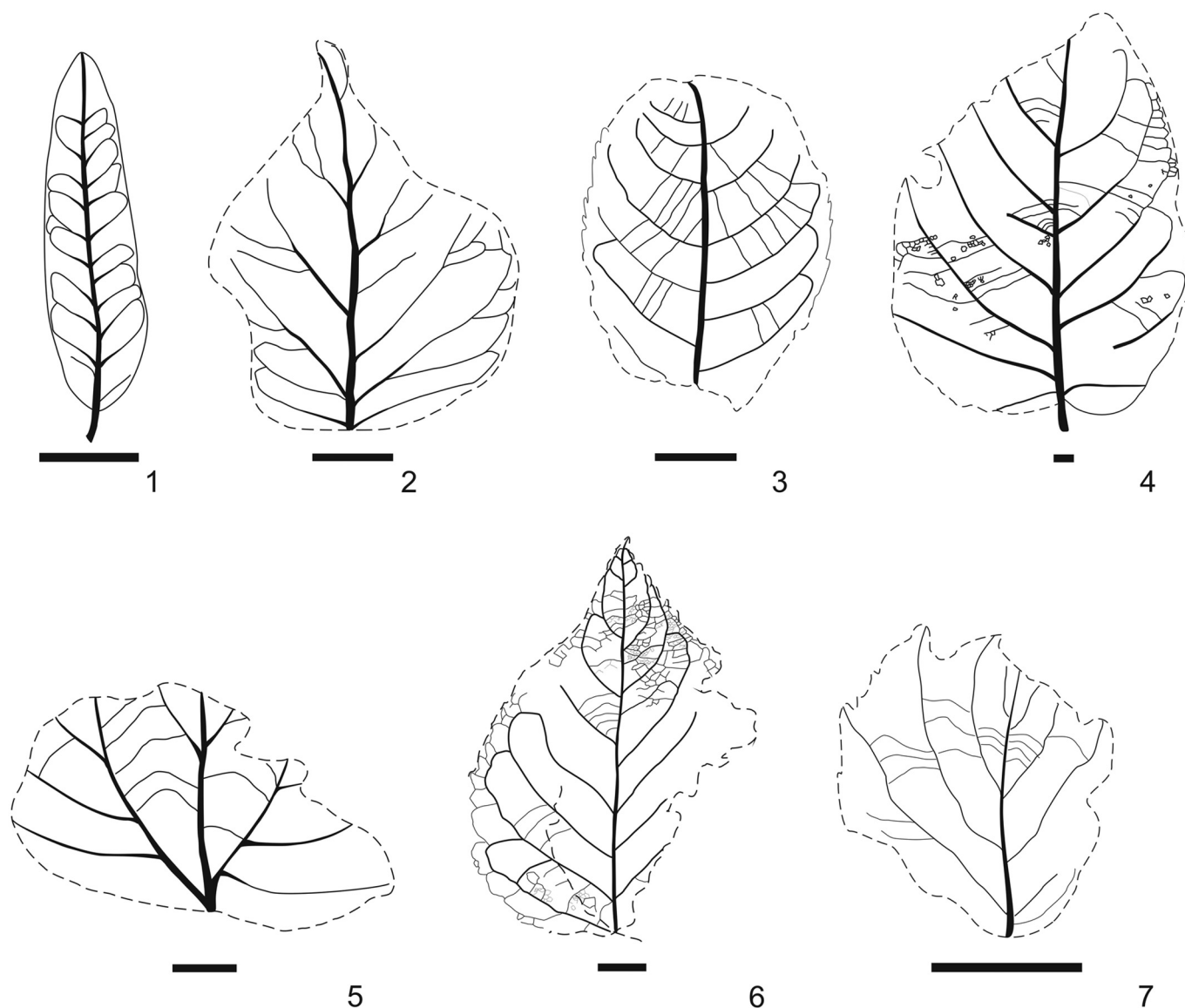
Fig. 5. Line drawing of some leaves from the Vallesian deposits of La Bisbal d'Empordà showing the characteristic foliar characters. 1: *Laurophyllum* sp. displaying the brochidodromous secondary veins (IPS109721). 2: *Populus balsamoides* with brochidodromous seconday veins (IPS109715). 3: Rosaceae 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.

veins rise from the midvein at 45°–60° and the attachment to the midvein is decurrent.

Remarks: This specimen was attributed to *Sapindus bilinicus* by Sanz de Siria Catalán (1981) in his fig. 12. A further specimen illustrated by Sanz de Siria Catalán (1981, pl. I, fig. 9) and named as *Laurophyllum princeps*, would be equivalent to this morphotype. A species-specific affinity was not assigned due to the high morphological variability of the Lauraceae and the limited material available. Based on Mihajlovič and Ljubotenski (1994) and Teodoridis (2003) cuticular preservation would be necessary to refine the attribution provided).

Order: PROTEALES Berchtold et Presl
Family: PLATANACEAE Lestibudois
Genus: **Platanus** Linnæus
Platanus sp.
(Plate III.3)
Material: IPS109709 is a proximal fragment of a blade with a strongly-marked venation pattern.

Description: The portion of the leaf blade available is 3.25 cm long and 4.5 cm wide. The base has a concave form. The margin is toothed with only one acute tooth preserved (concave shape in both flanks).

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

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

Order: Malpighiales Martius
Family: Salicaceae Mirbel
Genus: **Populus** Linnæus
Populus balsamoides Goeppert, 1855
(Plate III.4; Fig. 5.2)

1855 *Populus balsamoides* Goeppert, 23; pl. 15F (Goeppert, 1855)

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

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

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

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

The primary vein network is pinnate with one basal sympodial vein. The major secondary veins rise from the midveins with irregular spacing and uniform angles of 40°–50°. The attachment of the major secondaries to the midvein is decurrent and deflects the midvein. The first pair of secondary basal veins are thinner in width than other secondaries and at a greater angle to the midvein (70°) but are also brochidodromous.

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

Order: Rosales Perleb
Family: Rhamnaceae Durande
Genus: **Paliurus** Miller
Paliurus sp.
(Plate III.5)

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

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

Remarks: These specimens were also attributed to *Paliurus* sp. by Sanz de Siria Catalán (1981). Based on Burge and Manchester (2008) the receptacle shape allows for a distinction between two organ-species of Cenozoic *Paliurus* seeds. Unfortunately, this character is missing in the specimens studied.

Rosaceae gen. et sp. indet.
(Plate III.6; Fig. 5.3)

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

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

The primary vein framework is pinnate with one basal vein. The major secondaries are brochidodromous and are placed somewhat irregularly, but the distances between major secondary veins decreases distally. The angle of the major secondaries with the midvein is uniform at 60°–70^0, but they curve upwards towards the margins, before forming a loop with the adjacent secondary. The attachment of the major secondaries is excurrent. The intercostal tertiary fabric is straight to slightly sinuous, rising at 70° from the secondary veins.

Remarks: This specimen was attributed to *Alnus stenophylla* (Saporta et Marion) by Sanz de Siria Catalán (1981) due to what he interpreted as an emarginate apex. Here this feature is regarded as damage to the apex

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

Order: Fagales Engler
Family: Betulaceae Gray
Genus: **Alnus** Miller
Alnus gaudinii (Heer, 1859) Knobloch et Kvaček, 1976.
(Plate III.7; Fig. 5.4)

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

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

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

1976 *Alnus gaudinii* (Heer); Knobloch et Kvaček, 33; pl. 6, figs. 1, 3, pl. 7, figs. 1, 5, pl. 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, figs. 10–12. (Knobloch and Kvaček, 1976)

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

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

Material: IPS109707, IPS109722, IPS109726, IPS109738, IPS109759 and IPS109761 are incomplete blades and all of them lack the apex.

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

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

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

Genus: **Carpinus** Linnæus
Carpinus sp.
(Plate III.8)

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

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

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

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

Order: Sapindales Dumortier
Family: Sapindaceae Jussieu
Genus: **Acer** Linnæus
Acer tricuspidatum Bronn, 1838
(Plate III.9)

1823 *Phyllites trilobatus* Sternberg, 37; pl. 50, fig. 2. (Sternberg, 1820-1838)

? 1838 *Acer tricuspidatum* Bronn, 865; pl. 35, figs. 10a, b – missing holotype. (Bronn, 1838)

? 1845 *Acer trilobatum* Al. Braun, 172. (Braun, 1845)

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

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

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

1964 *Acer trilobatum* (Sternberg) Al. Braun; Walther, 59; pl. 21, pl. 22, figs 1–6, pl. 23, figs. 2, 5, 8.(Walther, 1964)

? 1968 *Acer tricuspidatum* Bronn; Walther, 363; pl. 2, fig. 1 – neotype. (Walther, 1968)

1972 *Acer tricuspidatum* Bronn; Walther, 78; pl. 15, figs. 1–12, pl. 45, figs. 2–10.(Walther, 1972)

1996 *Acer tricuspidatum* Bronn; Walther, 14; fig. 3.28.(Walther, 1996)

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

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

The primary vein network is basally actinodromous with five basal veins, three of which are primary veins, while the exterior two are secondaries. Principal primary veins terminate at the lobe apex. Simple veins run between the exterior primary veins and the margin (agrophic veins). These veins are craspedodromous and end at the tooth tip. The major secondary framework is craspedodromous and the spacing increases proximally while the angle between the central primary vein and the secondaries is uniform (40°–60°). The attachment of the major secondaries to the midvein is excurrent. The intersecondaries run a course that is parallel to the subjacent major secondaries and occur at a rate of <1 per intercostal area. They are <50% the length of major secondaries. The intercostal tertiary fabric is mixed percurrent, dominated by opposite percurrent veins at the proximal-most intercostal areas with consistent angles. Occasionally, some intercostal tertiary veins reach the apex of the tooth.

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

Order: Urticales Jussieu et Presl
Family: Ulmaceae Mirbel
Ulmus sp.
(Plate IV.1)

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

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

The primary vein framework is pinnate with one basal vein. The major secondary framework is semicraspedodromous with the principal veins terminating marginally at the tooth apices. The major secondary spacing is irregular at angles that are uniform at 40^0–55^0. The attachment of the major secondaries to the midvein is excurrent. The intercostal tertiary vein fabric is sinuous, however, the tertiaries that intersect the midvein form chevrons. The quaternary vein fabric is reticulate.

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

Genus: **Zelkova** Spach
Zelkova sp.
(Plate IV.2)

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

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

The primary vein framework is pinnate with one basal vein. The major secondary framework is semicraspedodromous with the principal veins terminating marginally at the tooth apices. The major secondary spacing is irregular at angles that are uniform at 40^0–55^0. The attachment of the major secondaries to the midvein is excurrent. The intercostal tertiary vein fabric is sinuous, however, the tertiaries that intersect the midvein form chevrons. The quaternary vein fabric is reticulate.

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

Genus: **Cedrelospermum**
Cedrelospermum sp.
(Plate IV.3)

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

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

The primary vein framework is pinnate. The major secondaries are craspedodromous and end at the apex of the teeth. They are regularly spaced (7 veins per cm) and arise at angles of 45°–80° from the midvein. The angle between the midvein and the secondary vein decreases towards the apex. The secondary vein attachment is excurrent. The intersecondaries appear to be parallel to the major secondaries but this is only seen in the distal third of the specimen. There is one intersecondary vein per intercostal area. The intercostal tertiary vein fabric is reticulate.

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

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.

by Jia et al. (2018) matches the leaf features from the specimen from La Bisbal d'Empordà, suggesting ascription to this genus.

Order: LAMIALES Bromhead
Family: OLEACEAE Hoffmanns et Link
Genus: **Fraxinus** Tourn. ex Linnæus

Fraxinus sp.
(Plate IV.4)
Material: Blades with excellent preservation of the venation but partial preservation of margins, apex or base in IPS109701, IPS109711, IPS109716, IPS109730, IPS109731, IPS109733, IPS109753, IPS109575, IPS109758, IPS109765 and IPS109766.

Specimen IPS109753 appears to be a compound leaf, with anatomically connected leaflets.

Description: Compound leaf comprising at least five leaflets. Leaflets arrangement is opposite or subopposite. The leaflets measure up to 3.2 cm in length and 1 cm in width and have a petiolule. The shape of the leaflet lamina is elliptic with both basal and medial symmetry. Usually, the apex and base of leaflets are acute, but they vary to rounded in some specimens. The margin is toothed. The tooth shape is straight at the proximal and distal flanks and the sinuses are angular. The teeth are regularly spaced, with up to 8 teeth per cm.

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

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

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

Incertae sedis
Undetermined magnoliopsid 1
(Plate V.1)
Material: IPS109718, a distal half of a blade with some damage to the apex and margin.

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

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

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

Undetermined magnoliopsid 2
(Plate V.2; Fig. 5.5)
Material: IPS109734 is an incomplete proximal part of a blade. Another leaf fragment is glued to the same specimen and this piece was recognised here as a counterpart piece of the specimen apex.

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

The primary vein framework is palmate with three actinodromous basal veins. Interior secondaries display a sinuous course. The secondary veins arise from the primary veins at 45°–110° and their spacing along the blade is irregular. The attachment of the major secondaries to the midvein is decurrent. The intercostal tertiary fabric is sinuous.

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

Undetermined magnoliopsid 3
(Plate V.3; Fig. 5.6)
Material: IPS109729 and IPS109766 are two incomplete blades, both missing the base.

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

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

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

Undetermined magnoliopsid 4
(Plate V.4; Fig. 5.7)
Material: IPS109767 is a deformed and incomplete blade. The apical and the basal part, some interior fragments and the right margin are damaged. Possible fragmentary material is also found in IPS109762.

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

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

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

Undetermined magnoliopsid 5
(Plate V.5)
Material: IPS109710 is a complete blade, lacking some details of the margin.

Description: The specimen studied measures 1 cm in length and 0.65 cm in width and the lamina has an elliptical shape. There is both
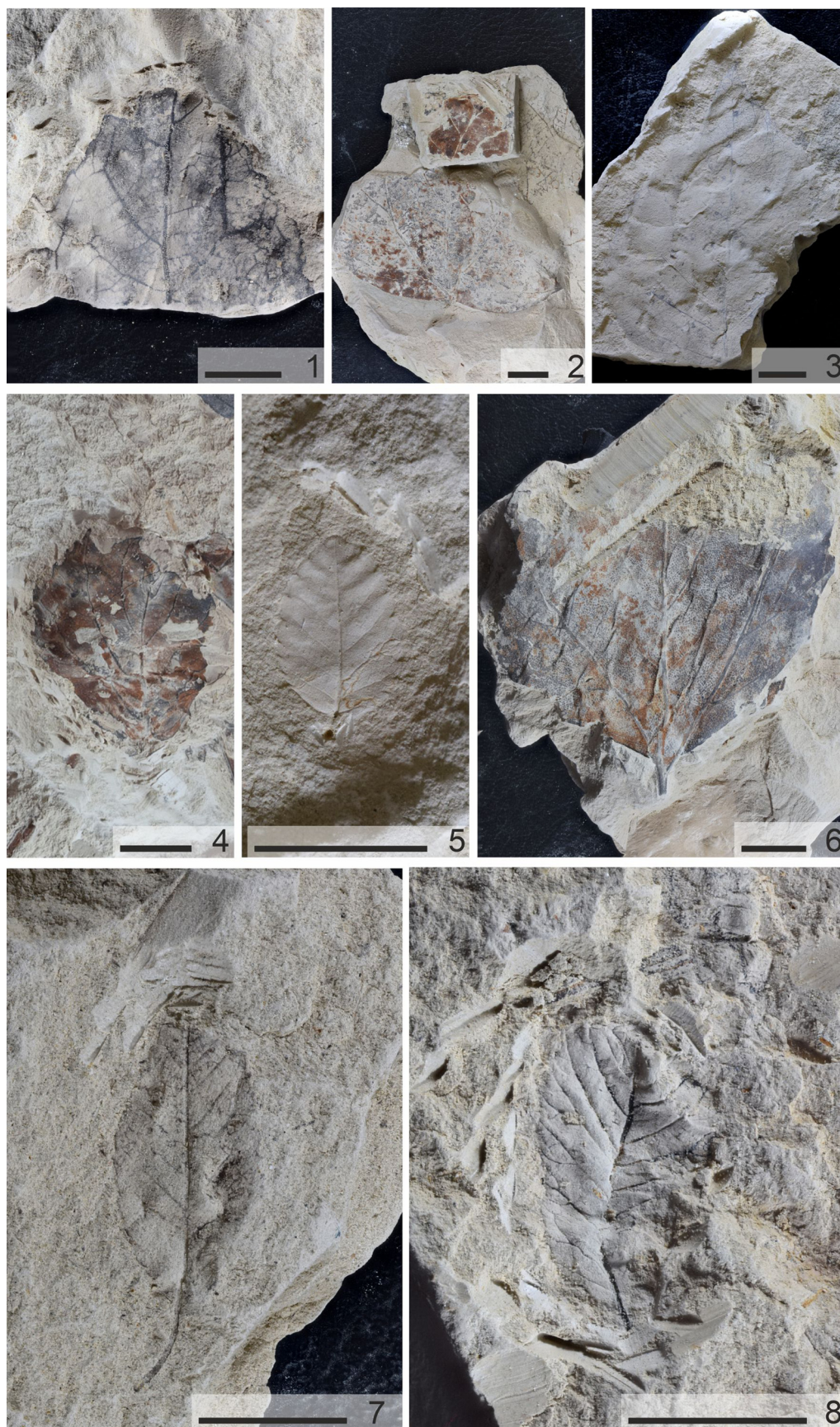
Plate V. Incertae sedis from the Vallesian deposits of La Bisbal d'Empordà (continued). 1: Undetermined magnoliopsid 1 (IPS109708). 2: Undetermined magnoliopsid 2 (IPS109734). 3: Undetermined magnoliopsid 3 (IPS109729). 4: Undetermined magnoliopsid 4 (IPS109767). 5: Undetermined magnoliopsid 5 (IPS109710). 6: Undetermined magnoliopsid 6 (IPS109708). 7: Undetermined magnoliopsid 7 (IPS109728). 8: Undetermined magnoliopsid 8 (IPS109765). Scale bar 1 cm.

medial and possible basal symmetry. The base is convex and the apex is straight, with an obtuse angle. The margin is toothed. The tooth shape is convex in the proximal and distal flank. They are closely and regularly spaced. The sinuses are acute.

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

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

Undetermined magnoliopsid 6
(Plate V.6)
Material: IPS109708 is an incomplete basal part of a blade, with damaged margins.

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

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

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

Undetermined magnoliopsid 7
(Plate V.7)
Material: IPS109771 is a complete blade with a preserved petiole but with poorly preserved veins.

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

The primary vein network is pinnate with one basal vein. The major secondary venation framework is craspedodromous with veins showing a regular spacing and uniform angles of 50°–55°. The attachment of the major secondaries to the midvein is excurrent. The principal secondary veins terminate at the apices of teeth. The intercostal tertiary venation fabric is percurrent to reticulating.

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

Undetermined magnoliopsid 8
(Plate V.8)
Material: IPS109728 is a damaged blade missing clear detail of the apex and basal parts of the lamina and with eroded margins.

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

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

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

4.3. Plant taphonomy and palaeoecology

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

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

Less than 20% of the samples bear helophytic plant stems, likened to reeds, and sometimes multiple stem portions occur in a given sample (Plate VI.2). These plant portions are 3–4 cm long and 1–2 cm wide. Furthermore, about 10% of the specimens are orbicular winged *Paliurus* seeds. Most of them are complete but a few show a small amount damage to the wing (Plate VI.3). *Fraxinus* leaflets are commonly isolated as seen in Plate IV.4, with just a single occurrence of a compound leaf, thought to belong to this genus (Plate VI.4).

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

The relatively abundant and almost intact winged seeds of *Paliurus* together with the absence of other organs of this plant such as leaves, indicate a clear plant organ selection. These taphonomic data are consistent with aerial transport. Based on the observations carried out by Ridley (1930), ripe winged seeds such as
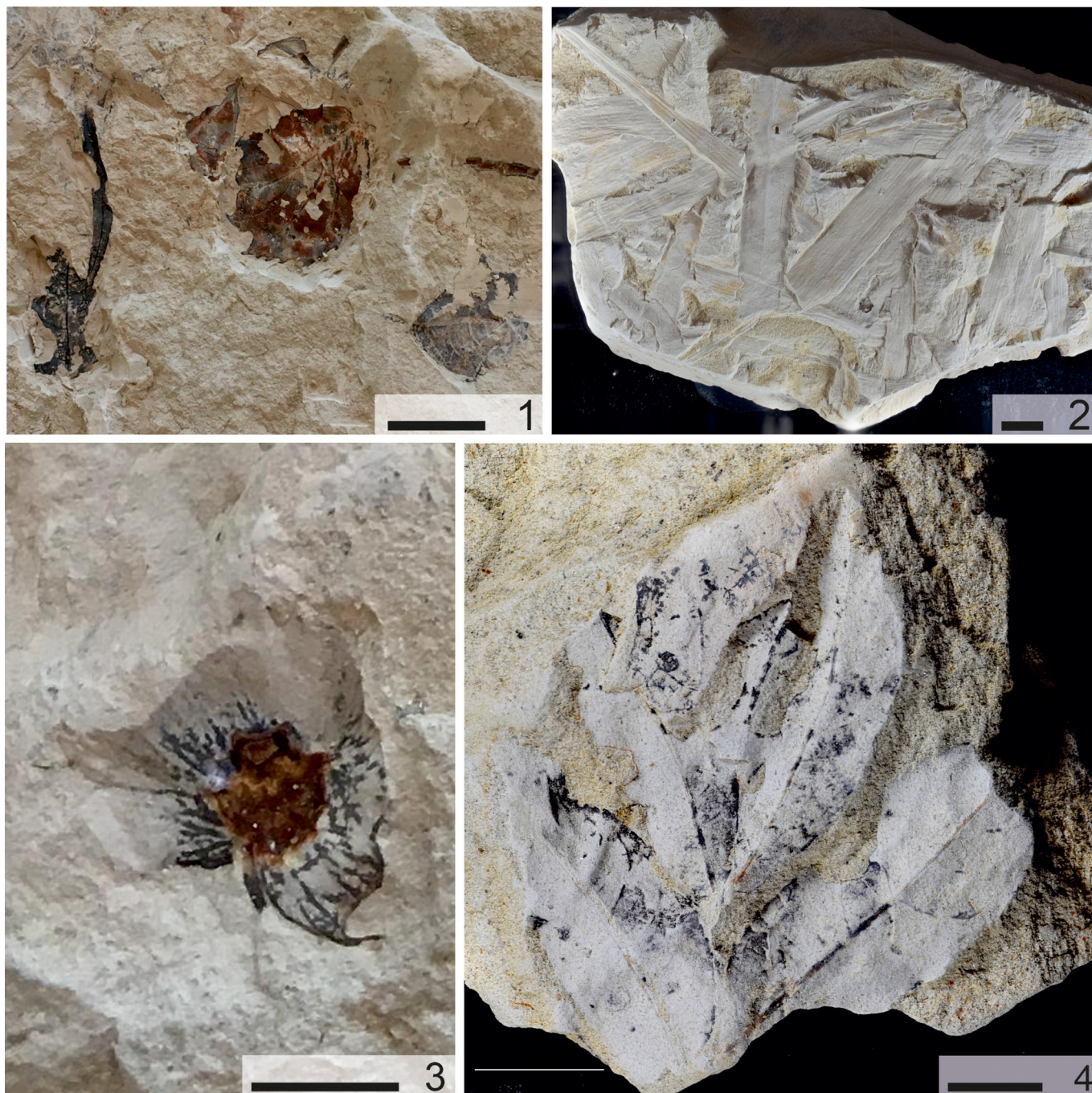
Plate VI. Taphonomic plant features from the Vallesian deposits of La Bisbal d'Empordà. 1: Torn leaf (IPS109740). 2: Helophytic plant portions forming a monospecific assemblage (IPS109769). 3: Almost intact *Paliurus* seed (IPS109718). 4: Leaf with anatomically connected leaflets of *Fraxinus* sp. (IPS109753). Scale bar 1 cm.

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

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

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

5. Discussion

The taxonomic description of the La Bisbal d'Empordà fossil leaf collection together with the sedimentological and taphonomic results are significant for the characterisation of the Vallesian lowland vegetation of this locality in the northeast of the Iberian Peninsula. Associated

small mammal fossils provide an independent and complementary source of information for palaeoenvironmental reconstruction.

5.1. Vallesian plant composition of La Bisbal d'Empordà

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

Sanz de Siria Catalán (1997) in his study of the macroflora of Terrassa (Vallès-Penedès Basin), also of late Vallesian age (MN10, 9.3 Ma; see Agustí et al., 2003), found certain similarities in plant composition with La Bisbal d'Empordà, but highlighted a clear dominance of five species in the latter collection (*P. fraxinifolia, Cinnamomum polymorpha,* *Platanus aceroides, Populus balsamoides* and *Acer trilobatum*) whereas the Terrassa assemblage is more balanced. However, our re-examination of the La Bisbal d'Empordà assemblage suggests that aside from the high abundance of *Fraxinus* sp., its composition is indeed more similar sharing many genera including, *Acer, Ulmus, Carpinus, Populus, Zelkova, Daphnogene* ("*Cinammomum*") and *Laurophyllum*.

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

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

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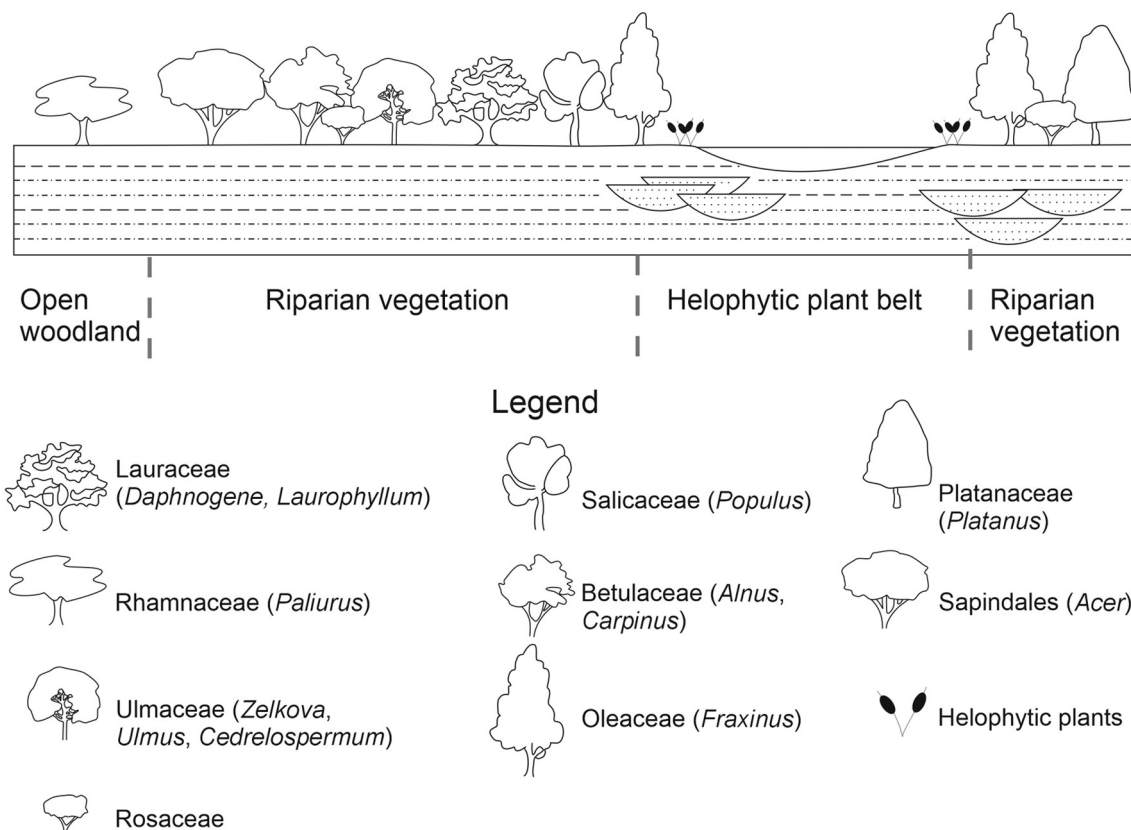

Fig. 6. Palaeoenvironmental reconstruction of the Vallesian from La Bisbal d'Empordà flora.

- Helophytic plant belt: This was mainly composed of reed plants, that were locally abundant. *Equisetum parlatorii* described and figured by Sanz de Siria Catalán (1981), could also be assigned to this plant community, but was not found in the studied collection here. This suggests that there were stable water tables capable of supporting a wetland community. This community is consistent with the edaphic features of the strata. However, this community is usually related to hydromorphic soils (Retallack, 2008), which is in contrast with the dominance of alfisols recognised in the field.

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

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

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

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

5.3. Comparison with the associated small mammal fauna

The mammal fauna found at the La Bisbal d'Empordà sites provides additional information on the palaeoenvironment. The exact provenance of the large mammal remains is uncertain. Although Villalta (1958) stated that the large mammal remains from this locality were found 1 km west of La Bisbal d'Empordà village, and thus near the Can Colomer clay pit, the exact bed is unknown and are not taken into consideration for palaeoenvironmental reconstruction herein.

The small mammal assemblages from La Bisbal d'Empordà are dominated by cricetids (hamsters and relatives) and ochotonid lagomorphs and include a few insectivores (Eulipotyphla) and arboreal taxa. The glirid *Muscardinus hispanicus*, which belongs to the same genus as the extant hazel dormouse (*Muscardinus avellanarius*), is the only presumably arboreal form in the whole assemblage and is only represented by 2 specimens (out of 56) in Can Colomer 2. Same as arboreal mammals, insectivorous mammals (mainly belonging to the order

Eulipotyphla) are more taxonomically diverse in more humid and forested habitats (Van Dam, 2006; Van Dam and Utescher, 2016). Not surprisingly, these are rare at the La Bisbal d'Empordà sites, only being represented by an undetermined soricid (shrew), an erinaceid (hedgehog) and the dimylid *Plesiodymylus* sp. at Can Colomer 2. Although the studied samples are limited, the rarity of such taxa indicates somewhat arid conditions. The presence of solely terrestrial squirrels (*Heteroxerus*, *Spermophilinus*) and none of the arboreal or gliding forms that are common at Miocene sites, reinforces this conclusion, together with the occurrence of the dormouse *Myodyromys hamadryas*, which is also believed to have favoured open environments (see Van der Meulen and De Bruijn, 1982). Finally, the moderately high-crowned molars of the cricetids *Hispanomys dispectus* and *Rotundomys freirensis*, which are common at the sites, are indicative of a diet that includes abrasive plants such as the grasses characteristic of open, relatively arid, landscapes (Van Dam and Weltje, 1999; Casanovas-Vilar and Agustí, 2007).

The composition of the Vallesian rodent faunas from the L'Empordà Basin contrasts with that of the nearby the Vallès-Penedès Basin situated 90 km to the southwest. The Vallès-Penedès sites often include a higher diversity of arboreal dormice and insectivores than La Bisbal d'Empordà, with the addition of flying squirrels which are absent at the latter (Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2016a). These differences might be due in part to the limited sample size of the La Bisbal d'Empordà sites or reflect taphonomic biases. Indeed, a remarkable proportion of specimens show taphonomical alterations produced by predators, such as partial dissolution of enamel and dentine by gastric acids (see Plate I.3, I.15–16). The degree of digestion ranges from moderate to heavy, as characteristic of certain aerial raptors (see digestion categories in Fernández-Jalvo and Andrews, 2016). The hunting range for aerial predators is generally broad, and these may have hunted in various habitats far from humid areas. Subsequently raptor pellets with undigested bones would have been regurgitated and ended up in the depositional site. Therefore, the small mammal assemblage would not only include taxa living near the depositional environment but also others that would have likely dwelled in the more open areas away from it. In summary, small mammal evidence from the Vallesian deposits from La Bisbal d'Emporda is congruent with the palaeobotanical reconstruction based on the plant collection, showing a mixture of taxa that inhabited humid and forested landscapes with others that likely preferred more open country. Taphonomic biases may partly account for the underrepresentation of the former.

6. Conclusions

Sedimentological and taphonomic evidence presented here challenges former interpretations of the depositional environment of the La Bisbal d'Empordà palaeobotanical site. Previously thought to correspond to a lake margin or to be of strictly alluvial fan facies, we now show that fluvial processes were dominant in the section, thus accounting for the preservation and composition of the plant assemblage.

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

The associated small mammal fauna coeval to the plant remains studied here is consistent with this environmental interpretation. The bulk of the micromammal fauna is defined by terrestrial species linked

to open landscapes, while arboreal species, such as *Muscardinus hispanicus* or insectivores associated with humid and forested environments, are rare in the assemblage. The apparent overrepresentation of open-landscape taxa may be explained by taphonomic factors.

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

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

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

References

Agustí, J., 1981. Roedores miomorfos del Neógeno de Cataluña. PhD ThesisUniversity of Barcelona, Barcelona, p. 284 (unpublished).

Agustí, J., Sanz de Siria, A., Garcès, M., 2003. Explaining the end of the hominoid experiment in Europe. J. Hum. Evol. 45, 145–153.

Allen, J.R.L., 1970. A quantitative model of grain size and sedimentary structures in lateral deposits. Geol. J. 7 (1), 129–146.

Allen, J.R.L., 1974. Studies in fluviatile sedimentation: lateral variation in some fining-upwards cyclothems from the Red Mark, Pembrokeshire. Geol. J. 9 (1), 1–16.

Barrón, E., 1992. Presencia de *Fraxinus excelsior* Linné (Oleaceae, Gentianales) en el Mioceno Superior de la depresión ceretana. Implicaciones tafonómicas y paleoecológicas. Rev. Esp. Paleontol. 7, 101–108.

Barrón, E., 1996a. Estudio tafonómico y análisis paleoecológico de la macro y microflora miocena de la Cuenca de la Cerdaña. Tesis doctoralUniversidad Complutense de Madrid, Madrid, p. 658.

Barrón, E., 1996b. Caracterización del género *Acer* Linné (Magnoliophyta) en el Vallesiense (Neógeno) de la comarca de la Cerdaña (Lérida, España). Bol. Geol. Min. 107 (1), 38–54.

Barrón, E., 1996c. Characteristics of the family Betulaceae S. F. Gray (Magnoliophyta), in the Vallesian (Neogene) of la Cerdanya (Lleida, Spain). Treballs Mus. Geol. Barcelona 5, 171–211.

Barrón, E., 1999. Estudio macroflorístico del afloramiento Mioceno de concreciones carbonáticas de Izarra (Álava, España). Aspectos tafonómicos, paleoecológicos y biostratigráficos. Rev. Esp. Paleontol. 14 (1), 123–145.

Barrón, E., 2003. Evolución de las floras terciarias en la Península Ibérica. Monogr. J. Bot. Córdob. 11, 63–74.

Barrón, E., Diéguez, C., 1994. Neogene species of the genus *Fagus* L. from La Cerdaña (Lérida, Spain). Taxonomic conclusions and phylogenetic considerations. Anal. J. Bot. Madrid 52 (1), 21–32.

Barrón, E., Postigo-Mijarra, J.M., 2011. Early Miocene fluvial-lacustrine and swamp vegetation of La Rinconada mine (Ribesalbes-Alcora basin, Eastern Spain). Rev. Palaeobot. Palynol. 165 (1–2), 11–26.

Barrón, E., Rivas-Carballo, R., Postigo-Mijarra, J.M., Alcalde-Olivares, C., Vieira, M., Castro, L., Pais, J., Valle-Hernández, M., 2010. The Cenozoic vegetation of the Iberian Peninsula: A synthesis. Rev. Palaeobot. Palynol. 162, 382–402.

Barrón, E., Postigo-Mijarra, J., Diéguez, C., 2014. The late Miocene macroflora of La Cerdanya Basin (Eastern Pyrenees, Spain): towards a synthesis. Palaeontogr. Abt. B. Paleobot. Paleophytol. 291, 85–129.

Barrón, E., Postigo-Mijarra, J., Casas-Gallego, M., 2016. Late Miocene vegetation and climate of La Cerdanya Basin (eastern Pyrenees, Spain). Rev. Palaeobot. Palynol. 235, 99–119.

Boggs, S., 2006. Principles of sedimentology and stratigraphy. Pearson Prentice Hall, Upper Saddle River, N.J, p. 676.

Braun, A., 1845. Die Tertiär-Flora von Öhningen. N. Jb. Min. Geogn. Geol. Petref.-Kunde 164–174.

Bronn, H.G., 1838. Lethaea Geognostica II. E. Schweizerbart's Verlagsbuchhandlung, Stuttgart, p. 865.

Burge, D.O., Manchester, S.R., 2008. Fruit morphology, fossil history, and biogeography of *Paliurus* (Rhamnaceae). Int. J. Plant Sci. 169 (8), 1066–1085.

Casanovas-Vilar, I., Agustí, J., 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 248, 169–189.

Casanovas-Vilar, I., Alba, D.M., Robles, J.M., Galindo, J., Carmona-Garcia, R., 2010. Rossegadors del Dipòsit Controlat de Vacamorta (= Can Colomer) (Cruïlles, Baix Empordà). Treballs Paleontol. Excavac. Paleontol. Catalun. 1, 128–149.

Casanovas-Vilar, I., Garcés, M., Van Dam, J., García-Paredes, I., Robles, J.M., Alba, D.M., 2016a. An updated biostratigraphy for the late Aragonian and Vallesian of the Vallès-Penedès Basin (Catalonia). Geol. Acta 14 (3), 195–217.

Casanovas-Vilar, I., Madern, A., Alba, D.M., Cabrera, L., García-Paredes, I., Van den Hoek Ostende, L.W., De Miguel, D., Robles, J.M., Furió, M., Van Dam, J., Garcés, M., Angelone, C., Moyà-Solà, S., 2016b. The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). Compt. Rend. Palevol. 15, 791–812.

Crusafont, M., 1962. Sobre la probable presencia del Mioceno continental en la cuenca del Ampurdán. Actas III Congreso Instituto Estudios Pirenaicos, Gerona, 1958. Instituto de Estudios Pirenaicos, CSIC, Zaragoza, pp. 57–65.

Denk, T., Grimm, G., 2005. Phylogeny and biogeography of *Zelkova* (Ulmaceae *sensu stricto*) as inferred from leaf morphology, ITS sequence data and the fossil record. Bot. J. Linn. Soc. 2005 (147), 129–157.

Ellis, B., Daly, D.C., Hickey, L.J., Johnson, K.R., Mitchell, J.D., Wilf, P., Wing, S.L., 2009. Manual of leaf architecture. The New York Botanical Garden, New York, p. 190.

Engelhardt, H., 1870. Flora der Braunkohlenformation im Königreich Sachsen. – Preisschrift. Fürstl. J. Ges. Leipzig 16, 1–69.

Erdei, B., Hably, L., Kázmér, M., Utescher, T., Bruch, A.A., 2007. Neogene flora and vegetation development of the Pannonian domain in relation to palaeoclimate and palaeogeography. Palaeogeogr. Palaeoclimatol. Palaeoecol. 253 (1–2), 115–140.

Fauquette, S., Suc, J.P., Jiménez-Moreno, G., Michels, A., Jost, A., Favre, E., Bachiri-Taoufiq, N., Bertini, A., Clet-Pellerin, M., Diniz, F., Farjanel, G., Feddi, N., Zheng, Z., 2007. Latitudinal climatic gradients in the Western European and Mediterranean regions from the Mid-Miocene (c. 15 Ma) to the Mid-Pliocene (c. 3.5 Ma) as quantified from pollen data. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.), Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies. The Micropalaeontological Society, Special Publications. The Geological Society, London, pp. 481–502.

Ferguson, D.K., 1985. The origin of leaf-assemblages - new light on an old problem. Rev. Palaeobot. Palynol. 46, 117–188.

Fernández-Jalvo, Y., Andrews, P., 2016. Atlas of Taphonomic Identifications: 1001 + Images of Fossil and Recent Mammal Bone Modification. Springer Netherlands, Cham, p. 359.

Fernández-Marrón, M.T., 1971. Estudio paleoecológico y revisión sistemática de la flora fósil del Oligoceno español. PhD thesis152. Universidad Complutense de Madrid Facultad de Ciencias, Serie A, p. 177.

Férnandez-Marrón, M.T., Olivé, A., Del Olmo, P., Portero, J.M., 1979. La flora terciaria del yacimiento de Izarra (Álava) y sus implicaciones cronostratigráficas. Bol. Geol. Min. 90 (1), 6–12.

Gibert, J., Agustí, J., Moyà, S., 1979. Bioestratigrafia de l'Empordà. Butll. Inform. Inst. Paleontol. Sabadell 11 (1–2), 43–47.

Gibert, J., Agustí, J., Moyà, S., 1980. Nuevos datos sobre la biostratigrafia del Ampurdán. Bol. Geol. Min. 91, 705–712.

Goeppert, H.R., 1855. Die Tertiäre Flora von Schossnitz in Schlesien. Görlitz, Heyn'sche Buchhandlung, p. 52.

Heer, O., 1855. Flora Tertiaria Helvetiae, I. J. Wurster et comp, Winterthur, p. 118.

Heer, O., 1856. Flora Tertiaria Helvetiae, II. J. Wurster et comp, Winterthur, p. 110.

Heer, O., 1859. Flora Tertiaria Helvetiae III. J. Wurster et comp, Winterthur, p. 378.

Ivanov, D., Utescher, T., Mosbrugger, V., Syabryaj, S., Djordjević-Milutinović, D., Molchanoff, S., 2011. Miocene vegetation and climate dynamics in Eastern and Central Paratethys (Southeastern Europe). Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 262–275.

Jia, L.-B., Su, T., Huang, Y.-J., Wu, F.-X., Deng, T., Zhou, Z.-K., 2018. First fossil record of *Cedrelospermum* (Ulmaceae) from the Qinghai–Tibetan Plateau: implications for morphological evolution and biogeography. J. Syst. Evol. 57 (2), 94–104.

Jiménez-Moreno, G., Fauquette, S., Suc, J.P., 2010. Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. Rev. Palaeobot. Palynol. 162 (3), 403–415.

Knobloch, E., 1961. Die oberoligozäne Flora des Pirskenberges bei Šluknov in Nord-Böhmen. – Sborník Ústředního ústavu geologického. Paleontologie 26, 241–315.

Knobloch, E., Kvaček, Z., 1976. Miozäne Blätterfloren vom Westrand der Böhmischen Masse. Rozpravy Ústředního ústavu geologického 42, 1–131.

Kovar-Eder, J., 2003. Vegetation dynamics in Europe during the Neogene. Distribution and Migration of Tertiary Mammals in Eurasia. 10, pp. 373–392.

Kraus, M.J., Aslan, A., 1999. Eocene hydromorphic paleosoils: significance for interpreting ancient floodplain processes. J. Sediment. Petrol. 63 (3), 453–463.

Kvaček, Z., 1971. Fossil Lauraceae in the stratigraphy on the North Bohemian Tertiary. Sborník Ústředního ústavu geologického, Paleontologie 13, 47–86.

Kvaček, Z., Walther, H., 1998. The Oligocene volcanic flora of Kundratice near Litoměřice, České středohoří Volcanic complex (Czech Republic). Acta Mus. Natl. Prag. Ser. B Hist. Nat. 54, 1–43.

Kvaček, Z., Walther, H., 2004. Oligocene flora of Bechlejovice at Děčín from the neovolcanic area of the České Středohoří mountains, Czech Republic. Acta Mus. Natl. Prag. Ser. B Nat. Hist. 60 (1–2), 9–60.

Llenas, M., Galobart, A., Agustí, J., 2002. Els petits mamífers del neogen i del quaternari inferior. In: Maroto, J., Ramió, S., Galobart, A. (Eds.), Els vertebrats fòssils del Pla de l'Estany. 23. Quaderns CECB, pp. 29–42.

Mai, D.H., 1963. Beiträge zur Kenntnis der Tertiärflora von Seifhennersdorf (Sachsen). Abh. Staatl. Mus. Mineral. Geol. Dresd. 1963, 39–114.

Manchester, S.R., Crane, P.R., Golovneva, L.B., 1999. An extinct genus with affinities to extant *Davidia* and *Camptotheca* (Cornales) from the Paleocene of North America and Eastern Asia. Int. J. Plant Sci. 160, 188–207.

Martín-Closas, C., Gomez, B., 2004. Taphonomie des plantes et interprétations paléoécologiques. Une synthèse. Geobios 37, 65–88.

Martín-Closas, C., Permanyer, A., Vila, M.J., 2005. Palynofacies distribution in a lacustrine basin. Geobios 38, 197–210.

Martín-Closas, C., Wójcicki, J., Fonollà, L., 2006. Fossil charophytes and hydrophytic angiosperms as indicators of lacustrine trophic change. A case study in the Miocene of Catalonia (Spain). Criptogamie-Algologie 27 (4), 357–379.

Miall, A.D., 1977. A review of the braided-river depositional environment. Earth Sci. Rev. 13, 1–62.

Miall, A.D., 1992. Alluvial deposits. In: Walker, R.G., James, N.P. (Eds.), Facies Models: Response to Sea Level Change. Cambridge University Press, pp. 119–142.

Miall, A.D., 2016. Stratigraphy: A Modern Synthesis. Springer International Publishing, Switzerland, p. 454.

Mihajlovič, D., Ljubotenski, T., 1994. Upper Eocene Flora of Ovce Polje, Macedonia. Geol. Carpath. 45, 203–210.

Nichols, G., 2009. Rivers and alluvial fans. Sedimentology and Stratigraphy. Wiley Blackwell, p. 432.

Picart, J., Solà, J., Mató, E., Llenas, M., Losantos, M., Beràstegui, X., Agustí, J., 1996. La sedimentación neógena en los márgenes de la cuenca del Empordà. Geogaceta 20, 84–87.

Pound, M.J., Haywood, A.M., Salzmann, U., Riding, J.B., 2012. Global vegetation dynamics and latitudinal temperature gradients during the Mid to Late Miocene (15.97–5.33Ma). Earth Sci. Rev. 112, 1–22.

Retallack, G.J., 2008. Soils of the Past: An Introduction to Paleopedology. Springer, Amsterdam, p. 520.

Ridley, H.N., 1930. The Dispersal of Plants Throughout the World. UK, Reeve, Ashford, p. 744.

Royer, D.L., Wilf, P., 2006. Why do toothed leaves correlate with cold climates? Gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. Int. J. Plant Sci. 167, 11–18.

Rufí-Casals, I., Orlandi-Oliveras, G., Solés-Coll, A., 2017. Presència de *Tetralophodon* Falconer, 1857 (Proboscidea) al Vallesià de la fossa de l'Empordà (Vaca Morta; Cruïlles, Monells i Sant Sadurní de l'Heura; Baix Empordà). Treb. Mus. Geol. Barcelona 23, 7–16.

Sanz, A., 1988. Els cormòfits. In: Gallemí, J. (Ed.), Registre fòssil. Història Natural dels Països Catalans, Enciclopèdia Catalana S.A., Barcelona. 15, pp. 151–196.

Sanz de Siria Catalán, A., 1981. Flora del Mioceno superior de La Bisbal (Baix Empordà). Butll. Inform. Inst. Paleontol. Sabadell 13, 57–68.

Sanz de Siria Catalán, A., 1985. Datos para el conocimiento de las floras miocénicas de Cataluña. Paleontol. Evol. 19, 167–177.

Sanz de Siria Catalán, A., 1997. La macroflora del Vallesiense superior de Terrassa (Barcelona) Datos paleoecológicos y paleoclimáticos. Paleontol. Evol. 30–31, 247–268.

Saula, E., Picart, J., Mató, E., Llenas, M., Losantos, M., Berástegui, X., Agustí, J., 1996. Evolución geodinámica de la fosa del Empordà y las Sierras Transversales. Acta Geol. Hisp. 29, 55–75.

Spicer, R.A., 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Park, Berkshire, England. Geol. Surv. Prof. Pap. 1143, 1–77.

Sternberg, K., 1820-1838. Versuch einer botanisch-geologischen Darstellung der Flora der Vorwelt. F. Fleischer, Leipzig, Ernst Breck's Witwe, Regensburg, J. Spurny, G. Hässe Söhne, Prag.

Teodoridis, V., 2003. Tertiary flora and vegetation of the locality Přívlaky near Žatec (Most Basin). Bull. Geosci. 78, 261–276.

Tosal, A., Verduzco, O., Martín-Closas, C., 2021. CLAMP-based palaeoclimatic analysis of the late Miocene (Tortonian) flora from La Cerdanya Basin of Catalonia, Spain, and an estimation of the palaeoaltitude of the eastern Pyrenees. Palaeogeogr. Palaeoclimatol. Palaeoecol. 564, 110186.

Tschan, G.F., Denk, T., Von Balthazar, M., 2008. *Credneria* and *Platanus* (Platanaceae) from the Late Cretaceous (Santonian) of Quedlinburg, Germany. Rev. Palaeobot. Palynol. 152, 211–236.

Uhl, D., Klotz, S., Traiser, C., Thiel, C., Utescher, T., Kowalski, E., Dilcher, D.L., 2007. Cenozoic paleotemperatures and leaf physiognomy - a European perspective. Palaeogeogr. Palaeoclimatol. Palaeoecol. 248, 24–31.

Utescher, T., Erdei, B., François, L., Mosbrugger, V., 2007a. Tree diversity in the Miocene forests of Western Eurasia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 253, 226–250.

Utescher, T., Djordjevic-Milutinovic, D., Bruch, B., Mosbrugger, V., 2007b. Climate and vegetation changes in Serbia during the last 30 Ma. Palaeogeogr. Palaeoclimatol. Palaeoecol. 253, 139–150.

Van Dam, J.A., 2006. Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: the use of small mammals as paleoprecipitation proxies. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238, 190–218.

Van Dam, J.A., Utescher, T., 2016. Plant- and micromammal-based paleoprecipitation proxies: comparing results of the coexistence and climate-diversity approach. Palaeogeogr. Palaeoclimatol. Palaeoecol. 443, 18–33.

Van Dam, J.A., Weltje, G.J., 1999. Reconstruction of the late Miocene climate of Spain using rodent paleocommunity successions: an application of end-member modelling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 1551, 267–305.

Van der Meulen, A.J., De Bruijn, H., 1982. The mammals from the lower Miocene of Aliveri (Island of Evia, Greece). II. The Gliridae. Proc. Koninkl. Akad. Wetensch. B 85, 485–524.

Villalta, J.F., 1958. La Néogene de l'Ampurdán. Bull. Soc. Géol. Franc. 6 (3), 947–948.

Walther, H., 1964. Paläobotanische Untersuchungen im Tertiär von Seifhennersdorf. Jb. Abh. Staatl. Mus. Mineral. Geol. Dresden 1–131.

Walther, H., 1968. Zur Nomenklatur von *Acer* "trilobatum". Monatsberichte der Königlichen Preussische Akademie der Wissenschaften zu Berlin 10, 630–638.

Walther, H., 1972. Studien über tertiäre *Acer* Mitteleuropas. Abh. Staatl. Mus. Mineral. Geol. Dresden 19, 1–309.

Walther, H., 1996. Das Tertiärvorkommen von Seifhennersdorf (Oberlausitz, Deutschland). N. Jb. Geol. Paläont. 200, 5–26.

Wang, Y.F., Ferguson, D.K., Zetter, R., Denk, T., Garfi, G., 2001. Leaf architecture and epidermal characters in *Zelkova*, Ulmaceae. Bot. J. Linn. Soc. 136, 255–265.

Westerhold, T., Marwan, N., Drury, A.J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J.S.K., Bohaty, S.M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D.A., Holbourn, A.E., Kroon, D., Lauretano, V., Littler, K., Lourens, L.J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R.H., Wilson, P.A., Zachos, J.C., 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. Science 369, 1383–1387.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292 (5517), 686–693.