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Peat-forming plants in the Maastrichtian coals of the Eastern Pyrenees

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ABSTRACT

The Lower Maastrichtian of Fumanya and neighbouring localities of the Vallcebre syncline (Eastern Pyrenees, Catalonia, Spain) provide the first taphonomic evidence for the hypothesis that cheirolepidiacean conifers were significant precursors of Maastrichtian Pyrenean coal. Most *Frenelopsis*-rich lignite beds do not bear rootlet marks, suggesting that the original peat was detrital. Sedimentological and taphonomic evidence indicates deposition on the margins of a lagoon after the transport of the cheirolepidiacean remains by flotation. The same parautochthonous assemblage includes complete impressions of *Sabalites longirhachis* leaves and large impressions of logs attributed to the same palm trees. Other parautochthonous or allochthonous plant megaremains include extremely rare cycadalean and monocot leaves and abundant minute angiosperm seeds. Rootlet marks associated with thin lignite beds occur at the top of some charophyte limestones. The charophyte association, dominated by *in situ* accumulation of *Peckichara* and *Microchara* gyrogonites, suggests that these limestones were deposited in shallow, freshwater lakes and that the corresponding peat mires were limnic rather than paralic in nature. The botanical affinity of plant remains associated with these root-bearing lignites is uncertain. Palynological analysis showed abundant bisaccates, with less abundant fern spores and freshwater algal oospores. Locally, the abundant rootlet marks were associated with large brush-like rooting structures attributed to *Sabalites longirhachis* palms. Our results show that, at the beginning of the Maastrichtian, cheirolepidiacean conifers were still significant peat-producing plants, although, unlike analogous Lower Cretaceous ones, they shared this role with rare angiosperms, such as palms.

KEYWORDS **Palaeobotany. Calcareous algae. Peat swamps. Upper Cretaceous. Pyrenees.**

INTRODUCTION

Cretaceous lignite from the Northern Hemisphere is generally attributed to the accumulation and diagenetic maturation of peat, caused mainly by taxodiacean conifers (Cross and Phillips, 1990; Greb *et al.*, 2006). Although these conifers may have been the main Cretaceous peat producers in particular sedimentary basins, this was not necessarily the rule everywhere. For instance, Kvaček and Herman (2004) showed that monocotyledons played an important role in the Cretaceous coal-forming wetlands of Grünbach (Austria). In the Iberian Peninsula, Cretaceous lignite forms significant deposits, which were intensively exploited in the past, in both the Albian of the Iberian Chain (mainly the Escucha Formation) and the Maastrichtian of the Eastern Pyrenees (Tremp Formation or "Garumnian" facies). The Iberian Lower Cretaceous coal deposits are not related to beds with taxodiacean megafossils but are instead associated with massive accumulations of cheirolepidiacean conifer remains, mainly *Frenelopsis* leafy axes, which suggests that the resulting lignite could have been produced by this extinct conifer (Gómez *et al.*, 2001, 2002). However, the Lower Cretaceous coal-bearing beds studied so far in Spain were not associated with rooting structures, indicating that they resulted from the accumulation of parautochthonous organic matter rather than *in situ* accumulation in peat mires. As a result, poor taphonomic evidence was available about the autochthonous production of these lignites (see Gómez *et al.*, 2001, 2002 for examples). A similar situation was reported in other European localities, such as the Cenomanian coal region of Bohemia (Uličný *et al.*, 1997).

The Maastrichtian of the Vallcebre syncline provides for the first time a case study, well documented in terms of its sedimentology and palaeogeography, to support the hypothesis that cheirolepidiacean conifers were indeed significant elements of Upper Cretaceous peat. The data gathered in the Vallcebre syncline also provide enough evidence to propose a taphonomic model of transport and deposition of plant remains in Maastrichtian wetlands.

MATERIALS AND METHODS

Four stratigraphic sections were measured to compile a 100-metre composite section of the Grey Garumnian unit in the Vallcebre syncline. They were located along the mountain road of Cal Sant (base coordinates N42º10'29" E01º49'44", top coordinates N42º10'33" E01º49'31") and in the inactive opencast coal mines of Font del Bullidor (base coordinates N42º10'30" E01º49'7", top coordinates N42º10'34" E01º49'3"), Fumanya Sud (base coordinates N42º10'50" E01º47'42", top coordinates N42º10'52" E01º47'47") and Mina Esquirol (base coordinates N42º11'8" E01º47'51", top coordinates N42º11'7" E01º47'52"), which were exploited during the last third of the 20th century. These sites are located between the village of Fígols and the Coll de Fumanya (Figs. 1-2), to the north of the town of Berga (Catalonia, Spain). Combined sedimentological analyses and descriptions of plant taphofacies were investigated in order to ascertain the palaeoenvironmental and palaeoecological setting of plant remains. Most marly levels and limestone beds were sampled for charophytes, and 31 samples were collected. Charophyte gyrogonites were obtained by both direct picking on the surface of marls and the usual micropalaeontological sieving and picking procedure. Charophyte thalli were studied under the optical microscope in thin sections, about 30μm thick, cut parallel and perpendicular to the bedding surface. Several lignite, organic marls and marlstone beds were sampled for pollen and cuticles. The preparation of samples for palynological analysis involved established procedures of crushing, followed by hydrochloric (HCl) and hydrofluoric (HF) acid treatments. Six samples were collected for palynological analysis. Between 100 and 200 grains were counted in three of them; the other samples were very poor, allowing only a qualitative (presence/absence) analysis. Because the plant-rich localities are protected by the cultural heritage law 9/1993 of the Catalan government, replicas of the largest megafossil plant remains were prepared in the field, and only small specimens or fragments were removed for study in the laboratory. Cuticle fragments were obtained after maceration with HCl and/or hydrogen peroxide (H_2O_2) followed by Schulze's reagent without treatment with ammonia. Later, cuticles were cleaned with HF. For some samples, peels were also made, with the acetate peel technique (Galtier and Phillips, 1999). Cuticles and peels were examined under a Light Microscope (LM) and photographed. Charophyte gyrogonites and plant cuticle samples were studied and photographed with Hitachi S1300 and Quanta 200 Scanning Electron Microscopes (SEM) at the Serveis Cientificotècnics of the Universitat de Barcelona.

Charophyte samples are stored in the charophyte collection of the Departament d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona. Megafossil plant remains are housed in the collection of the Institut Català de Paleontologia. Palynological slides prepared are housed at the UEI de Paleontología, Instituto de Geociencias (CSIC-UCM).

GEOLOGICAL SETTING

The Maastrichtian of the Eastern Pyrenees was deposited in a set of elongated, largely non-marine depocentres aligned at each side of the axis of the

Pyrenean range. In the Pyrenean Southern Foreland these depocentres are, from East to West, Vallcebre, Coll de Nargó, Tremp and Àger (Ardèvol *et al.*, 2000). They were formed and separated from each other by the uplift of successive thrust-sheets, which during the Cenozoic finally led to the formation of piggy-back basins and to the uplift of the whole Pyrenean range (Muñoz *et al.*, 1986; Puigdefàbregas *et al.*, 1986). Although Maastrichtian coal-bearing deposits are recognized in all these depocentres, they are best developed in the Vallcebre syncline, which is the subject of the present study.

The Vallcebre syncline is situated in the Lower Pedraforca thrust sheet and has minor decametric to hectometric thrusts at its core (Vergés *et al.*, 1994) (Fig. 1). The basin infilling was almost continuous from the Santonian to the Thanetian. There are three main sedimentary units in the basin, which are stratigraphically conformable. The lower unit is Late Santonian to Late Campanian in age and consists of basinal turbidites (Vallcarga Formation, Mey *et al.*, 1968). The second unit is Late Campanian in age and consists of near-shore calcarenitic limestones with foraminifera, bryozoans, brachiopods, ostracodes, bivalves, gastropods, corals and echinoderms (Terradets Formation, Pons, 1977). The upper unit, Latest Campanian to Thanetian in age, is mainly formed by fluvial red beds with subsidiary coal, lacustrine limestones and transitional marls of the Tremp Formation (Mey *et al.*, 1968), regionally called "Garumnian" (Leymerie, 1862).

The Tremp Formation or Garumnian in the Vallcebre syncline is up to 850m thick (Vergés *et al.*, 1994) and was divided by Rosell *et al.* (2001) into four lithological units, one of which is the subject of our study: the transitional basal unit (Grey Garumnian). The latter is formed by a heterolithic succession, up to 100m thick in this syncline, containing grey lutites and marls with intercalations of lignite, charophyte limestones and sandstones.

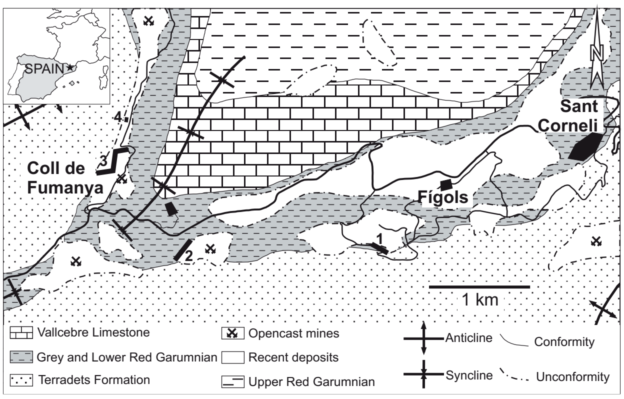

FIGURE 1 | Geological map of the study area with location of the stratigraphic sections shown in Figure 2.

Feist and Colombo (1983) reported a charophyte assemblage formed by *Microchara cristata* and *Peckichara cancellata* from limestones, lignites and organic marls in the lower part of the unit, while *Septorella brachycera* and *Peckichara sertulata* were found in variegated lutites, at the top of the section. These assemblages indicate a Lower Maastrichtian age for the Grey unit in the Vallcebre syncline. Recent palaeomagnetic data show that marlstones with dinosaur trackways in the lower part of the section are close to the Campanian-Maastrichtian boundary (Oms *et al.*, 2007).

The Fígols-Vallcebre composite section studied here includes the Grey Garumnian unit and shows three distinct intervals: lower, middle and upper (Fig. 2). In this study we focused on the middle Grey Garumnian, which contains the coal-bearing horizons and most of the plant remains in the succession.

Lower Grey Garumnian

It is formed by up to 11.5m of laminated, grey, marlstones, laminated lime mudstones and marls. This unit was called the "concrete beds" by local miners. The laminated marlstones contain abundant bivalves and gastropods, and a few centimetres-long, fragmented leafy axes of *Frenelopsis*. The laminated lime mudstones commonly contain abundant ostracodes. Several mudstone beds are topped with ferric crusts and *Thalassinoides* burrows. The bioturbation is filled by sand and fragments of ostracodes and charophyte thalli. This basal part of the Grey Garumnian unit is attributed to deposition in a protected brackish to freshwater lagoon (Rosell *et al.*, 2001) or tidal mudflat (Riera et al, 2010), the salinity being indicated by the invertebrate fossil content, formed by a mixture of marine-brackish mollusc taxa (*Cerastoderma*, *Saccostrea* shells with incrustated bryozoans, anomiids, *Cerithium*) along with freshwater-brackish genera (*Corbicula*, *Pyrgulifera*). The presence of bioturbation along with the formation of ferric crusts is indicative of episodical bottom stabilization and sediment starving.

Middle Grey Garumnian

This part of the Grey Garumnian unit is made up of 47m of black organic marls alternating with lignite and light-coloured charophyte lime wackestones-packstones. Minor intercalations of clays, siltstones and fine sandstones occur. Organic marls (facies 1) are abundant in the whole middle part of the Grey Garumnian and may contain low-diversity assemblages of molluscs dominated by euryhaline taxa (abundant *Corbicula laletana*, *Cerithium* sp., *Melanopsis* sp., oysters and *Pyrgulifera* sp. with rare *Cerastoderma* sp., *Deianira* sp., "*Pseudomelania*" shells). A few, but well preserved, shells of the terrestrial snail *Lychnus* sp. were

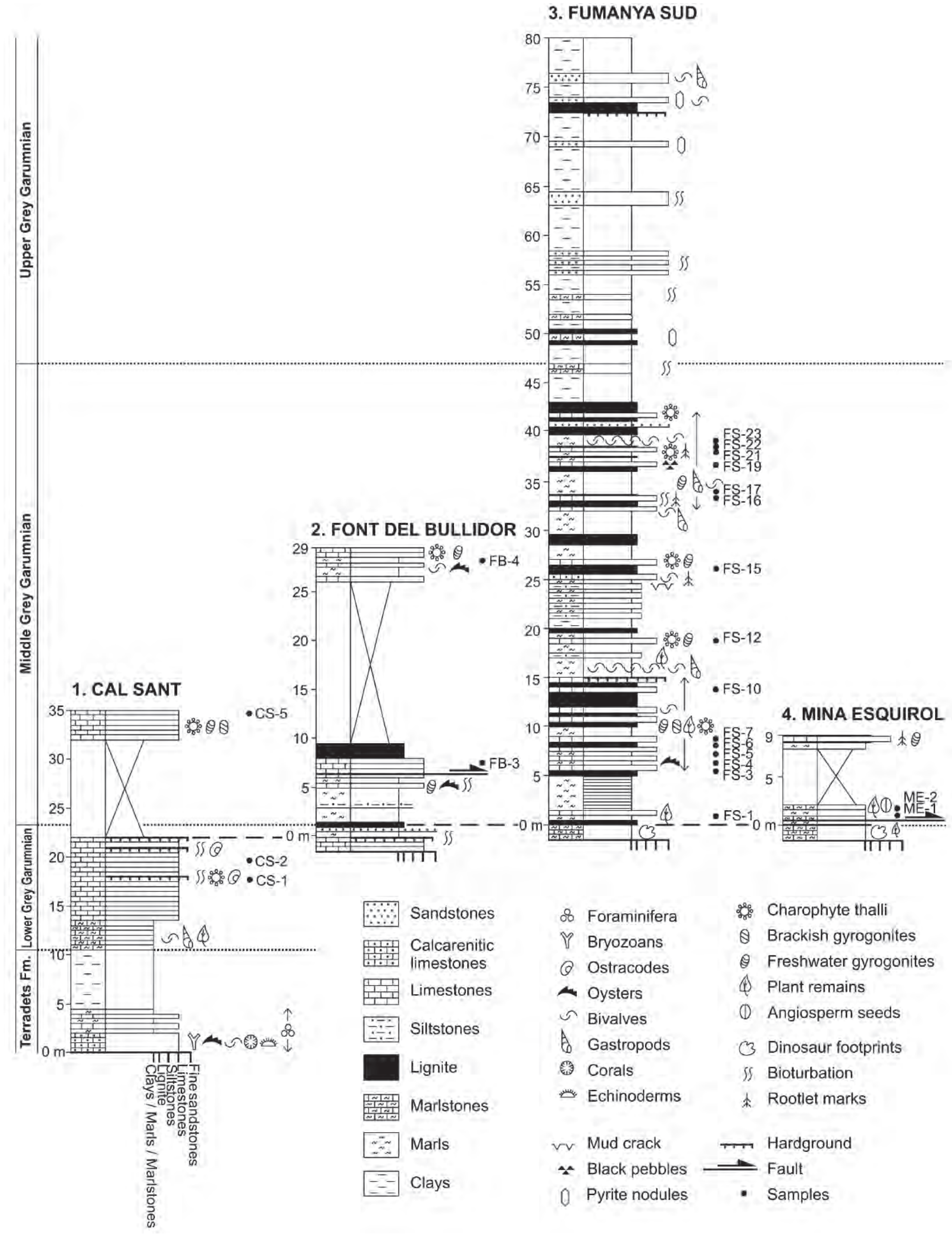

FIGURE 2 | Stratigraphic sections studied in the Fígols-Vallcebre area. See Figure 1 for the situation of columns.

also found in these organic marls. Other horizons with the unionid "*Unio" garumnica* indicate freshwater conditions. Babinot *et al.* (1983) also reported brackish ostracodes from this facies.

Lignite (facies 2) overlying previous marls forms tabular beds, less than 1.5m thick and with a lateral continuity of more than 1km. Petrologically, it is humic in composition and sub-bituminous in rank (García-Vallès *et al.*, 1994). According to these authors, the coal macerals are mainly from the vitrinite group and would indicate coal deposition in a forest swamp. The base of the first lignite seam at Coll de Fumanya shows abundant dinosaur trackways (Vila *et al.*, 2005), abundant *Sabalites longirhachis* adpressions (Marmi *et al.*, 2008, 2010) and massive accumulations of *Frenelopsis* sp. internodes. These lignite beds do not show root traces at their bases. The water salinity under which these lignites accumulated is unknown and may be variable in the Vallcebre syncline.

Limestones are well-bedded wackestones-packstones, up to 1.5m thick, and contain abundant gyrogonites and charophyte thalli. Four different types of carbonate microfacies (facies 3-6) were defined (Fig. 3):

Facies 3. Wackestones of porocharacean gyrogonites belonging to *Feistiella malladae* (Bataller) Villalba-Breva and Martín Closas nov. comb. associated with *Charaxis* sp. thalli. They were found in basal limestones mainly at Cal Sant and exceptionally in Fumanya Sud. Monotonous assemblages of porocharaceans are known to indicate brackish water conditions in the Cretaceous (Mojon, 1989).

Facies 4. Massive packstones of large charophyte thalli of the *Clavatoraxis* sp. type, showing a high degree of articulation and associated with small characean gyrogonites.

Facies 5. Laminated packstones formed by large collapsed charophyte thalli of the *Charaxis* sp. type, associated with gyrogonites of the genus *Peckichara* without anatomical connection. An assemblage of gyrogonites belonging to *Peckichara cancellata* was obtained at the top of some limestone beds.

Facies 6. Wackestones-mudstones of charophyte thalli of the *Clavatoraxis* sp. type, with *Microchara* sp. gyrogonites in anatomical connection, and abundant calcified filaments of *Girvanella* sp. attributed to cyanobacteria.

Limestones dominated by the genus *Peckichara* (facies 5) are dominant throughout the sections studied. This genus appears to be limited to lacustrine facies (Massieux *et al.*, 1987).

At the top of some of these charophyte-rich limestone beds, a different type of lignite was found (facies 7). These are up to 10-cm-thick lignite beds showing organic rootlet marks penetrating the underlying limestones, which suggests that the lignite resulted from an autochthonous accumulation of peat. The occurrence of lacustrine green algae, such as Oedogoniales in palynological sample FS-23, suggests fresh-water conditions during the deposition of this peat. In conclusion, root-bearing lignites may represent small peat-mires developed along the lakeshores, finally covering the lacustrine facies when lacustrine shallowing processes occurred.

The sedimentary succession of the middle Grey Garumnian shows small-order sedimentary cycles (Fig. 3). The most abundant facies association (Fig. 3A) is formed by basal organic marls (facies 1), followed by

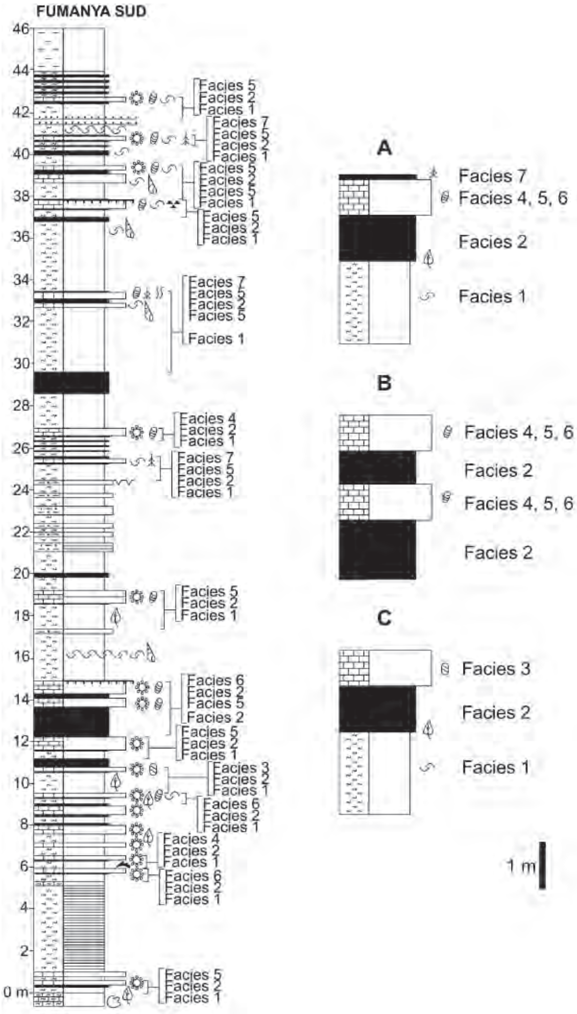

FIGURE 3 | Detail of Fumanya Sud section with indication of the seven facies defined in the middle Grey Garumnian. Conceptual cycles resulting from the three facies associations (A-C) are shown on the left hand side. See legend of Figure 2.

lignite (facies 2), charophyte limestones (facies 4-6) and root-bearing lignite at the top (facies 7). These cycles are repeated dozens of times and represent a repeated tendency to upward shallowing of the lagoon. In parallel, aquatic conditions pass from brackish to freshwater (Fig. 3A). Brackish water is represented by marls with euryhaline molluscs (facies 1), while freshwater deposits include most of the charophyte limestones studied (facies 4-6) and the thin root-bearing lignite beds overlying these limestones (facies 7). Accumulation of parautochthonous plant remains (facies 2) is uninformative about water salinity during its deposition. Another type of cycle is built up from the reiteration of the accumulation of parautochthonous organic matter and lacustrine limestones (Fig. 3B). Finally, a third type of facies association (Fig. 3C) includes brackish charophytes (assemblages of *Feistiella malladae*) even in the top limestones of each cycle (facies 3).

Upper Grey Garumnian

The upper part of the Grey Garumnian is up to 34m thick and shows a succession of brownish clays intercalated with light marlstones and fine sandstones. Clays are up to 8m thick, variegated in colour. Minor lignite horizons with ferric crusts are intercalated; they do not show root traces at their bases, which suggests that they resulted from an accumulation of parautochthonous organic matter. Marlstones and fine sandstones are generally yellowish in colour and form up to 1.5m-thick lenticular beds of about 30-50m in continuity, and look nodular when weathered. Abundant vertical or sinuous burrows, less than one centimetre in diameter and sometimes with a meniscus infilling occur across the whole bed. These burrows have been attributed to the ichnogenus *Spirographites*, which has been related to non-marine arthropod galleries, probably of crustaceans, spiders or insects (Mayoral and Calzada, 1998). Fine sandstones are found at the top of the section. In large outcrops, they show continuity of several hundred metres and wedge laterally into the variegated clays.

In short, the upper part is related to deposition in a non-marine, probably fluviatile, floodplain. Lenticular, fine sandstone bodies represent extremely lax channels of a low hydrodynamic regime. Variegated clays are overbank deposits with hydromorphic soil profiles. Marlstones represent deposition in shallow ponds with high oscillations in the water table and late colonization by non-marine arthropods. Lignite horizons represent small permanent and vegetated ponds. A well-preserved assemblage of megaspores of *Minerisporites succrasulus* and *Parazolla* sp., belonging to freshwater lycophytes and ferns, respectively, was reported by Médus *et al.* (1988) and supports the view that these deposits were non-marine and oligohaline.

PALAEOBOTANY

Plant assemblages from the Maastrichtian of Pyrenees have been poorly studied to date. Charophyte assemblages were analyzed with a biostratigraphic perspective by Feist and Colombo (1983) and Masriera and Ullastre (1988), while Villalba-Breva and Martín-Closas (2011) studied the rich-charophyte microfacies of Vallcebre. Most of the information about vascular plant assemblages was provided by palynological studies. Porta *et al.* (1985), Ashraf and Erben (1986), Médus *et al.* (1988), López-Martínez *et al.* (1999), Mayr *et al.* (1999) and Fernández-Marrón *et al.* (2004a, b) carried out these studies mainly in the western depocentres of Tremp and Àger. Only one preliminary study was devoted to the Cretaceous megafossil plant remains in the Tremp syncline (Vicente, 2002). The accounts of megafossil plants (*Frenelopsis* sp., *Sabalites longirhachis*) from the Vallcebre syncline were given by Marmi *et al.* (2008, 2010) and Riera *et al.* (2010). An overview of present knowledge of the palaeobotany and palynology of the Pyrenean Maastrichtian is provided by Nichols and Johnson (2008).

Intensive sampling of meso and megafossil plant remains in the Grey Garumnian of the Vallcebre syncline resulted in a relatively diverse assemblage of charophytes, vascular megafossil plant remains and palynomorphs. As a detailed description of these remains was outside the remit of this study, only a brief account of their main characters is given below.

Charophytes

Feistiella malladae (Bataller) Villalba-Breva and Martín-Closas nov. comb. (Fig. 4A)

This species presents very large porocharacean gyrogonites (950-1175µm high and 900-1000µm wide), ellipsoidal to subspherical in shape with an isopolarity index of 110-120. Six to seven large convolutions are visible in lateral view, giving the gyrogonite a characteristic low-celled appearance. The apex is truncated, showing an apical pore of 120-200µm in diameter. This species was previously reported from the Maastrichtian of the Southern Pyrenean basins in the Tremp and Àger depocentres, but is described for the first time in the Vallcebre syncline.

Peckichara cancellata Grambast (Figs. 4B-E)

Gyrogonites are large, often 850-100µm high and 900-925µm wide, ovoidal to spheroidal in shape with an isopolarity index of 100-105. The number of convolutions is 5-8 (most frequently, 7). The apex is flat or convex, and shows a poorly marked periapical depression. Apical nodules are irregular in shape (Fig. 4D). The base shows a shallow funnel (Fig. 4E). Ornamentation consists of small perpendicular rods at each side of a mid-cell crest (Figs. 4B-C). The rods range from regularly spaced, resulting in a reticulate pattern, to more irregular in shape and distribution.

Microchara cristata Grambast and Gutiérrez (Figs. 4F-J)

Gyrogonites are ovoidal-spheroidal, rarely ellipsoidal, small in size, 375-525µm high (often 425-450µm) and 325-575µm wide (often 400-475µm). The isopolarity index ranges from 90-146 (often 95-105). Five to seven, most frequently six, convolutions are visible in lateral view. Spiral cells are 80-100µm wide and ornamented with wide, regular wavy mid-cell crests (Figs. 4F-H), which disappear around the apex and continue as far as near the basal pore. The apex is flat or pointed, without periapical modifications but with prominent nodules (Figs. 4F, 4I). The base is rounded or pointed. The basal pore is pentagonal, 20-60µm in diameter (Fig. 4J).

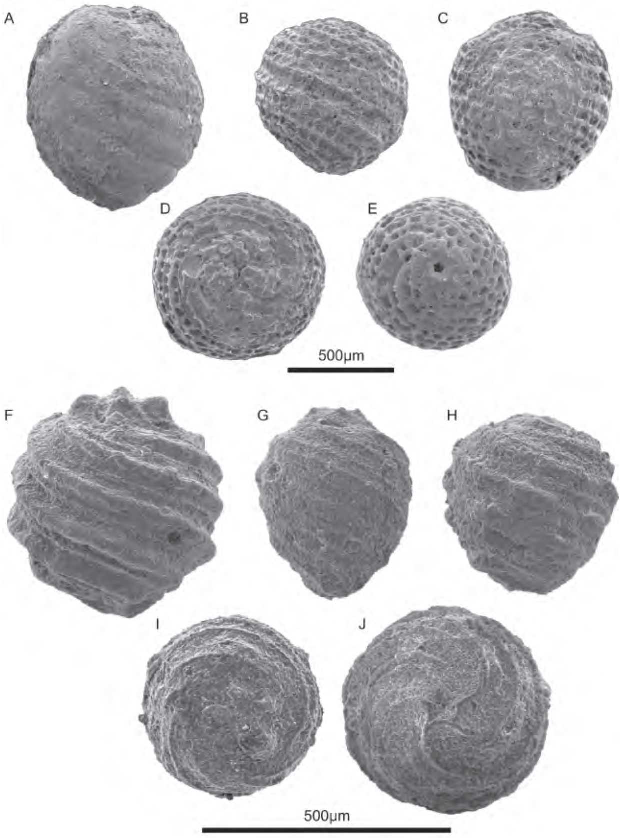

FIGURE 4 | Charophytes from the Lower Maastrichtian of the Vallcebre syncline. A) *Feistiella malladae*, sample FS-5, lateral view. B to E) *Peckichara cancellata*, sample FS-7, B and C) lateral views, D) apex, E) base. F. to J) *Microchara cristata*, sample FB-4, F to H) lateral views, I) apex, J) base.

Vascular megafossil plant remains

Conifers (Cheirolepidiaceae)

Frenelopsis sp. (Figs. 5A-C, Figs. 6A-C)

Remains of *Frenelopsis* sp. are identified from adpressions of very rarely branched leafy axes, isolated leafy whorls and some cuticle fragments. The remains consist of compressed cylindrical leafy axes, 0.5-3.0mm wide and with isolated or successive attached leafy whorls showing three distal free tips (Figs. 5B, C). Free parts of leaves are triangular and 0.6-1.1mm long (Fig. 5C).

Longitudinal parallel dotted lines of some specimens are interpreted as stomatal rows (Fig. 5C). Cuticle remains available show stomata more or less arranged in parallel rows with a density of 11-14 rows per mm^2 (Fig. 6A). The estimated stomatal density is 147-180 per mm^2. The stomatal apparatus has a diameter 40-65µm and 4-6 poorly preserved massive papillae, each borne by a subsidiary cell (Fig. 6B). Ordinary epidermal cells are square, rectangular to polygonal, and also form rows between the stomatal rows (Fig. 6C). They are 31-40µm long and 16-19µm wide.

Cycadales? (Figs. 5D-E)

A single specimen has been collected. It consists of three pinnae (Fig. 5D). Each pinna bears 18 pairs of pinnules alternating distically in the ultimate-order rachises. Pinnules are inserted on the upper part of the rachis in a butterfly-like arrangement. The pinnules slightly overlap each other, the proximal part of the next distal pinnule covering the distal part of the previous proximal pinnule. The pinnules are obovate, asymmetrical, longer (2.5-3.5mm) than wider (1.4-1.8mm) and with entire margins. Five or six major veins rise separately from the base of pinnules and branch dichotomously once or twice (Fig. 5E).

The specimen may be interpreted as a partial bipinnated leaf of a Cycadale. In many cases, pinnae of cycads display dichotomizing venation lacking midrib (Stevenson *et al.*, 1996). Diagnostic features of cycads, such as the inverted-omega-shaped pattern of vascular bundles in the petiole-rachises and cuticle anatomy, are not available in the specimen studied. In addition, leaves of cycads may be very similar in shape to those of Bennettitales, making them very difficult to distinguish in the absence of cuticular data. However, the youngest remains of Bennettitales were reported in the Early Campanian (Rothwell and Stockey, 2002).

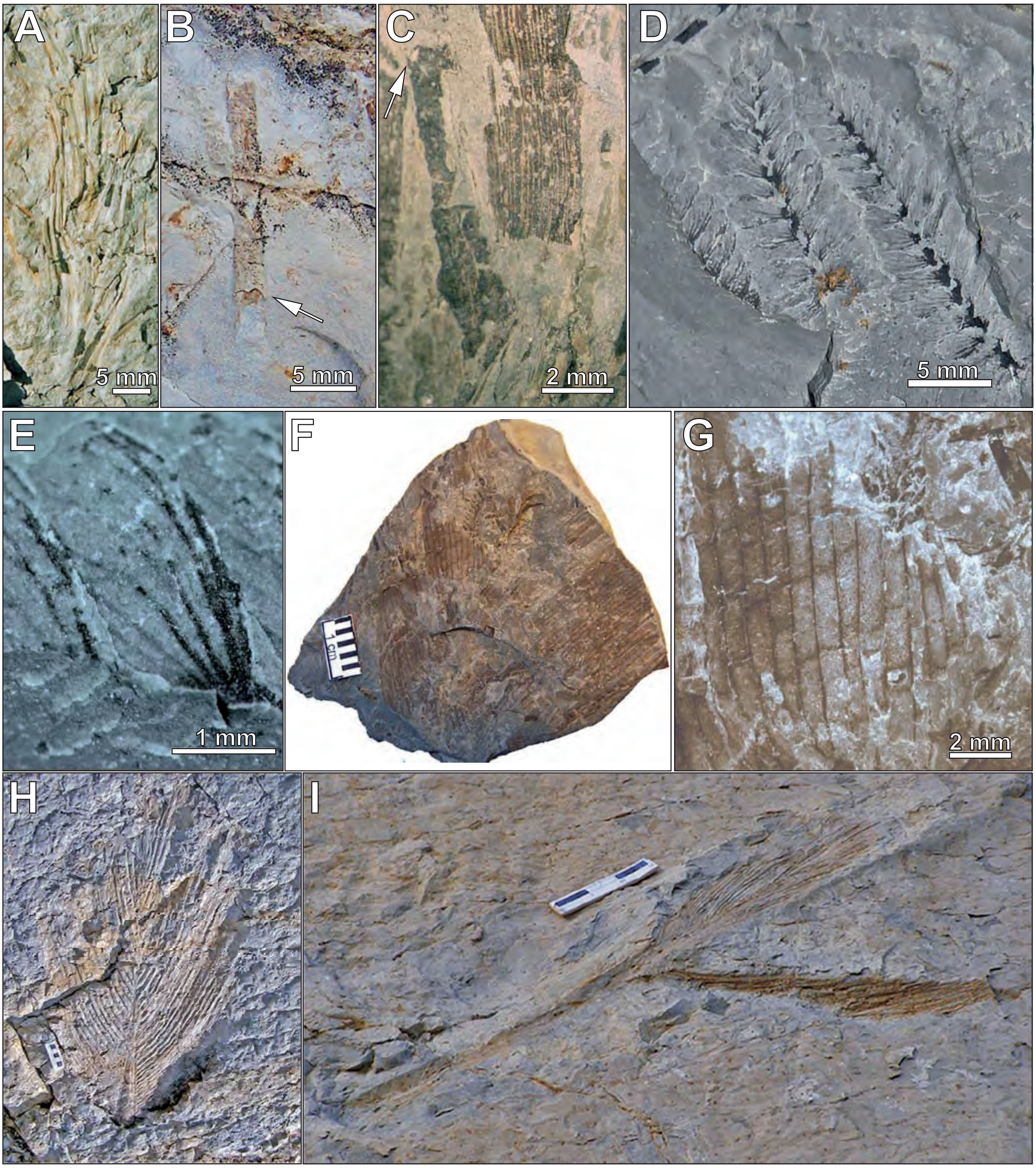

FIGURE 5 | Vascular plants from the Lower Maastrichtian of the Vallcebre syncline. A to C) remains of *Frenelopsis* sp.; A) branched axes, B) two fragmented and connected internodes showing leaf tips (arrowed), C) two internodes, one of them showing longitudinal parallel dotted lines. One leaf tip is arrowed. D and E) Cycadalean foliage; D) general view of specimen showing three pinnae, E) detail of a pinnule showing venation. F and G) Monocot foliage; F) fragments of leaves, G) detail of F showing venation. H and I) *Sabalites longirhachis* complete leaves; H) complete lamina of a mature leaf (scale bar=5cm), I) complete marcescent leaf showing petiole (scale bar=15cm).

Angiosperms

Monocot leaves (Figs. 5F-G)

Several ribbon-shaped leaf fragments with parallel venation were collected (Fig. 5F). They show a single order of longitudinal veins, 12-14 veins per cm and 0.56-0.89mm wide between veins. Vein width ranges from 0.11-0.19mm. The smallest transversal veins are oblique to perpendicular compared to the main longitudinal venation (Fig. 5G).

The specimens have similarities with Pandanaceae leaves. For instance, the specimens share diagnostic characters with the genus *Pandanites*, especially regarding the venation pattern: one-order parallel veins (of the same width) and obliquely or perpendicularly oriented transversal thin veins. Vein thicknesses and density of veins per centimetre are consistent with those given by Kvaček and Herman (2004) for *Pandanites trinervis* (Ettingshausen). However, more material and better conservation are needed for more accurate determination.

Sabalites longirhachis (Unger) Kvaček and Herman (Figs. 5H-I)

Adpressions of leaves, sometimes with complete laminae and the petioles attached, were first documented from the Vallcebre syncline by Marmi *et al.* (2008). These leaves are costapalmate and ovalo-lanceolate in shape (Fig. 5H). The most complete leaf laminae are 43-75cm long and 10-41cm wide. The base angle of the leaf lamina is acute, lower than 90°. Base and apex are convex. The leaf lamina is composed of approximately 25-30 pairs of opposite, induplicate and fused segments that are nearly linear and generally get wider in their apical part. The petioles are 44-53cm long, exceeding in some cases the lamina lengths in the smallest leaves. A detailed description of these leaves and a reconstruction of the tree habit of the plant were recently provided by Marmi *et al.* (2010).

Angiosperm seeds (Figs. 6D-E)

Small monocot-like angiosperm seeds are found in massive accumulations. They are rounded to oval in shape, 1.1-3.0mm long and 0.8-1.7mm wide (Figs. 6D-E). The seed coat clearly shows two integuments. The hilum and micropyle are located at opposite poles, indicating that the ovule was orthotropous (Fig. 6E).

Palynology

Médus *et al.* (1988) provided the only palynological data available to date from Vallcebre. However, their productive samples were mainly from the upper Grey Garumnian and overlying beds, which are of limited interest to the objectives of this study. Six palynological samples were taken in key beds from the coal-bearing deposits of the middle Grey Garumnian. Up to 42 taxa were identified (Table 1, Fig. 7).

Three samples were highly productive and represent three significant facies. Sample ME-1 from a marlstone bed with angiosperm seeds located just below the first coal was formed mostly by conifer bisaccate pollen grains (93%). Spores of lycophytes and ferns were in a minority (5%), with species of *Hamulatisporis*, *Kuklisporites*, *Leiotriletes*, *Polypodiaceoisporites* and *Verrucatosporites* (Figs. 7D, 8). Finally, angiosperms accounted for only 2% of the assemblage and comprised pollen grains of *Rugulitriporites pflugi*, *Tricolporopollenites* sp. and *Megatriopollis* sp. (Figs. 7R-S, 8).

The association of sample FS-17 from organic marls represents the most diverse assemblage found. It contained abundant (56%) trilete spores of bryophytes, lycophytes and ferns (Figs. 7C, E-M, 8), with Cyatheaceae (species of *Cyathidites*, Figs. 7I-J) and Schizaeaceae (species of *Chomotriletes, Klukisporites* and *Leiotriletes*, Figs. 7E-H) being dominant. Pollen grains of conifers and cycadales (Figs. 7N-O, Q, 8) were minority (7%), with the Pinaceae *Pinuspollenites ruginosa* (Fig. 7Q) being the most abundant. Angiosperms (Figs. 7T, 8) only made up 4% of the assemblage and included two pollen taxa attributed to palms, *Monocolpopollenites* cf. *tranquillus* and *Spinizonocolpites* cf. *baculatus* (Fig. 7T), the latter generally related to the mangrove palm *Nypa* (Baksi and Deb, 1980; Mahmoud and Schrank, 2007). Finally, 33% of the assemblage included freshwater green algae living in alkaline ponds (*Oedogonium cretaceum* and *Ovoidites spriggi*, Figs. 7A-B, 8).

The third rich sample (FS-23) from lignite with rootlet-marks had very little diversity. It consisted almost exclusively (95%) of conifers, especially *Pinuspollenites ruginosa* (Fig. 8). Spores only comprised 3% of the assemblage and included species of *Leiotriletes, Cyathidites* and *Gabonisporis* (Fig. 8). An oospore of *Oedogonium cretaceum* was also identified (Fig. 8).

Three more samples from grey marls (samples FS-1, FS-6, FS-15 in Fig. 2) also supplied palynomorphs, but they were scarcer and poorly preserved. In sample FS-1, conifer pollen grains (*Pinuspollenites* sp.) along with fern spores of *Leiotriletes* sp. and fungal spores (*Pluridellaesporites* sp.) were recorded. Sample FS-6 was practically sterile, with a few unidentified fungal spores, conifer pollen grains (*Pinuspollenites ruginosa*, *Pinuspollenites* sp.) and angiosperms (*Triporopollenites* sp.). In sample FS-15 the association consisted of a few fern spores (*Leiotriletes balinkaense*, *Cyathidites australis* and cf.

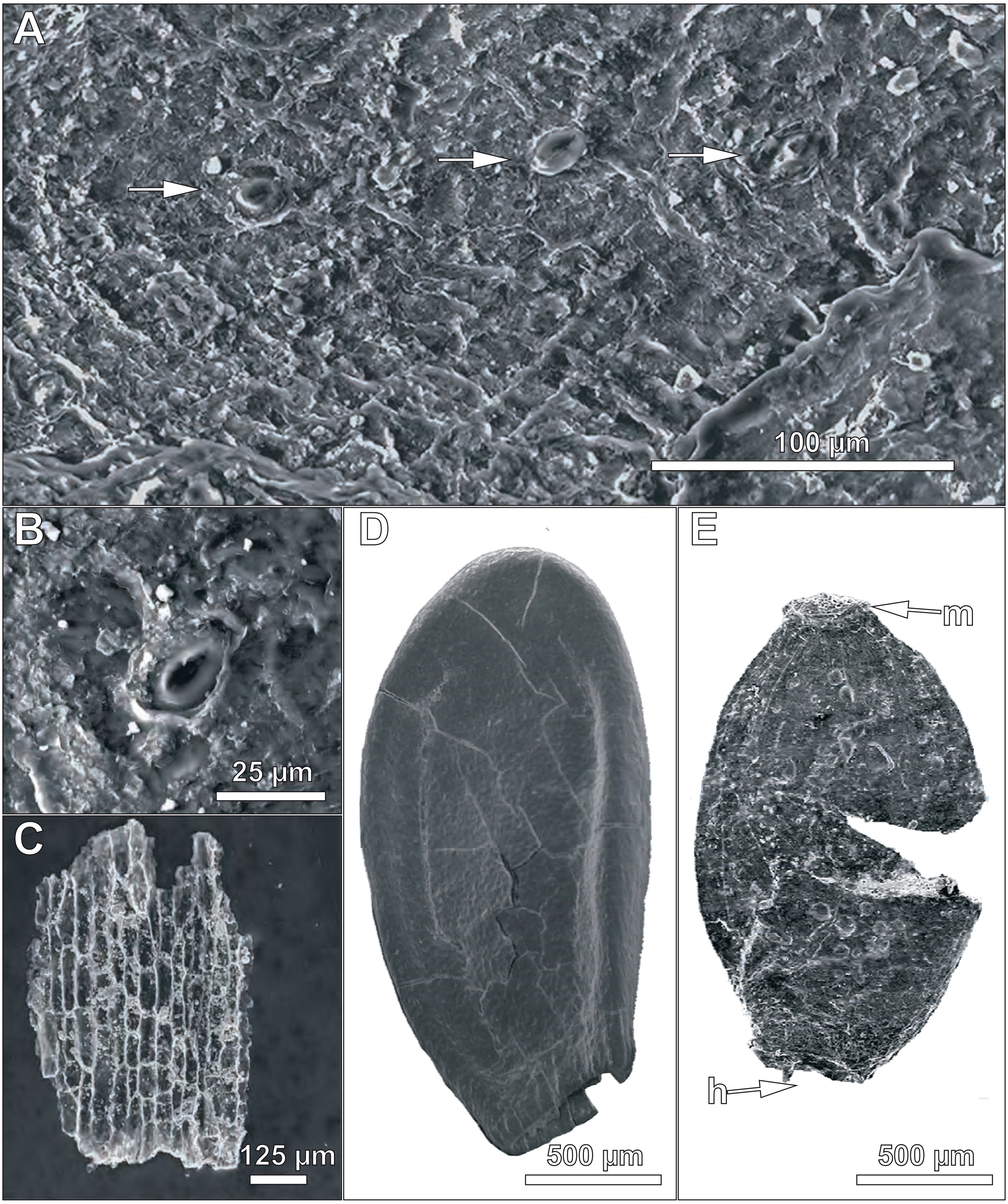

FIGURE 6 | Vascular plants from the Lower Maastrichtian of the Vallcebre syncline (continued). A) external view of the cuticle showing three aligned stomata forming a row and stomatal pits. B) detail of stomatal pit around a ring with remains of at least four subsidiary cells. C) fragment of cuticle assigned to *Frenelopsis* with long epidermal cells. D and E) angiosperm seeds showing outer; D) and inner E) integuments. The micropyle (m) and hilum (h) are arrowed on photograph E.

TABLE 1 | Palynological composition of samples from the Grey Garumnian unit of the Vallcebre syncline

	FS-1	FS-6	FS-15	FS-17	FS-23	ME-1
Chlorophyta						
Fam. Oedogoniaceae						
Oedogonium cretaceum Zippi			X	X	X	
Oedogonium sp.				X		
Zygnematophyta						
Fam. Zygnemataceae						
Ovoidites spriggi (Cookson & Detmann) Zippi				X		
Bryophyta						
Zlivisporis blanensis Pacltova				X		
Licophyta						
Hamulatisporis sp.						X
??*Echinatisporis* sp.				X		
Filicophyta						
Fam.Schizaeaceae						
Chomotriletes fragilis Pocock				X		
Klukisporites (*Ischyosporites) scaberis* (Cookson & Dettmann) Dettmann				X		X
Leiotriletes adriennis (Pot. & Gell.) Krutzsch				X		
Leiotriletes balinkaense Kedves			X	X	X	
Leiotriletes dorogensis Kedves				X		
Leiotriletes maxoides Krutzsch				X		
Leiotriletes sp.	X			X	X	X
Fam. Cyatheaceae						
Cyathidites australis Couper			X	X		
Cyathidites minor Couper				X		
Cyathidites sp.				X	X	
Fam. Polypodiaceae						
Polypodiaceoisporites sp.				X		X
cf. *Verrucatosporites* sp.				X		X
Fam. Marsiliaceae						
Gabonisporis vigourouxii Boltenhagen				X	X	
cf. *Gabonisporis* sp.			X			
Pteridophyta incertae sedis						
Biretisporites croxtoniae Kedves				X		
Biretisporites potoniaei Delcourt & Sprumont				X		
Triplanosporites sinuosus Pflug				X		
Triplanosporites sp				X		
Cycadophyta						
Cycadopites carpenteri Delcourt & Sprumont			X			
Cycadopites minor (Kedves) Kedves				X		
Cycadopites sp.			X	X		
Coniferophyta						
Fam. Araucariaceae						
Araucariacites australis Cookson			X			
cf. *Araucariacites* sp.				X	X	
Fam. Pinaceae						
Pinuspollenites ruginosa (Stanley) Oltz		X	X	X	X	X
Pinuspollenites cf. *sphaerisaccus* Brenner						X
Pinuspollenites sp.	X	X			X	X
Fam. Podocarpaceae						
Podocarpidites sp.						X
Angiospermophyta						
Magnoliopsida (Dicots)						
cf. *Polyporopollenites* sp.				X		
Rugulitriporites pflugi Kedves						X
Rugulitriporites sp.				X		
Tricolpopollenites sp.				X		
Triporopollenites sp.		X				X
Megatriopollis sp.						X
Liliopsida(Monocots)						
Fam. Arecaceae						
Monocolpopollenites cf. *tranquillus* (Pot.) Thomson & Pflug				X		
Spinizonocolpites cf. *baculatus* Müller				X		
Fungi						
Pluricellaesporites sp.	X					
unidentified fungal spores		X				

Gabonisporis sp.), pollen grains of cycadales (*Cycadopites carpenter*, *Cycadopites* sp.), conifers (*Pinuspollenites* sp., *Araucariacites australis*, Fig. 7P) and oospores of freshwater green algae *Oedogonium cretaceum*.

The assemblages from Vallcebre can be compared with other assemblages collected from similar coal-bearing deposits of the Pyrenean Maastrichtian, such as those from Coll de Nargó (Médus, 1972; Ashraf and Erben, 1986), Barranc de la Posa in the Tremp depocentre (Porta *et al.*, 1985) and Fontllonga in the Àger depocentre (López-Martínez *et al.*, 1999; Fernández-Marrón *et al.*, 2004b). Thus, assemblage FS-17 is similar to other Pyrenean localities in showing dominant trilete spores of similar taxa. In contrast, samples FS-23 and ME-1 were distinct from most other Pyrenean Maastrichtian localities in being dominated by bisaccates. On the other hand, some other Pyrenean localities showed a higher proportion of palm-related monocolpates.

PLANT TAPHONOMY AND PALAEOECOLOGY

The taphonomic information about the taxa reported above enables us to put forward some testable hypotheses about the Lower Maastrichtian plant community from the Vallcebre syncline. Most taphonomic data, gathered from facies 1-7, corresponded to marls, lignites and limestones of the middle Grey Garumnian.

Organic marls and lignite without rooting structures (facies 1 and 2)

The base of the lignites overlying marls does not show any evidence of rooting structures at a macroscopic scale. The precursory peat was deposited on the edges of a brackish lagoon, represented by marls with euryhaline molluscs, and contains the highest diversity of megafossil plant remains. Most taphonomic data gathered come from the base of the first lignite seam, which is the best exposed contact surface on marlstones of the lower Grey Garumnian in the outcrops studied. Here, *Frenelopsis* is by far the most abundant megafossil plant, the bed surface being covered by adpressions of their leafy axes. Generally, the remains are disarticulated and broken at nodes (Fig 9A). In articulated conifers this type of fragmentation is usually formed after shoot abscission and drying in the leaf litter. The accumulation and orientation of the *Frenelopsis* sp. shoots at the base of the first lignite was attributed to short transport and reworking by low-regime tidal flows (Riera *et al.*, 2010). The abundance of *Frenelopsis* sp. axes at the base of this type of coal seam, along with the abundance of coal macerals of conifer origin described by García-Vallès *et al.* (1994), strongly suggests that cheirolepidiacean conifers provided most of the organic matter precursory of coal.

The second most abundant megafossil plant remains are *Sabalites longirhachis* leaves (Figs. 5H-I). They are complete or almost complete laminae, some of them with their petioles in anatomic connection. Since, as a rule, palm leaves remain attached to the stem for long periods after their death and even decay when still attached to the parental plant, these isolated leaves were probably abscised traumatically by storms or strong winds (Martín-Closas and Gomez, 2004). The great variability in size and opening of the palm fans is attributed to diverse growth stages (*i.e.* green or marcescent leaves), which suggests that there was no selection in the supply of these leaves in the depositional setting (Marmi *et al.*, 2008, 2010). Associated with *Sabalites longirhachis* leaves, there are impressions of large logs, 2.5-13.8m long and 16-22cm at their maximum width, some of them attributed to the same plant (Fig. 9D). A few of them show ellipsoidal scars, 1.0-1.8cm long and 0.3-0.6cm wide (Fig. 9E). These features are reminiscent of adventitious roots and may represent the basal part of the palm stems. The taphonomic attributes of palm remains suggest that the *Sabalites longirhachis* leaves and logs are parautochthonous at the base of the coal layers. These remains were deposited there after short-distance flotation.

Other leaf remains found at the base of lignite seams are extremely scarce monocot and possible cycadalean foliage (Figs. 5D-G). The scarcity and high fragmentation of these remains and the absence of rooting marks belonging to these plants suggest that these leaves are parautochthonous or allochthonous. The accumulation of monotonous assemblages of angiosperm seeds in these horizons (Fig. 9G) is considered an indication of allochthony or massive supply of seeds from a monospecific vegetation source (Martín-Closas and Gomez, 2004; Steinhardt and Selig, 2009, respectively). The above observations, and the fact that most coal seams of facies 2 are not associated with rooting structures, strongly suggest that all the organic matter precursory to this lignite resulted from detritic accumulation of parautochthonous plant remains, mainly *Frenelopsis* sp. leafy axes, at some distance from the site of growth.

Dealing with palynology, only samples ME-1 and FS-17 are rich enough and not altered during the diagenesis to allow for a taphonomic (biostratinomic) analysis. They show contrasting compositions and taphonomic features. ME-1, from the base of the first coal, is mostly formed by pinaceous pollen grains (93%). As is well-known, bisaccate pollen is produced in vast numbers and is easily transported long distances by water and wind due to the buoyancy of its structure. Therefore, the composition of this largely monotypic palynological assemblage probably bears no direct relation to local vegetation and should be considered allochthonous. Moreover, the palynofacies components of sample ME-1 give black phytoclasts that are usually attributed to charcoal, which is a highly buoyant plant remain (Tyson, 1995).

The association of sample FS-17, representing organic marls, is dominated (56%) by trilete spores, mainly from ferns, and also includes abundant oospores of freshwater green algae (33%). Generally, fern spore-dominated assemblages are not transported far from their source (Traverse, 2008) and the association is probably parautochthonous. The absence of megafossil fern remains associated with their

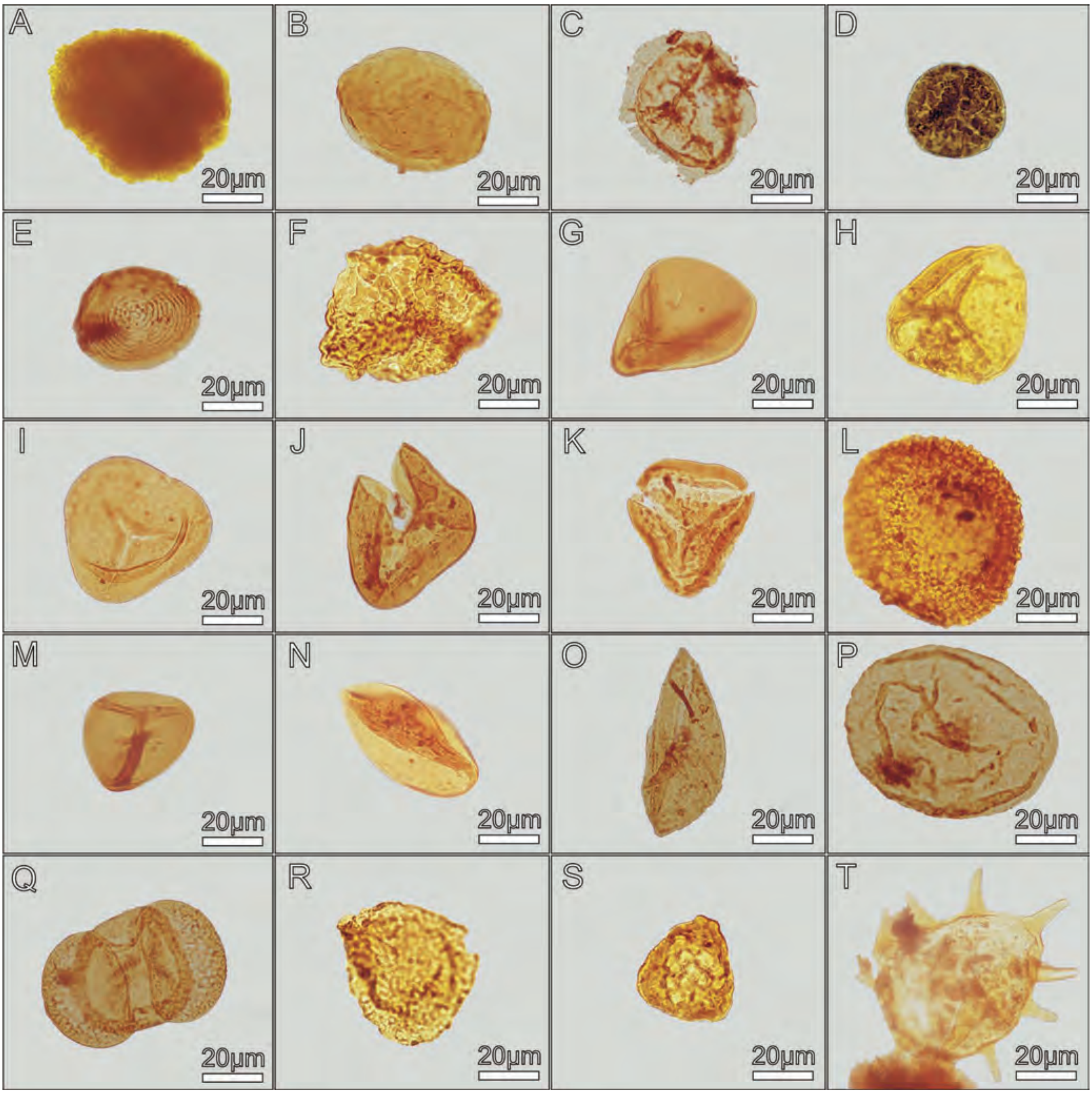

FIGURE 7 | Palynomorphs from the middle Grey Garumnian of Vallcebre syncline. A) *Oedogonium cretaceum* Zippi, sample FS-23. B) *Ovoidites spriggi* (Cookson and Dettmann) Zippi, sample FS-17. C) *Zlivisporis blanensis* Pacltova, sample FS-17. D) *Hamulatisporis* sp., sample ME-1. E) *Chomotriletes fragilis* Pocock, sample FS-17. F) *Klukisporites (Ischyosporites) scaberis* (Cookson and Dettmann) Dettmann, sample ME-1. G) *Leiotriletes balinkaense* Kedves, sample FS-17. H) *Leiotriletes* sp., sample ME-1. I) *Cyathidites australis* Couper, sample FS-17. J) *Cyathidites* sp., sample FS-17. K) *Polypodiaceoisporites* sp., sample FS-17. L) *Gabonisporis vigourouxii* Boltenhagen, sample FS-23. M) *Triplanosporites* sp., sample FS-17. N) *Cycadopites minor* (Kedves) Kedves, sample FS-17. O) *Cycadopites* sp., sample FS-15. P) *Araucariacites australis* Cookson, sample FS-15. Q) *Pinuspollenites ruginosa* (Stanley) Oltz, sample FS-15. R) *Rugulitriporites pflugi* Kedves, sample ME-1. S) Megatriopollis sp., sample ME-1. T) *Spinizonocolpites* cf. *baculatus* Müller, sample FS-17.

spores may be probably explained by the generally poorly cutinized leaves of this plant group, which makes their preservation difficult. The relative abundance of freshwater green algae in this assemblage informs about the prevailing freshwater conditions of this particular sample. However, the occurrence of a pollen that is close to *Nypa* in the assemblage supports the interpretation of a wide area of brackish water existing beyond the freshwater lakes. *Nypa* pollen is relatively large in size and with a prominent sculpture, which makes its long distance transport by wind or water unlikely.

The absence of *Classopollis* in the palynomorph assemblages from organic marls and coals without rootlet marks is in clear contradiction with the abundance of *Frenelopsis* in the corresponding megafossil plant assemblages. A number of explanations can be provided for this lack of correspondence, but selective sorting during transport and deposition appears to be the most probable reason for it. Taugourdeau-Lanz *et al.* (1982) noted that pinaceous bisaccates and cheirolepidiacean circumpolloid pollen grains had opposite taphonomic behaviour, the latter being not easily transported by water. This may account for the absence of *Classopollis* in the allochthonous palynological assemblage of sample ME-1 (coals without rootlet marks). In contrast, the absence of *Classopollis* in sample FS-17 (parautochthonous assemblages of ferns in organic marls) is more difficult to ascertain and may be attributed to a number of reasons, such as local absence, low production of *Classopollis* pollen in the source plants or others. Unfortunately, these explanations remain speculative, given the information to hand.

Charophyte limestones (facies 3-6)

Charophyte limestones form the third lithology analyzed for taphonomic purposes. Four facies (facies 3-6) are defined. Facies 3 is dominated by porocharacean remains (*Feistiella malladae*) associated with corticated thalli of the *Charaxis* sp. type. Charophyte thalli and some gyrogonites are broken, suggesting that transport occurred before deposition in lakeshore facies of brackish lakes, directly limited to the seashore. In contrast, facies 4-6 are dominated by *Clavatoraxis* and *Charaxis* thalli and gyrogonites attributed to genera *Peckichara* and *Microchara* elsewhere. The degree of articulation suggests that facies 4 corresponds to *in situ* accumulation in a charophyte meadow below lacustrine wave action; whereas facies 5 and 6 correspond to parautochthonous and allochthonous charophyte remains. The lamination of facies 5 suggests that charophyte remains were deposited on a quiet, anoxic lake bottom devoid of bioturbation, after undergoing short lateral transport, while the high content in mud and the good articulation of plant remains in facies 6 suggest that this facies was formed in relatively deeper zones of the lake, where only cyanobacterial mats were growing *in situ* (Villalba-Breva and Martín-Closas, 2011). These taphonomic results are relatively explicit about the habitat of charophytes and point towards the occurrence of rare brackish lakes dominated by *Feistiella malladae* (basal charophyte limestones in Cal Sant and Fumanya Sud sections) and abundant freshwater lakes dominated by *Peckichara* and *Microchara* elsewhere.

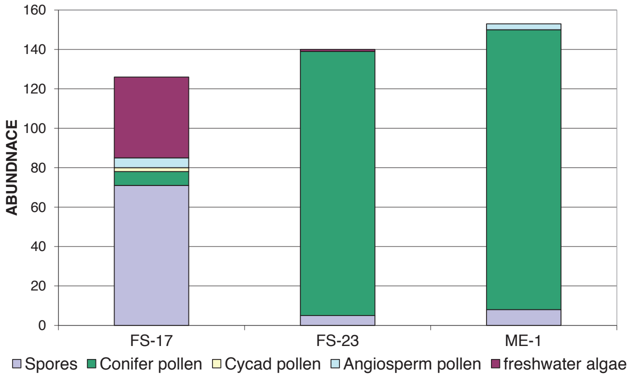

FIGURE 8 | Diagram showing the abundance of the most representative morphological groups of palynomorphs in the studied samples.

Lignite with rooting structures (facies 7)

Thin coal seams with rooting structures of facies 7 occur at the top of some lacustrine limestones and provide the unique taphonomic evidence of *in situ* growth of land plants in the basin. Two types of rooting structures are observed:

1) Small tap roots are ca. 10cm long, largely conical, unbranched organic structures penetrating at right angles from thin lignite beds into the underlying charophyte limestones (Fig. 9C). They form dense assemblages of about 400-500 rootlets/m^2 at the top of some limestones at Fumanya Sud (Fig. 9B). Though the overlying coal is not explicit about the composition of the producing plant, probably because of the poor preservation of organic matter in such thin coal beds. The palynomorph association (sample FS-23) consists almost exclusively of conifers (95% bisaccates). As explained above, conifer pollen is usually over-represented and may be transported for long distances. Therefore, the pollen is probably allochthonous.

2) Large, brush-like rooting systems occur at the top of a charophyte limestone at Mina Esquirol (Fig. 9F), associated with the previous type of rootlet. The best preserved specimen consists of a central circular mark, 19cm across, from which about 16 rectilinear, slightly curved rays, 0.9-1.3cm in diameter, emerge to form a conical structure. The diameter of the whole structure is 140cm at maximum. Other less

FIGURE 9 | Plant taphonomic features from the Lower Maastrichtian of Vallcebre syncline. A) Base of the first Fumanya Sud coal showing an accumulation of *Frenelopsis* internodes. The coin for scale is 2cm in diameter. B) Densely perforated top of charophyte limestone attributed to rootlets at Fumanya Sud. The hammer for scale is 30cm long. C) Small tap roots (arrows) in the Fumanya Sud coal mine. Rootlets penetrate a charophyte limestone starting from the overlying lignite, located on the right hand side. D) Large impression of log attributed to a palm at the base of the first coal of Mina Esquirol. E) External cast of a decayed palm log portion showing marks of adventitious roots. Base of the first coal seam in Fumanya Sud. F) Large brush-like rooting structure attributed to a palm, upon a charophyte limestone at Mina Esquirol coal mine. G) Monotonous accumulation of minute angiosperm seeds at the base of first coal at Mina Esquirol.

well-preserved rooting systems do not show any central element but show the same radial pattern around a central depression. All these brush-like structures are attributed to rooting systems of palms (Marmi *et al.*, 2010). The circular central mark or depression may correspond to the palm stump and falls within the range of the maximum diameters of logs reported above for *Sabalites longirhachis* palms. The radiating structures are attributed to palm adventitious rootlets. The best preserved rooting system is completely replaced by coarser sediment dominated by charophyte remains. This is attributed to the post-mortem decay and infilling of the stump and adventitious roots.

In summary, the two types of rooting structures indicate that the peat-forming plants in the Fumanya wetlands lived in freshwater contexts, directly bordering charophyte lakes. However, there are insufficient evidences to determine the plant community that grew in these peat-mires.

PALAEOENVIRONMENTAL RECONSTRUCTION

The combination of palaeontological results, including taxonomy, taphonomy and palaeoecology, and sedimentological analysis leads to the characterization of the depositional setting and the palaeoenvironment (Fig. 10). In sedimentological terms, the Fígols-Vallcebre composite section records a regression from marine to continental facies. The underlying Terradets Formation is interpreted as deposited on a shallow shelf of moderate energy (Pons, 1977). The basal marlstones of the lower Grey Garumnian are interpreted as deposited in a tidally influenced mudflat (Riera *et al.*, 2010) or protected lagoon (Rosell *et al.*, 2001). Overlying this unit, there are small-order sedimentary cycles that show a transition from brackish deposits (organic marls with euryhaline molluscs of facies 1, and limestones with *Feistiella malladae* of facies 3) to freshwater deposits (*Peckichara*-dominated limestones of facies 4-6 and root-bearing lignite of facies 7). The water salinity under which detrital peat was deposited (lignite of facies 2) is unknown and may be variable. The cyclic progradation and retreat of the whole system could have resulted in the development of cycles of the type shown in Fig. 10B. Finally, clays, sandstones and marlstones of the upper part are related to deposition in a fluvial terrigenous floodplain and cover the whole peatland system to the top of the Grey Garumnian deposition.

The sedimentological and taphonomic evidences are relatively explicit about the habitat of charophytes in the lakes and land plants growing on the lakeshores. Two types of lakes are documented. Shallow, freshwater lakes were dominated by the charophytes *Peckichara* and *Microchara*, whereas rare brackish lakes were dominated by the charophyte *Feistiella malladae*. Peat mires grew in the last infilling stages of the freshwater lakes. Evidence for this is mainly provided by two kinds of rooting structures. The most abundant were small tap roots of unknown botanical affinity. The second type, which occurs only on one of the basalmost charophyte limestones of the Mina Esquirol mine, is brush-like roots attributed to palms. The habitats of other plants represented by parautochthonous and allochthonous remains are difficult to ascertain. They could have grown in the same peat mires, but in less abundance, giving little chance to find their roots. Alternatively, they may have grown outside the depositional setting, *i.e.* away from the peat-mires and brackish swamps. In summary, the present results lead us to the conclusion that the only vegetated areas of the Lower Maastrichtian wetlands of the Vallcebre syncline were the limnic parts, since all the rooting structures were found on lacustrine limestones. In contrast, the brackish deposits were devoid of roots indicating that the corresponding environment probably looked like a bare water table most of the time.

Absence of rooted horizons at the base of most lignite beds on brackish organic marls suggests that these coal

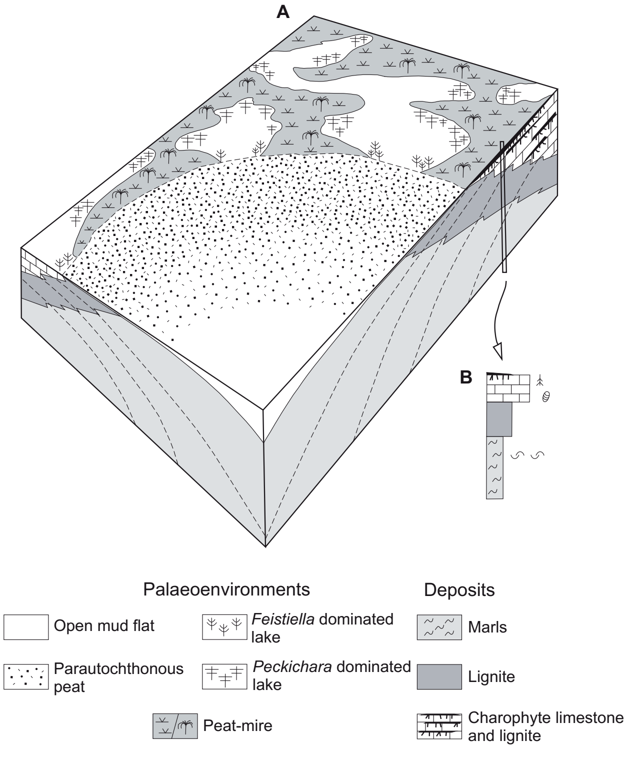

FIGURE 10 | Palaeoenvironmental and taphonomic reconstruction from the Maastrichtian wetlands of the Vallcebre syncline. Not to scale. A) Palaeoenvironmental and taphonomic diagram showing transport and deposition of plant remains. B) Section showing the vertical development of a basic sedimentary cycle, as shown in Figure 3A.

seams resulted from the parautochthonous accumulation of plant remains, mainly *Frenelopsis* leafy axes. The transport of organic matter could have been effected by flotation, depending on its density and buoyancy.

DISCUSSION

The Maastrichtian lignite of the Eastern Pyrenees has been the subject of a number of petrological studies in the past, which showed that it contained abundant woody remains attributed to conifer forest swamps (see García-Vallès *et al.*, 1994 for summary). These authors provisionally related the plant remains to taxodiacean elements, by comparison with Tertiary and extant forest swamps. However, the taxonomic and taphonomic evidence given here suggests that the parent plants that provided the organic matter which was precursory of most of the Garumnian lignite were mainly cheirolepidiacean conifers and, to a lesser extent, arecacean angiosperms. Also, the main coal seams exploited industrially during the 20th Century in the now closed opencast mines of Vallcebre correspond to parautochthonous organic matter deposited in marginal marine settings, while the autochthonous peat, deposited in freshwater peat-mires, represents an extremely small part of the total coal volume of the coal basin.

A modern analogue of parautochthonous and allochthonous peat deposition in a marginal marine setting could be the tropical Mahakam River delta in Borneo (Indonesia). In this case, Gastaldo *et al.* (1993) suggested that fluvial distributory channels are the principal means by which plant parts are transported to the delta front, where they are reworked principally by waves and tides, forming a detrital peat.

In the Early Cretaceous, gymnosperms dominated the brackish water-related environments, whereas the first angiosperms were confined to freshwater-related environments (Coiffard *et al.*, 2006, 2007). In the latter, competition was limited to non-vascular plants, mainly charophytes (Martín-Closas, 2003). Subsequently, the ecological range of angiosperm trees extended. In the Cenomanian, angiosperms were already well diversified, recorded in channel margins and even in brackish-related environments, although conifers were still the main component of the mangrove-like vegetation (Coiffard *et al.*, 2007). During the Campanian, palms are first recorded in swamps, apparently starting a progressive replacement of the Cenomanian conifers (Coiffard *et al.*, 2006; Coiffard and Gomez, 2010). The results documented here indicate that the cheirolepidiacean conifer *Frenelopsis* might still inhabit wetlands associated with *Sabalites longirhachis* palms at the beginning of the Maastrichtian in the Iberian Peninsula.

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