Els caròfits de les fàcies continentals i transicionals del Garumnià basal (Cretaci superior) del Pirineu Oriental

Sheila Villalba Breva

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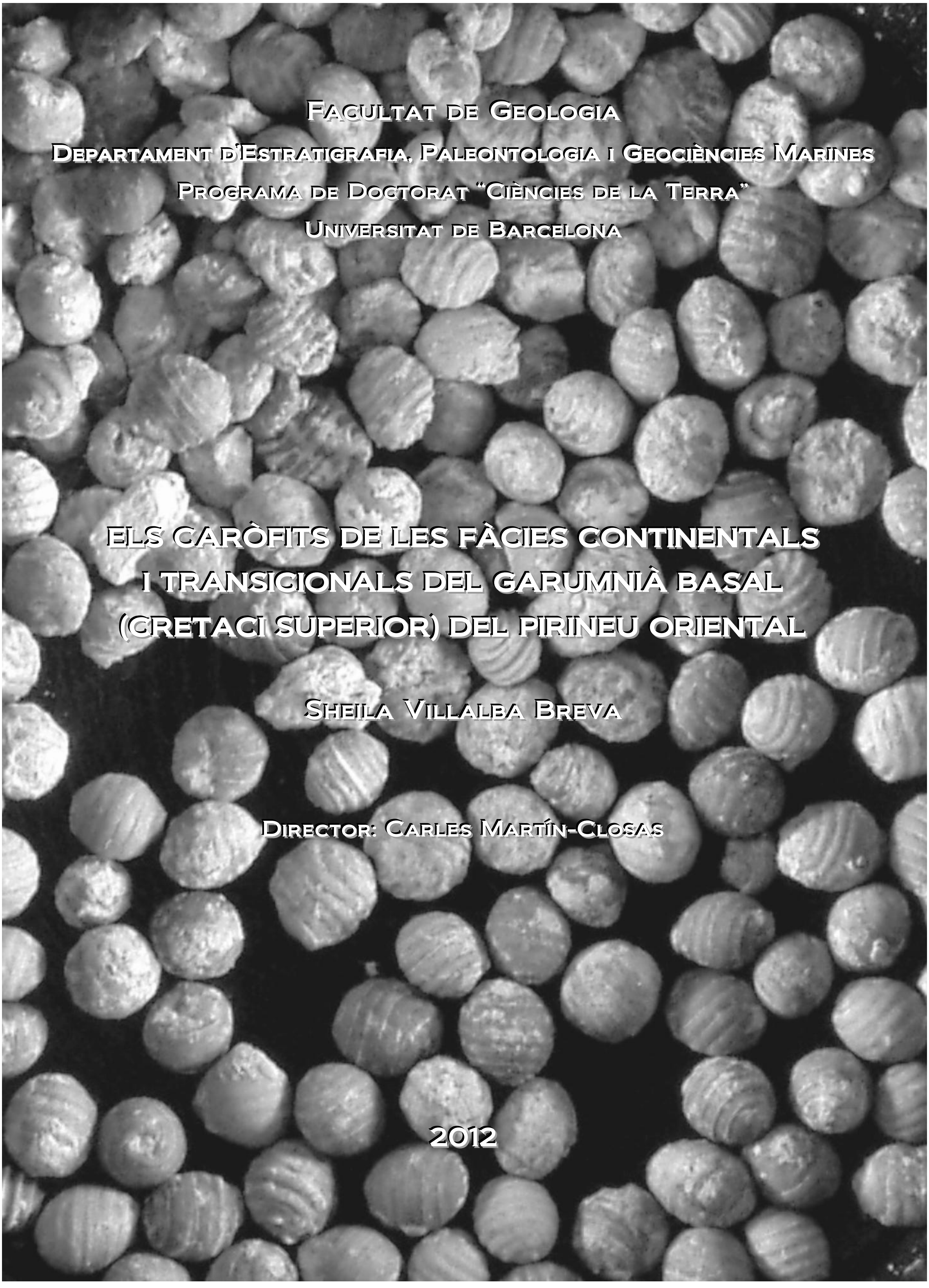

Facultat de Geologia
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ELS CARÒFITS DE LES FÀCIES CONTINENTALS I TRANSICIONALS DEL GARUMNIÀ BASAL (CRETACI SUPERIOR) DEL PIRINEU ORIENTAL

Sheila Villalba Breva

Director: Carles Martín-Closas

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Memòria presentada per Sheila Villalba Breva per optar al grau de Doctor dins del Programa de Doctorat "Ciències de la Terra" de la Univesitat de Barcelona

DIRECTOR
Carles Martín-Closas

A les persones que estimo

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RESUM

Aquesta tesi té com a objectiu fonamental la caracterització taxonòmica, biostratigràfica i paleoecològica de les associacions de caròfits de les fàcies lacustres i transicionals del Garumnià basal (Cretaci superior) de les Conques de Vallcebre, Coll de Nargó, Tremp i Àger. L'altre objectiu d'aquesta tesi és la caracterització tafonòmica i paleoecològica de les restes fòssils de plantes vasculars productores dels lignits garumnians.

La flora de caròfits del Garumnià basal està constituïda per girogonits de *Feistiella malladae*, *Peckichara cancellata*, *P. sertulata*, *Microchara cristata*, *M. parazensis*, *Platychara caudata*, *P. turbinata* i *Dughiella obtusa*, i utricles de *Clavator brachycerus*. Pel que fa als òrgans vegetatius les calcàries garumnianes son molt riques en tal·lus de grans dimensions de *Charaxis* sp. associats a *Peckichara* sp., i de tal·lus més gràcils de *Clavatoraxis microcharophorus* Villalba-Breva et Martín-Closas 2011, portadors de *Microchara* sp. També és freqüent la presència de *Munieria grambastii* associada a vegades a *Clavator brachycerus*.

Des del punt de vista biostratigràfic, les associacions de caròfits de les conques d'Àger i Vallcebre pertanyen a la biozona de caròfits Peckichara cancellata (Campanià superior - Maastrichtià inferior basal), mentre que les associacions de caròfits de les conques de Coll de Nargó i Tremp pertanyen a la biozona Septorella ultima (Maastrichtià inferior). En base a l'estudi estratigràfic i sedimentològic i l'anàlisi de microfàcies s'ha determinat que la sedimentació a la Conca d'Àger està formada majoritàriament per calcàries lacustres organitzades en centenars de seqüències de somització, que van des de fàcies lacustres profundes, passant per ambients marginals, ben il·luminats dominats per herbeis de caràcies, fins a fàcies de vora de llac dominades per herbeis de clavatoràcies. A les conques de Vallcebre, Coll de Nargó i Tremp, la sedimentació del Garumnià basal està organitzada en diversos cicles, els quals comencen amb dipòsits salabrosos formats per margues amb mol·luscs eurihalins a la base , seguits per lignits i calcàries d'ambients salabrosos dominades per porocaràcies, i calcàries d'aigua dolça amb caràcies i clavatoràcies. Les diferències en el registre sedimentari i la flora de caròfits mostren que les conques sud pirinenques presentaven una polaritat de fàcies sud-nord durant l'inici de la sedimentació continental del Cretaci superior, i que aquesta continentalització va començar al sud i desprès va continuar al nord, d'est a oest.

L’estudi de la macroflora del Garumnià basal de les conques de Vallcebre, Coll de Nargó i Tremp indica que la comunitat vegetal dels aiguamolls del Maastrichtià inferior estava dominada per la conífera queirolepidiàcia *Frenelopsis*, que va ser la planta productora de la matèria orgànica precursora del lignit. Associada a aquestes coníferes hi havia la palmera *Sabalites longirhachis*, i en alguns casos altres angiospermes d’aiguamoll, representades per les seves llavors, especialment *Bergacarpon viladricii* Marmi, Gomez, Villalba-Breva et Martín-Closas 2012. Altres plantes vasculars significatives encara que menys abundants eren les falgueres, cicadals i pandanals.

ABRIDGED ENGLISH VERSION

1. Introduction

This PhD thesis is mainly devoted to the study of charophytes from the basal non-marine Upper Cretaceous deposits (lower Garumnian) of the Southern Pyrenees from the point of view of taxonomy, biostratigraphy and palaeoecology. The previous knowledge about these charophytes was extremely focused on the characterisation of the Cretaceous – Tertiary boundary, leaving the lower part of the non marine record, mainly Late Campanian to Early Maastrichtian, largely unstudied. However, this PhD thesis aims not only to fill in this gap in the knowledge on Pyrenean charophytes but also to contribute to the knowledge on the evolution of the Pyrenean Basin during the Upper Cretaceous. The Garumnian facies represent the first continentalisation of the Pyrenean Basin, which is a central event of the basin evolution. This process remained poorly studied to date. In particular, there was no agreement either about the age or about the palaeoenvironmental conditions under which this continentalisation occurred. For this reason, the two other aims of this thesis were (1) to clarify the relative age of the basal Garumnian on the basis of charophyte biostratigraphy combined with magnetostratigraphic results from previous authors and (2) to improve the palaeogeographical and palaeoenvironmental knowledge of this first continentalisation. In relation with this latter objective, we studied with particular interest the coal-bearing deposits of the Vallcebre, Coll de Nargó and Tremp basins. Although this lignite has been the subject of different petrological studies in the past, there was little information about the precursory plants of this coal and the sedimentary setting of the organic matter accumulation. Sedimentological analysis and the study of taxonomy, taphonomy and palaeoecology of the vascular plant remains from the basal Garumnian of the Southern Pyrenean Basins allowed us to shed new light onto these questions.

2. Geological and stratigraphic settings

The studied area is located in the South-eastern Pyrenees. The Pyrenees are the Alpine fold-trust belt that was formed by the collision between the Iberian and the European continental plates from the Late Cretaceous (Santonian-Campanian) to the Miocene (Teixell 2004). The mountain belt consists of a Hercynian basement and a sedimentary cover that developed from the Late Permian to Early Cretaceous in rift basins and later from the Late Cretaceous to the Oligocene in foreland and piggy-back basins (Puigdefàbregas et al. 1986; Muñoz, 1989; Teixell 2004). As a consequence, the Southern Pyrenean Basin was segmented in several sub-basins or depocentres (López-Martínez et al. 1999; Ardèvol et al. 2000). The Eastern Pyrenean sub-basins are the subject of the present study. In particular we studied the Vallcebre Basin, Coll de Nargó Basin, Tremp Basin, located in the Montsec-Pedraforca thrust sheet, and the Àger Basin in the Serres Marginals thrust sheet (Fig.1).

2.1. Vallcebre Basin

The Vallcebre Basin forms a syncline located in the Pedraforca thrust sheet (Fig. 2). The basin infilling was almost continuous from the Santonian to the Thanetian and according to Vergés et al. (1994) there are three main sedimentary units in the basin. The upper unit, Latest Campanian to Thanetian in age, corresponds to the Tremp Formation (Mey et al. 1968), regionally called Garumnian (Leymerie 1862), and is mainly formed by fluvial red beds with subsidiary coal, lacustrine limestones and transitional marls. The Tremp Fm was divided by Rosell et al. (2001) into four lithological units, of which the transitional basal unit or Grey Garumnian has been object of study.

The Grey Garumnian is formed by a heterolithic succession, up to 100 m thick (Fig. 3). Micritic marlstones comprise the dominating lithology at the base and contain frequent dinosaur trackways at the top. These trackways are close to the Campanian-Maastrichtian boundary as indicated by palaeomagnetic data (Oms et al. 2007). Micritic marlstones are covered by a succession of alternating organic marl, lignite and charophyte limestones, which supplied the charophytes and plants studied. A succession of variegated siltstone with dinosaur eggshells represents the top of the Grey Garumnian. This succession was deposited in peritidal to supratidal environments, including brackish lagoons at the base, followed by well-developed wetlands with brackish marshes and freshwater lakes and ending with flood plains to the top (Rosell et al. 2001).

2.2. Coll de Nargó Basin

The Coll de Nargó Basin forms a small syncline located in the Monstec thrust sheet (Fig. 4). The Upper Cretaceous basin infilling is subdivided in four lithostratigraphic units according to Willems (1985), from which the upper corresponds to the Tremp Fm or Garumnian, Maastrichtian to Thanetian in age. Willems (1985) divided the Tremp Fm in three members, of which the basal or Lower Garumnian has been object of study.

The basal Garumnian from the Coll the Nargó Basin is up to 60 m thick and is made of marls, intercalated with lignites and charophyte limestones, which supplied the charophyte samples studied (Fig. 5). This succession has been attributed to a transition from lagoon facies to freshwater lacustrine conditions (Willems 1985).

2.3. Tremp Basin

The Tremp Basin forms a broad syncline located in the Montsec thrust sheet (Fig. 6). The Upper Cretaceous basin infilling is subdivided into seven lihostratigraphical units (Caus and Gómez-Garrido 1989). The uppermost unit, called the Tremp Group or Garumnian, Late Campanian to Thanetian in age, is mainly formed by lagoonal and coastal-swamp lacustrine marls and limestones, intercalated sometimes with lignites, which are covered by fluvio-lacustrine red beds. The base of the Tremp Group, largely formed by non-marine carbonates was described by Liebau (1973) and later by Cuevas (1992) as La Posa Formation and has been the object of our study.

The La Posa Fm is up to 130 m thick and shows alternating organic marls, lignite, and charophyte limestones, which supplied the charophytes and plants studied. A succession of variegated lutites with an intercalation of a rudist-horizon formed by *Hippuritella castroi* marks the top of the La Posa Fm (Fig. 7).This succession has been attributed to deposition in a coastal-swamp environment connected with shallow freshwater lakes (Nagtegaal 1972).

2.4. Àger Basin

The Àger Basin is located in the Serres Marginals thrust sheet (Fig. 8). According to Caus and Gómez-Garrido (1989) the Upper Cretaceous basin infilling was continuous from the Campanian to the Thanetian. The upper unit (Garumnian) is Late Campanian to Thanetian in age and is mainly formed by lacustrine limestones and fluvial red beds, described by Colombo and Cuevas (1993) as the Fontllonga Group. These authors recognized four different formations in the Fontllonga Group, from which the basal unit, called La Maçana Fm, has been the object of our study.

The La Maçana Fm is up to 100 metres thick and is built up mainly by charophyte-rich limestones with a characteristic colour banding of white wackestones and dark grey packstones corresponding to small-order lacustrine cycles (Fig. 9). Towards the top of this interval, marls are intercalated with dark grey wackestones topped with brecciation, ferric crusts and dinosaur footprints. This succession has been attributed to deposition in lacustrine-palustrine environments with protected areas in which the preservation of organic matter occurred under anoxic conditions (Colombo and Cuevas 1993). The brecciation observed towards the top of the formation is an edaphic feature suggesting the occurrence of vegetation in periods of lacustrine restriction or water table fluctuations.

3. Material and Methods

3.1. Field and laboratory work

Several representative stratigraphic sections were studied and sampled in the four basins. Cal Sant, Font del Bullidor, Fumanya Sud and Mina Esquirol sections were studied in the Vallcebre Basin; the Mina Santaeulàlia section was studied in the Coll de Nargó Basin; the Barranc de la Posa, Riera Barcedana, Alzina and Montrebei sections were studied in the Tremp Basin; and finally the Cal Magí, La Maçana, Fontllonga and Millà sections were studied in the Àger Basin. Physical stratigraphy and sedimentology of these sections were first studied. Systematic sampling of all charophyte-bearing marl and limestone beds resulted in the selection of over 100 samples for carbonate microfacies analysis and charophyte palaeontology and biostratigraphy.

Charophyte gyrogonites and utricles were obtained from unconsolidated marls after disaggregation in a solution of water and hydrogen peroxide, sieving with sieve mesh apertures of 0.2, 0.5 and 1 mm and hand-picking under a binocular microscope. Fructifications were studied and measured under a Wild M5A binocular microscope with micrometer incorporated, and photographed with a Quanta 200 scanning electron microscope at the "Serveis Cientificotècnics" of the Universitat de Barcelona. Two research stays were conducted at the Institut des Sciences de l'Évolution of the Université Montpellier II (June 2009 and October-November 2010, funded by AGAUR, Generalitat de Catalunya), in order to review the taxonomical determinations by Dr. Monique Feist, who is expert in Upper Cretaceous charophytes. On the other hand, thin sections, about 30 μm thick, were prepared from oriented rock slabs cut parallel and perpendicular to the bedding surface. About a dozen 2.5x5 cm slides were prepared for each rock sample and studied under a Motic B3-220ASC optical microscope. Each charophyte portion was oriented with reference to the producing plant, and in one species there was sufficient data to reconstruct the whole plant tridimensionally. In other cases, however, only fragmentary data on the thalli were obtained. These remains were only used for palaeoecological purposes in combination with taphonomic and sedimentological analyses. Samples are housed in the charophyte collection of the Dept. Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona and in the Museu Geològic del Seminari Conciliar de Barcelona (MGSCB).

In the Vallcebre Basin, several lignite, organic marls and marlstone beds were sampled for plant mega- and mesoremains and pollen and combined sedimentological analyses and descriptions of plant taphofacies were investigated in order to ascertain the palaeoenvironmental and palaeoecological setting of plant remains. The preparation of samples for the study of plant cuticles and mesoremains was undertaken by Dr. Bernard Gomez and Dr. Josep Marmi at the Université de Lyon 1, following the methodological procedures detailed in Marmi et al. (2010, 2012) and Villalba-Breva et al. (2012). Mega- and mesofossil plant remains are housed in the collection of the Institut Català de Paleontologia. The preparation of samples for palynological analysis was performed at the Laboratory of Palaeontology from the Universitat de Barcelona, by Mr. Alejandro Gallardo, and involved the well-known procedures of crushing, followed by hydrochloric (HCl) and hydrofluoric (HF) acid treatments detailed in Villalba-Breva et al. (2012). Palynological samples were then studied by Dr. María Teresa Fernández-Marrón from the Universidad Complutense, Madrid, and slides are housed at the UEI de Paleontología, Instituto de Geociencias of Madrid (CSIC-UCM).

In the Tremp Basin, a palaeontological excavation was conducted in the basal Garumnian around the town of Isona in collaboration with Dr. Josep Marmi and other staff members of the "Grup del Mesozoic" of the Institut Català de Paleontologia. The fossils found were provisionally housed at the Museu d'Isona i Conca Dellà and later the plant remains were studied in the Université de Lyon 1, in June 2011, during a research stay supervised by Dr. B. Gomez and in part financed with a grant from the Faculty of Geology, UB. This stay allowed me to learn many of the methodological procedures necessary for the study of plant cuticles (Kerp and Krings 1999) and to begin the accurate description of fossil leafs from line drawings in camera lucida.

3.2 Biostratigraphy

Charophyte assemblages were assigned to biozones defined by M. Feist in Riveline et al. (1996) and in Hardenbol et al. (1998). Later, these biozones were calibrated with magnetozones defined by Oms et al. (2007) and Galbrun et al. (1993) in the Vallcebre and Àger basins respectively, and correlated with shallow marine fossils, especially benthic foraminifera (Willems 1985; Caus and Hottinger 2009) in the Coll de Nargó and Tremp basins. In addition, the presence of marine beds with rudists in the Tremp and Àger basins (Pons 1977, 1982; Gallemí et al. 1983; Vicens et al. 2004) allowed correlation of charophyte biozones with rudist horizons defined by J. Philip in Hardenbol et al. (1998).

3.3. Taphonomy and palaeoecology

The palaeoecology of charophyte assemblages from the basal Garumnian of the Eastern Pyrenees was characterized in transitional and strictly freshwater facies, based on depositional analysis, taphonomic study of microfacies and comparison with other palaeobiological indicators (foraminifera, ostracods and molluscs). In addition, the relation of vascular plants of the Vallcebre Basin with other biota (invertebrates and dinosaur ichnites) was determined.

4. Results

4.1. Systematic Palaeobotany

The charophyte assemblages from the Àger Basin are formed by *Feistiella malladae* (BATALLER 1945) nov. comb. VILLALBA-BREVA ET MARTÍN-CLOSAS, *Microchara cristata* GRAMBAST 1971, *M. parazensis* MASSIEUX 1987, *Dughiella obtusa* GRAMBAST ET GUTIÉRREZ 1977, *Peckichara cancellata* GRAMBAST 1971, *P. sertulata* GRAMBAST 1971, *Platychara caudata* GRAMBAST 1971, *P. turbinata* GRAMBAST ET GUTIÉRREZ 1977 and *Clavator brachycerus* (GRAMBAST 1962) MARTÍN-CLOSAS 1996. These species were taxonomically described by Villalba-Breva and Martín-Closas (under revision) (Figs. 10 and 11). In the Vallcebre and Tremp basins the charophyte assemblage is formed by *Feistiella malladae*, *Microchara cristata*, *Peckichara cancellata*, *P. sertulata* and *Clavator brachycerus*, although homogeneous associations of *Feistiella malladae* are the most abundant (Villalba-Breva et al. 2012; Villalba-Breva and Martín-Closas under revision) (Figs. 10 and 11).

Besides fructifications, the charophyte thalli were also taxonomically studied. Three types of charophyte thalli were distinguished. The first type corresponds to *Munieria grambastii* BYSTRICKÝ 1976. All the thalli show transversal sections with irregular, mainly triangular, outlines in contrast to the typically rounded shape of this species. This peculiar shape probably results from diagenetic deformation. The second type is very large isostichous thalli of *Charaxis* HARRIS 1939. These thalli form characteristic megaplant assemblages in the Vallcebre and Tremp Garumnian charophyte limestones, but showed only low degrees of articulation hindering an accurate taxonomic description. The thalli are only calcified in the intercellular area between the internodal and the cortical cells, leading to the accumulation of collapsed intercellular fragments, typically triangular in shape. The third type of thallus corresponds to the genus *Clavatoraxis* MARTÍN-CLOSAS ET DIÉGUEZ 1998. The exceptional preservation of these thalli enabled us to describe the new species *Clavatoraxis microcharophorus* VILLALBA-BREVA ET MARTÍN-CLOSAS (Figs. 12 and 13). The new species *C. microcharophorus* is characterized by relatively small isostichous thalli with spine cell rosettes, which bore *Microchara* sp. gyrogonites attached to bract-cell rosettes of branchlets (Fig. 12A). Each gyrogonite was covered completely by an expanded bract cell (Fig. 12B), which corresponds to a structural tunica (Villalba-Breva and Martín-Closas 2011).

The megafossil plant associations from the basal Garumnian of the Vallcebre and Coll de Nargó basins are very similar; both are formed mainly by leafy axes of the cheirolepidiacean conifer *Frenelopsis* (SCHENK 1869) WATSON 1977, which provided most of the organic matter precursory of coal (Villalba-Breva et al. 2012). The second most abundant megafossil plant remains are *Sabalites longhirachis* (UNGER) J. KVAČEK ET HERMAN palm leaves. These remains were found associated to palm logs and rooting systems in the Vallcebre Basin, which allowed Marmi et al. (2010) reconstructing the palm tree bearing *S. longirhachis* leaves (Fig. 14). In the Vallcebre Basin other megafossil plant remains include extremely rare cycadalean and monocot (probably pandanacean) leaves and abundant minute angiosperm seeds (Villalba-Breva et al. 2012) (Fig. 15). Most of these seeds belong to the new species of angiosperm seed *Bergacarpon viladricii* MARMI, GOMEZ, VILLALBA-BREVA ET MARTÍN-CLOSAS 2012 attributed to a monocot (probably a commelinid) based on the presence of a micropylar lid in the orthotropous (atropous) seed (Marmi et al. 2012).

The Isona flora from the Tremp Basin is more diverse than the flora from the Vallcebre and Coll de Nargó basins. This flora was preliminary studied by Vicente (2002) but little was known about the precise taxonomy and the taphonomical and stratigraphical context of the assemblage. Some taxa occur in the three basins, such as *Frenelopsis* sp. leafy twigs and *Sabalites longirhachis* palm leaves, but the Isona flora include other conifers and, particularly, a large variety of angiosperms, especially dicot leaves (Fig. 16). The megafossil plants found correspond mainly to very fragmented leaves preserved as compressions and impressions, but a few well-preserved leaves allow for detailed description (in progress). Also, angiosperm seeds similar to *Bergacarpon viladricii* were found in Isona.

Finally, palynological analysis from the basal Garumnian of the Vallcebre Basin showed that three samples, from a marlstone bed with angiosperm seeds, organic marls and a lignite with rootlet-marks respectively, were highly productive and consisted of abundant bisaccates (especially *Pinuspollenites ruginosa*), with less abundant fern spores (species of *Cyathidites*, *Chomotriletes*, *Klukisporites* and *Leiotriletes* being dominant) and freshwater algal oospores (*Oedogonium cretaceum* and *Ovoidites spriggi*) (Villalba-Breva et al. 2012) (Figs. 17 and 18).

4.2. Biostratigraphy

The charophyte assemblage of the Àger Basin is dominated by *Peckichara cancellata*, and *Clavator brachycerus*. The species *Peckichara cancellata* is biostratigraphically significant and represents the index species of the homonymous charophyte biozone. According to Riveline et al. (1996), this biozone has been calibrated with chrons C32r and C32n, middle and upper part of the Late Campanian in age (Villalba-Breva and Martín-Closas under revision). These results are compatible with the age inferred for the basal Garumnian based on the age of the underlying formation according to Caus and Gómez-Garrido (1989) and Vicens et al. (2004) based on foraminifera (*C. lecalvezae*, *I. decussatus*) and rudists (*Hippurites radiosus, Radiolites pulchellus*) respectively.

In the Vallcebre Basin the charophyte assemblage is also dominated by *Peckichara cancellata* and belongs to the Peckichara cancellata biozone. However, new magnetostratigraphic data from this basin by Oms et al. (2007) allowed the extension of the top of the biozone to chron C31r at least, i.e. the Earliest Maastrichtian (Villalba-Breva et al. 2012). These results are compatible with biostratigraphic data obtained by Feist and Colombo (1983).

The charophyte assemblage of the Tremp Basin is formed by *Feistiella malladae*, *Peckichara sertulata*, *Microchara cristata* and *Clavator brachycerus*. The two species *Microchara cristata* and *Clavator brachycerus* have a wide range from the Middle Campanian to the Late Maastrichtian. However, this range can be limited to the Early Maastrichtian by the occurrence of homogeneous assemblages of *Peckichara sertulata*, considered to develop in the Septorella ultima biozone, Early Maastrichtian in age (Villalba-Breva and Martín-Closas under revision). In the Barranc de la Posa section, this biozone can be correlated with the lowest occurrence of the rudist *Hippuritella castroi* (Early Maastrichtian) defined by J. Philip in Hardenbol et al. (1998). These results are compatible with biostratigraphic data obtained by Feist et al. (1983), Gallemí et al. (1983) and Caus and Gómez-Garrido (1989). However they do not agree with the age obtained from sequence stratigraphic interpretations by Ardèvol et al. (2000) and Vicens et al. (2004).

Finally, the charophyte assemblage found in Santaeulàlia Mine from the Coll de Nargó Basin is formed only by *Feistiella malladae.* This species has a wide range from the Late Campanian to the Late Maastrichtian. However, Feist and Colombo (1983) found homogeneous assemblages of *Peckichara sertulata* in equivalent beds from another section of the basin, allowing to assign them to the Early Maastrichtian (Septorella ultima biozone), as in the Tremp Basin. These results are compatible with biostratigraphic data obtained by Willems (1985) based on foraminifera.

In sum, the charophyte biozones defined in the Southern Pyrenean Basins, Peckichara cancellata and Septorella ultima, can be correlated with the lowest occurrences of rudists *Hippurites radiosus* and *Hippuritella castroi*, and calibrated with magnetozones C32r, C32n and C31r, as shown in Table 1.

4.3. Sedimentology, taphonomy and palaeoecology

The basal Garumnian in the Àger Basin is organised into hundreds of small order sedimentary cycles, generally less than one meter thick, formed by basal marls, followed by white wackestones and topped by dark-grey packstones (Villalba-Breva and Martín-Closas under revision). From a palaeoecological point of view the charophyte assemblage is dominated by *Peckichara cancellata*. Charophyte-rich microfacies have enabled to distinguish a number of facies belts (Fig. 19A). The lakeshore belt is represented by facies of fragmented charophyte remains and bioclasts; the shallow lake is represented by three different types of charophyte meadows, respectively dominated by (1) *Munieria grambastii* and *Clavator brachycerus*, (2) *Charaxis* sp. and *Peckichara* associated with submerged vascular plants, probably angiosperms and (3) *Clavatoraxis microcharophorus* and *Microchara*. The repeated change in the shallowing-upward cycles from white wackestones of *Charaxis* - *Peckichara* and *Clavatoraxis* - *Microchara* to dark-grey packstones with *Munieria grambastii* and *Clavator brachycerus* suggests that this last meadow grew in very shallow environments. In contrast, the *Charaxis – Peckichara* and *Clavatoraxis microcharophorus – Microchara* meadows occurred in relatively deeper parts of the shallow lake. The fact that clavatoraceans occurred in the shallower and better illuminated vegetation belt is remarkable since *Clavator brachycerus* represents one of the last clavatoraceans, occurring shortly before the extinction of the family during the Maastrichtian.

In contrast, the basal Garumnian in the Vallcebre, Coll de Nargó and Tremp basins is organised in a few cycles, several meters thick, formed by basal marls, followed by lignite and grey wackestone-packstones at the top (Villalba-Breva et al. 2012; Villalba-Breva and Martín-Closas under revision). Charophyte-rich microfacies have enabled to distinguish one meadow of brackish facies dominated by *Feistiella malladae* and, again, three charophyte meadows of freshwater lacustrine facies dominated by: (1) *Munieria grambastii*, (2) *Charaxis* sp. and *Peckichara*, and (3) *Clavatoraxis microcharophorus* and *Microchara*.

The lateral relationships between these three meadows and their relative abundance are different in the three basins. In the Vallcebre Basin the brackish environments were dominated by *Feistiella malladae* with subsidiary *Platychara* sp. In the lacustrine environments the *M. grambastii* and *Charaxis – Peckichara* meadows appear to have grown in very shallow parts, while *Clavatoraxis microcharophorus* meadows grew in deeper areas. The *Charaxis – Peckichara* meadow was dominant, while the others only occurred locally, under particular conditions (Fig. 19B). Instead, in the Coll de Nargó and Tremp basins the most abundant meadow was dominated by *Feistiella malladae*. In the freshwater lakes meanwhile, the different types of charophyte meadows only occur locally and the lateral relationships between these three meadows are poorly known (Fig. 19C).

4.4 Palaeogeography

The first non-marine deposits (Garumnian) of the Southern Pyrenean Basins of Vallcebre, Coll de Nargó, Tremp and Àger show contrasting chronostratigraphical, sedimentological, and palaeoecological features. These differences are important from a palaeogeographical point of view since they suggest that the Southern Pyrenean Basin displayed a south to north shift of facies during the Campanian-Maastrichtian boundary (Fig. 20). This facies polarity was superimposed to the well-known east to west polarity of the Garumnian basins (Ardèvol et al. 2000). Thus, in the Late Campanian (Peckichara cancellata biozone, chron C32r to C32n) the more proximal, strictly lacustrine facies, were deposited to the south (La Maçana Fm, Àger Basin) whilst in the north (Vallcebre, Coll de Nargó and Tremp basins) more distal, strictly marine facies of the nearshore Areny Fm occurred (Fig. 20A). In the Campanian-Maastrichtian boundary (Peckichara cancellata biozone, chron C31r) the same south to north facies polarity occurred again, along with an east to west polarity. This time, the facies were fluviatile in the Àger basin, to the south (Figuerola Fm); in the north the sedimentation ranged from the transitional facies and minor freshwater lakes of the Vallcebre Basin (Northeast), to the marine facies of the Areny Fm in the north-west, i.e in the Coll de Nargó and Tremp basins (Fig. 20B). Finally, in the Early Maastrichtian (Septorella ultima biozone) in the west (Coll de Nargó and Tremp basins) the sedimentation displayed transitional facies of coastal-swamp environments connected with shallow freshwater lakes (La Posa Fm), whereas in the south and west (Àger and Vallcebre basins respectively) the facies were already fluviatile (Fig. 20C).

5. Discussion

5.1. Charophyte taxonomy

a) Clavatoraceae

Grambast (1971, 1974) proposed that the distinction between the last clavatoracean species *Clavator brachycerus* GRAMBAST 1971 and *C. ultimus* (GRAMBAST 1971) MARTÍN-CLOSAS 1996 was based on the presence/absence of an apical pore. Later Massieux et al. (1979) showed that the apical pore of *C. brachycerus* was in fact a mechanical artefact produced by fragmentation and that in both species the apex of the utricle was closed. The studied samples from the Southern Pyrenean Basin confirm that the distinction between the two species refers only to the utricle size and to a different number of bract cells, since the apical pore is closed in *Clavator brachycerus* utricles. The structure of the utricle is especially significant for the species distinction. Thus, utricles of *C. brachycerus* display 5-7 bract cells whilst *C. ultimus* utricles bear 8-9 bract cells. In addition, clavatoracean utricles related to *Clavator brachycerus* are locally associated with thalli of *Munieria grambastii*, which allows us to assign this type of thallus to the aforementioned clavatoracean fructification, as already suggested by Fabre-Taxy and Chatelet (1971).

b) Porocharaceae

Feist and Colombo (1983), Massieux et al. (1985, 1987) and Masriera and Ullastre (1988) identified a single porocharacean species in the Late Cretaceous of the Pyrenees, *Porochara mallladae*. We observed that the fructifications of *Porochara malladae* have a unicellular basal plate, and correspond in fact to genus *Feistiella* SCHUDACK 1986. Thus the new combination *Feistiella malladae* (BATALLER 1945) VILLALBA-BREVA ET MARTÍN-CLOSAS nov. comb. is proposed in Villalba-Breva and Martín-Closas (in revision).

c) Characeae

Microchara parazensis has only been reported from the Maastrichtian of the France by Massieux et al. (1987). Here we report for the first time its occurrence in the Late Campanian of the Southern Pyrenees. *Dughiella obtusa* and *Platychara turbinata* are two exclusively Iberian species; however, previously they were unknown from the Àger Basin.

This is the first time a whole plant fossil of a charophyte has been reconstructed from thin sections of lacustrine limestones. In addition, the anatomical connection between characean fructifications and a *Clavatoraxis* thallus clearly shows that this type of thallus is not exclusive of clavatoraceans, as previously thought, and provides significant new characters for a better distinction between *Microchara* and *Chara*. Although these genera show similar gyrogonites, they were attached to extremely different type of thalli. Now we know that *Microchara* is attached on *Clavatoraxis* thalli whilst *Chara* is borne on *Charaxis*-type thalli. On the other hand, the constant association of the very large *Charaxis* thalli with *Peckichara* gyrogonites suggests that they belonged to the same plant.

5.2. Vascular plants taxonomy

a) *Frenelopsis* sp.

The studied coniferous remains from the Vallcebre Basin belong to *Frenelopsis* because they present several diagnostic characters provided by Gomez et al. (2002): stomata more or less arranged in parallel rows (11-14 files per mm^2), with 4-6 massive papillae, each borne by a subsidiary cell, and ordinary epidermal cells are square, rectangular to polygonal in shape (31-40 µm long and 16-19 µm wide).

b) *Sabalites longhirachis*

Palm leaves studied in the Vallcebre Basin are identified as *S. longirhachis* based on gross morphology and venation features. These leaves show all macroscopic characters reported by Kvaček and Herman (2004) in the diagnosis of *Sabalites longirhachis* from the Lower Campanian of the Grünbach Formation (Austria), and a venation pattern similar: leaves costapalmate, induplicate, lanceolate; thick long costa; leave segments fused, nearly linear, slightly wider towards the apex, each of them V-shaped in transversal section and emerging at an acute angle from the costa; mid-vein and four parallel vein orders for each segment. The logs found associated to these leaves show external features typical of living palms: they are straight, of nearly uniform width, or tapered upwards, and slender, there is no evidence of spines, but only ellipsoidal structures and holes attributed to adventitious roots in basal parts of the palm stems. The rooting marks attributed to *Sabalites longirhachis*-bearing palm are preserved as adpressions and internal casts without anatomical details. Moreover, they can be interpreted as palm rooting systems based on their great similarity in shape and size to those of living palms. The circular central mark may correspond to the palm stump and falls within the diameter range of logs reported from the Vallcebre Basin. In addition, rooting systems of other vascular plants identified are different to palms in many features: conifers and most angiosperms usually have axonomorph rooting systems, cycadalean roots consist of a taproot with small, branched lateral roots arranged in two rows, pandanaceous trees produce many thick stilt roots near the trunk base to provide support.

c) *Bergacarpon viladricii*

All seeds studied in the Vallcebre Basin belong to a single species, *Bergacarpon viladricii*, as they share similar morphology, size and sculpture. They are orthotropous and have a micropylar cap. Opercular seeds are best known in monocots, especially in members of Commelinids, but also in Nymphaeales and in some Eudicots. Nymphaeales are mostly anatropous and usually have more than two ovules per carpel and fleshy fruits; Begoniaceae and Cactaceae have anatropous and campylotropous ovules, respectively, and probably originated during the Cenozoic. Thus, these seeds may have been produced by a commelinid.

d) Other megafossil plant remains

A specimen collected in the Vallcebre Basin may be interpreted as a partial bipinnated leaf of a Cycadale. But, diagnostic features of cycads 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.

Several leaf fragments, collected also in the Vallcebre Basin, 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) KVAČEK ET HERMAN. However, more material and better conservation are needed for more accurate determination.

5.3. Biostratigraphy

The biostratigraphic study contributed to the calibration of Upper Campanian and Lower Maastrichtian biozones on the basis of magnetostratigraphy. Thus, the Peckichara cancellata biozone defined by M. Feist in Riveline et al. (1996) was directly calibrated with the magnetozones C32r to C32n (Galbrun et al 1993), reaching possibly the top of chron C33n (Westphal and Durand 1990), which represent the middle and upper part of the Late Campanian as to present knowledge based on the geochronological scale of Gradstein (2004). However, new magnetostratigraphic data by Oms et al. (2007) from the Vallcebre Basin allowed us to enlarge the top of the biozone to the Earliest Maastrichtian, magnetozone C31r. This modification is compatible with the correlation of Peckichata cancellata biozone and Lower Maastrichtian palynofloras (Médus et al. 1988).

On the other hand, the charophyte assemblages of the Tremp Basin do not contain any index species of the charophyte biozonation defined also by M. Feist in Riveline et al. (1996). According to Grambast (1971) and Riveline et al. (1996), *Peckichara sertulata* forms homogeneous assemblages only associated to *Clavator ultimus*, index species of the Septorella ultima biozone. Thus, despite the absence of *C. ultimus*, probably due to palaeoecological limitations, the occurrence of *P. sertulata* is enough to date the basal Garumnian as Early Maastrichtian in the Tremp Basin.

5.4. Sedimentology, taphonomy and palaeoecology

a) Charophytes

Sedimentological analysis combined with microfacies and taphonomic analyses allows description of the habitat of charophytes in freshwater lakes and provides the key to recognizing the facies of deeper lake bottoms with poor oxygenation and inhabited by loose cyanobacterial mats as favourable to the preservation of well-articulated charophyte remains. In contrast, the in situ charophyte meadows resulted in an accumulation of a large number of collapsed charophyte thalli with only a relatively small portion of sediment, forming lime packstone-grainstones where the detailed anatomical structures and especially the attachment of gyrogonites and thalli are difficult to recognize or absent altogether.

A comparison of the Vallcebre, Coll de Nargó, Tremp and Àger reveals that the lakes of these basins had three similar types of charophyte-rich facies, dominated respectively by *Clavatoraxis microcharophorus*, *Charaxis* sp. and *Munieria grambastii* thalli, sometimes with abundant remains of submerged macrophytes. However, species richness in the basal Garumnian of the Àger Basin is much higher than in the Vallcebre, Coll de Nargó and Tremp Basins, as is to be expected when charophyte assemblages from freshwater lakes are compared with assemblages from brackish water (García 1999). Also, the species composition between the basins is different, since lacustrine facies from La Maçana Formation in the Àger Basin show assemblages dominated by characeans, especially *Peckichara cancellata*, in the marginal lake and clavatoraceans

(*Clavator brachycerus*) in the lakeshores, whilst in the other basins the most abundant species was the porocharacean *Feistiella malladae*. These palaeoecological differences, coupled with the sedimentological differences described from the basins studied show that there was a significant palaeogeographical control of facies and species distribution.

b) Vascular plants

Combined sedimentological and taphonomical analyses were also performed to elucidate the habitat of vascular plants. 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 (García-Vallès et al. 1994). These authors related the plant remains to taxodiacean elements, by comparison with Tertiary and extant forest swamps. However, the taphonomic evidence obtained in the Vallcebre Basin suggests that the parent plants that provided the organic matter precursory of most of the Garumnian lignite were cheirolepidiacean conifers (*Frenelopsis* sp.) and, to a lesser extent, arecacean angiosperms (*Sabalites longirhachis*). Also, the absence of rooted horizons at the base of most lignite beds on brackish organic marls suggests that these coal seams resulted from the detrital accumulation of plant remains, mainly *Frenelopsis* leafy axes. The transport of organic matter could have been carried out by flotation, depending on its density and buoyancy.

In contrast, peat mires grew in the last infilling stages of the freshwater lakes. Evidence for this is mainly provided by two kinds of rooting structures preserved in charophyte limestones from the Fumanya Sud and Mina Esquirol mines (Vallcebre Basin). The most abundant were small tap roots of unknown botanical affinity. However, given that these roots occur associated to thin lignite beds with *Frenelopsis* sp. the working hypothesis is proposed that this plant inhabited the peat mires. The second type of roots is brush-like roots attributed to *Sabalites longirhachis* palms. Also, the occurrence of lacustrine green algae in root-bearing lignites suggests freshwater conditions during the deposition of this peat.

Scarcity, high fragmentation and the absence of rooting marks related to other plants found in the Vallcebre Basin (fern, cycadalean and monocot foliage suggest that these plants were parautochthonous to allochthonous in the coal bearing deposits. Therefore, the habitats of these plants 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. On the other hand, the seeds and fruits studied in Vallcebre are concentrated in a marlstone bed. The accumulation of monotonous assemblages of the angiosperm seed *Bergacarpon viladricii* was likely influenced by ecological constraints of a local plant source (monospecific plant community) or by taphonomic, mainly transport processes. In fact, this is one of the oldest monotypical angiosperm seed accumulations found so far in the fossil record.

The palynological assemblages from the Vallcebre Basin were compared with other assemblages collected from similar coal-bearing deposits of the Pyrenean Maastrichtian, such as those from the Coll de Nargó Basin (Médus 1972; Ashraf and Erben 1986), Barranc de la Posa in the Tremp Basin (Porta et al. 1985) and Fontllonga in the Àger Basin (López-Martínez et al. 1999; Fernández-Marrón et al. 2004b). The assemblages from Vallcebre were distinct from most other Pyrenean Maastrichtian localities in being dominated by bisaccates and showing a lower proportion of palm-related monocolpates. However, some assemblages were similar to other Pyrenean localities in showing dominant trilete fern spores of similar taxa. On the other hand, the contradictory absence of the cheirolepidiacean conifer pollen *Classopollis* in beds with abundant *Frenelopsis* sp. leafy remains can be explained by selective sorting during transport and deposition, as noted by Taugourdeau-Lanz et al. (1982). However it cannot be ruled out that this absence is related to a low production of *Classopollis* pollen in the source plants. Elucidating this question would be highly significant since the last cheirolepidiacean conifers occur in the time span represented by the Garumnian record and the absence of male reproductive organs in the assemblage could be a reasonable hypothesis to explain the extinction of this important Mesozoic conifer family near the K-T boundary.

5.5. Palaeogeography

The south to north shift of facies found in the Southern Pyrenean Basin during the Campanian-Maastrichtian boundary is somewhat reminiscent of the distribution of facies reported for Lower Cretaceous Pyrenean Basins by Peybernès (1976). However, in the Late Cretaceous it was superimposed onto the well-known east to west polarity, related to Southern Pyrenean Basin infilling and to the anticlockwise rotation of Iberia (Capote et al. 2002). This distribution shows that, since the beginning of non-marine sedimentation of the Late Cretaceous, the Montsec-Pedraforca thrust sheet was a sedimentary high that separated a domain clearly more continental located south of the rise (Àger Basin) and a domain with marine influence in the north (Tremp, Coll de Nargó and Vallcebre basins).

Conclusions

The charophyte assemblages from the basal Garumnian of the Vallcebre, Coll de Nargó, Tremp and Àger basins have been studied from the point of view of taxonomy, biostratigraphy and palaeoecology. The charophyte flora is formed by girogonites of *Feistiella malladae*, *Peckichara cancellata*, *P. sertulata*, *Microchara cristata*, *M. parazensis*, *Platychara caudata*, *P. turbinata*, *Dughiella obtusa*, and utricles of *Clavator brachycerus*. Taxonomy of this thesis conforms to the system proposed by previous authors, especially Grambast (1971). However, some precisions were incorporated. The distinction between *Clavator brachycerus* and *C. ultimus* is limited to the size and a different number of bract cells, not by the presence/absence of an apical pore. Also, the occurrence of genus *Feistiella* as the only porocharacean genus represented in the Late Cretaceous of the Pyrenees is confirmed. From the biogeographical viewpoint most of the flora was already known from the Pyrenees. However, *Microchara parazensis* and *Dughiella obtusa* are reported for the first time in the Late Campanian of the Southern Pyrenean Basin and the species *Platychara turbinata* is recorded for the first time in the Àger Basin. An innovative approach in the taxonomy of fossil charophytes of the basal Garumnian of the Southern Pyrenean Basin is the description of three types of charophyte thalli: *Munieria grambastii*, *Charaxis* sp. and the new characean species *Clavatoraxis microcharophorus* VILLALBA-BREVA ET MARTÍN-CLOSAS 2011. This thallus showed features unknown in extant characeans, such as isostichous cortication with spine-cell rosettes and gyrogonites coated by an expanded bract cell, which corresponds to a structural tunica. Furthermore, the reconstruction of this new species shows that this type of thallus is not exclusive of clavatoraceans, and provides significant new characters for a better distinction between *Microchara* and *Chara* based on their vegetative organs. Finally, this is the first time that a whole-plant fossil characean has been reconstructed from thin sections.

From the point of view of biostratigraphy, the basal Garumnian of the Àger Basin was first characterised biostratigraphically, whilst the biostratigraphy of the Vallcebre, Coll de Nargó and Tremp basins was revised with new data on hand. The age of the basal Garumnian (La Maçana Formation) in the Àger Basin is Late Campanian and in the Vallcebre Basin the non marine Grey Garumnian began in the Earliest Maastrichtian. Both records belonged to the Peckichara cancellata biozone defined by Feist in Riveline et al. (1996). In contrast the first non marine deposits of the basal Garumnian in the Coll de Nargó and Tremp basins were Early Maastrichtian in age (Septorella ultima biozone), based on the occurrence of homogeneous assemblages of *Peckichara sertulata*. As a consequence, the onset of the non-marine sedimentation in the Late Cretaceous (Garumnian) began first in the south (Serres Marginals thrust sheet), and followed later in the Montsec-Pedraforca thrust sheet from east to west, showing a clear diachronism. The whole continentalisation process in the Southern Pyrenean Basins lasted for about 6-7 Ma.

From a palaeoecological point of view, the charophyte assemblages from the Àger Basin indicate freshwater conditions whilst the assemblages from the Vallcebre, Coll de Nargó and Tremp basins contain homogeneous assemblages of porocharaceans, which are more characteristic of brackish water conditions. This result suggests that the Southern Pyrenean Basin displayed a south to north shift of facies, at the beginning of the continental sedimentation in the Late Cretaceous. In the basins with a significant brackish influence, charophyte limestones were regularly intercalated with coal (lignite). Taxonomic and taphonomic evidence suggest that the main Garumnian coal seams result from the accumulation of detrital organic matter, mainly *Frenelopsis* leafy axes, in marginal marine settings, while the autochthonous peat, deposited in freshwater peat mires, represents an extremely small part of the total coal volume. Moreover, the rooting structures found on charophyte limestone of the Vallcebre Basin suggest that the only non submerged vegetated areas of the Lower Maastrichtian wetlands were the limnic parts; in contrast, the brackish environments looked like a bare water table most of the time. The study of megafossil plant remains from the basal Garumnian of the Vallcebre, Coll de Nargó and Tremp basins indicates that the cheirolepidiacean conifer *Frenelopsis* were the main component of the wetlands vegetation associated with *Sabalites longirhachis* palms, and in some cases with other angiosperms, such as the plant bearing *Bergacarpon viladricii* MARMI, GOMEZ, VILLALBA-BREVA ET MARTÍN-CLOSAS 2012, probably a commeliniid. Palynological analyses show abundant bisaccates, with less abundant fern spores and freshwater algal oospores. Surprisingly the pollen from *Frenelopsis*, *Classopollis* was absent, as it is the rule in most Upper Cretaceous Southern Pyrenean Basins. These differences may be explained by taphonomic biases or by the low productivity of male organs.

INTRODUCCIÓ

La present tesi doctoral tracta de l'estudi dels caròfits del Cretaci superior no marí (Garumnià basal) del Pirineu Oriental des d'un punt de vista taxonòmic, biostratigràfic i paleoecològic. En començar aquesta tesi, el coneixement de la taxonomia i la biostratigrafia dels caròfits del Cretaci superior dels Pirineus estava extremadament focalitzat en la identificació del límit Cretaci – Terciari (K – T). Per això, un dels objectius inicials va ser estendre aquest coneixement a la base del registre del Cretaci superior continental (Garumnià basal). D'altra banda, el Garumnià correspon a la formació o fàcies que marca l'inici de la continentalització de la Conca Sud Pirinenca entre el Cretaci superior i el Paleocè. Aquest esdeveniment, que és cabdal per entendre l'evolució de la conca pirinenca, romania també poc conegut, especialment des del punt de vista cronostratigràfic i paleoambiental. Per tal de cobrir aquest buit, un segon objectiu va ser la caracterització del Garumnià basal des d'un punt de vista biostratigràfic, paleoecològic i paleogeogràfic. Donat que els carbons garumnians representen una de les litologies mes significatives del Garumnià basal i la gènesi de les calcàries de caròfits de moltes de les conques estudiades estava íntimament lligada a la dels carbons, ha calgut aportar nova informació referent a la paleobiologia i la sedimentologia de la matèria orgànica precursora del carbó garumnià explotat durant el segle XX a la Conca Sud Pirinenca.

La tesi doctoral que es presenta s'ha dut a terme a les conques de Vallcebre, Coll de Nargó, Tremp i Àger. Aquesta tesi s'estructura en base a les dades de tres articles fonamentals, un d'ells publicat, un altre en premsa i un darrer en revisió, tots ells a revistes indexades de reconegut prestigi internacional (SCI):

1. **Villalba-Breva, S.**, Martín-Closas, C., Marmi, J., Gomez, B., Fernández-Marrón, M. T. 2012. Peat-forming plants in the Maastrichtian coals of the Eastern Pyrenees. *Geologica Acta*, doi: 1133 101344/105000001711 (en premsa).

2. **Villalba-Breva, S.**, Martín-Closas, C. 2011. A characean thallus with attached gyrogonites and associated fossil charophytes from the Maastrichtian of the Eastern Pyrenees (Catalonia, Spain). *Journal of Phycology*, 47: 131-143.

3. **Villalba-Breva, S.**, Martín-Closas, C. The onset of the non-marine sedimentation in the Upper Cretaceous of the Central Southern Pyrenean Basins

(Catalonia, Spain) from charophyte biostratigraphy and palaeoecology. *Facies* (en revisió).

A més a més, a l'Annex 2 es presenten dos treballs complementaris relacionats amb la caracterització paleobotànica dels carbons de la Conca de Vallcebre, publicats igualment en una revista indexada del SCI:

1. Marmi, J., Gomez, B., Martín-Closas, C., **Villalba-Breva, S.** 2010. A reconstruction of the fossil palm *Sabalites longirhachis* (Unger) J. Kvaček et Herman from the Maastrichtian of Pyrenees. *Review of Palaeobotany and Palynology*, 163: 73-83.
2. Marmi, J., Gomez, B., **Villalba-Breva, S.**, Martín-Closas, C. 2012. *Bergacarpon viladricii* gen. et sp. nov., angiosperm seeds and associated fruits from the early Maastrichtian of the eastern Pyrenees (Catalonia, Spain). *Review of Palaeobotany and Palynology*, 171: 83-94.

Finalment, per tal d'oferir una visió global el més uniforme possible de les àrees estudiades, en els casos on la informació encara no s'ha estructurat en una publicació (Conca de Coll de Nargó) es presenten resultats inèdits de forma resumida.

Objectius

1. Estudiar la taxonomia i la sistemàtica de la flora de caròfits del Garumnià basal del Pirineu Oriental. Es pretén completar i ampliar el coneixement existent dels caròfits a partir de la taxonomia de les fructificacions sedassades de les famílies Characeae, Clavatoraceae i Porocharaceae. Aquest estudi taxonòmic s'ha estès de manera molt innovadora a la reconstrucció 3D de tal·lus a partir de làmines primes. L'estudi dels tal·lus pot aportar dades importants sobre la sistemàtica d'alguns gèneres difícils de caracteritzar només a partir dels girogonits.
2. Estudiar la biostratigrafia dels caròfits, incloent l'assignació de les associacions estudiades a les biozones de caròfits definides per M. Feist a Riveline et al. (1996) i a Hardenbol et al. (1998), i la seva correlació amb les biozones de rudistes i amb les magnetozones definides per autors anteriors. En base a aquest estudi biostratigràfic es pretén aclarir l'edat relativa dels primers dipòsits no marins del Cretaci superior (Garumnià basal) de les conques de Vallcebre, Coll

de Nargó, Tremp i Àger. Alhora que es millora i precisa la biozonació de caròfits per aquest període de temps.

3. Caracteritzar la paleoecologia de les associacions de caròfits definida a partir de l'anàlisi deposicional, l'estudi tafonòmic a partir de les microfàcies i la comparació amb altres indicadors paleobiològics (foraminífers, ostracodes i mol·luscs). Aquest estudi paleoecològic permetria aconseguir una comprensió integrada de les paleobiotes. A més a més, amb l'anàlisi de microfàcies riques en caròfits es contribueix a millorar el coneixement paleoambiental de la primera continentalització del Cretaci superior dels Pirineus.
4. Estudiar les restes fòssils de plantes vasculars del Garumnià basal de les conques sud pirinenques des d'un punt de vista tafonòmic i paleoecològic amb l'objectiu de conèixer quines van ser les plantes precursores dels lignits garumnians i contrastar hipòtesis sobre el seu hàbitat. A més a més, l'anàlisi sedimentològica d'aquests lignits combinada amb l'estudi tafonòmic esmentat permetrà saber on es va formar i dipositar la matèria orgànica precursora dels carbons, que constitueixen una litofàcies estretament lligada a les calcàries de caròfits. Concretament es volia saber ens quins casos els carbons provenien de torberes i en quins casos eren dipòsits de matèria orgànica detrítica.

Problemàtica

Entre els sediments marins cretàcics i els nivells de l'Ilerdià se situa una sèrie continental i lacustre, formada per margues vermelles, calcàries lacustres i lignits, molt característica del Pirineu, l'atribució estratigràfica exacta de la qual ha constituït un motiu constant de discussió entre els geòlegs, des de que aquests materials van ser definits com el darrer pis del Cretaci superior, el Garumnià, per Leymerie (1862).

La denominació de "Garumnià" encara s'utilitza en diversos treballs regionals. Així, alguns autors l'han emprat amb accepció d'estatge cronostratigràfic mentre que en l'actualitat la majoria l'utilitzen per denominar els materials, en fàcies continentals, existents al trànsit Cretaci – Terciari (K – T). Altres autors, per evitar les confusions que podria portar aquest terme, prefereixen obviar-lo i emprar el de Formació Tremp (Mey et al. 1968).

En general, el Garumnià ha rebut l'atenció de molts autors especialment des de la dècada dels anys 1980' per la seva importància en la cronostratigrafia del límit entre el Cretaci i el Terciari (límit K-T). Per aquesta raó la majoria d'estudis (estratigràfics, sedimentològics, paleontològics, de paleomagnetisme i de geoquímica) s'han centrat en els materials pròxims a aquest límit. Això va conduir a que la informació referida als materials basals del Garumnià, estudiats en aquesta tesi, fos fins a l'actualitat molt reduïda. La majoria d'autors descriuen aquesta part inferior del Garumnià com formada principalment per lutites grises, carbons, calcàries amb caròfits i gresos, però no hi ha acord ni en l'edat ni en les condicions paleoambientals sota les quals va tenir lloc la primera continentalització de les conques sud pirinenques.

La datació d'aquests primers dipòsits no marins del Cretaci superior dels Pirineus ha sigut controvertida. Per començar, aquests dipòsits no s'han datat mai amb precisió a la Conca d'Àger, i fins ara s'havia inferit una edat Campanià superior en base a estudis biostratigràfics i magnetostratigràfics dels materials suprajacents (Galbrun et al. 1993, recalibrat segons Gradstein et al. 2004). D'altra banda, l'edat dels dipòsits basals del Garumnià a les conques de Vallcebre, Coll de Nargó i Tremp estava originalment acceptada com Maastrichtià inferior en base a foraminífers bentònics, rudistes, pol·len i espores, biostratigrafia de caròfits i magnetostratigrafia (Liebau 1973; Pons 1977, 1982; Feist i Colombo, 1983; Gallemí et al. 1983; Ullastre i Masriera 1983; Porta et al. 1985; Willems 1985; Médus et al. 1988; Caus i Gómez-Garrido 1989; Oms et al. 2007). No obstant això, interpretacions més recents de l'edat dels primes dipòsits no marins a les conques sud pirinenques centrals basats en estratigrafia seqüencial han suggerit que aquests primers dipòsits eren sincrònics i pertanyien al Campanià superior (Ardèvol et al. 2000; Vicens et al. 2004). Com a resultat d'aquests resultats contrastats existeix certa confusió sobre l'edat de la primera continentalització de les conques sud pirinenques.

Des d'un punt de vista paleoambiental, també existeix cert desacord en quant a les fàcies dels primers dipòsits no marins del Cretaci superior. El Garumnià basal de la Conca de Tremp està àmpliament acceptat com corresponent a dipòsits de *lagoon* i pantà costaner de salinitat variable, relacionats lateralment amb gresos marins d'illa barrera de la Fm. Areny (Nagtegaal 1972; Díaz-Molina 1987). A la conca de Vallcebre, segons Oms et al. (2007) aquests materials correspondrien a ambients de fangars (*mud-flat*) de salinitat variable que passen a planes d'inundació sorrenques. A la Conca d'Àger, Cuevas et al. (1989) i Colombo i Cuevas (1993) havien mostrat que els dipòsits del Garumnià basal pertanyien a ambients lacustres d'aigua dolça mentre que Rosell et al. (2001) consideraven que en aquesta conca no hi estava representat Un escenari alternatiu va ser proposat encara per López-Martínez et al. (2009), que interpretaven el Garumnià basal com dipòsits perimareals i d'estuari més o menys homogeni a totes les conques sud pirinenques.

Al camp de la paleontologia del Garumnià basal, hi ha nombrosos treballs referents als dinosaures (per exemple, López-Martínez 2000; López-Martínez et al. 1999, 2001; Vila et al. 2005, 2011; Riera et al. 2009, entre altres), mentre que la paleobotànica ha estat poc estudiada fins a l'actualitat i en general els estudis paleobotànics sempre han estat focalitzats envers el límit Cretaci – Terciari. En el cas dels treballs de caròfits cal destacar els publicats per Feist i Colombo (1983), Masriera i Ullastre (1983, 1988, 1990), Ullastre i Masriera (1983), Médus et al. (1988), Galbrun et al. (1993) i Mayr et al. (1999), tots ells amb l'objectiu de caracteritzar biostratigràficament el límit K – T. Tot i constituir una bona base, aquests treballs necessitaven ser ampliats al Garumnià basal i completats en quant a temes com la sistemàtica de tal·lus, la biostratigrafia, l'anàlisi de microfàcies riques en caròfits o la paleoecologia.

Referent a les plantes vasculars dels carbons associats a calcàries de caròfits, la majoria d'informació ha sigut proporcionada per estudis palinològics. Així, Médus (1972), Ashraf i Erben (1986), Porta et al. (1985), Médus et al. (1988), López-Martínez et al. (1999), Mayr et al. (1999) i Fernández-Marrón et al. (2004a, b) van dur a terme aquests estudis principalment a les conques d'Àger i Tremp amb una perspectiva biostratigràfica per localitzar, també, el límit K – T. Pel que fa a les macrorestes de plantes fòssils del Cretaci superior només s'havia realitzat un estudi preliminar a la Conca de Tremp (Vicente 2002) i més recentment s'havien publicat dos treballs a la Conca Vallcebre, un de caràcter taxonòmic sobre les palmeres *Sabalites longirhachis* (Marmi et al. 2008) i un altre més sedimentològic i tafonòmic sobre les restes de *Frenelopsis* sp. (Riera et al. 2010); per tant encara es mantenien moltes qüestions obertes sobre les associacions de plantes vasculars del Garumnià basal dels Pirineus, tant taxonòmiques com paleoecològiques. En aquest sentit, cal destacar el coneixement fragmentari que es tenia sobre les plantes precursores dels lignits garumnians de Berga, Tremp i Àger. De fet, García-Vallès (1990) i García-Vallès et al. (1993, 1994, 2000) van realitzar diversos estudis sobre la petrologia orgànica i inorgànica d'aquests carbons, mentre que Domínguez i Sáez (1988) van caracteritzar els lignits de la Conca de Vallcebre des d'un punt de vista tectono-sedimentari. Poc es coneixia doncs sobre l'origen paleobotànic d'aquests lignits i quin va ser el seu medi deposicional en detall (torbera *in situ* o dipòsits detrítics de matèria orgànica).

MARC GEOLÒGIC I ESTRATIGRÀFIC

Marc geològic

La zona d'estudi se situa a la vessant meridional del Pirineu Oriental. L'estructuració de l'Orogen Pirinenc és el resultat de la convergència entre les plaques ibèrica i europea, que s'inicià al Cretaci superior (Santonià – Campanià) i es perllongà fins al Miocè (Teixell 2004). La situació extensional de la Conca Pirinenca del Cretaci inferior s'invertí durant el Cretaci superior i va passar a un estat de marge passiu afectat per episodis transgressius (Cenomanià – Campanià), i després a una conca d'avantpaís (Maastrichtià), que continuà durant gran part del Terciari (Simó 2004). La Serralada Pirinenca es va estructurar en plecs i encavalcaments propis de nivells corticals alts, afectant a un sòcol hercinià, d'edat paleozoica, i una cobertora sedimentària que es va desenvolupar del Permià superior al Cretaci inferior en conques de rift i posteriorment del Cretaci superior a l'Oligocè en conques d'avantpaís i de collibè (*piggy-back*) (Puigdefàbregas et al. 1986; Teixell 2004).

En un primer estadi, els encavalcaments es formaren per inversió de les falles distensives del rift Mesozoic (Muñoz i Puigdefàbregas 1992). Com a conseqüència d'aquesta inversió tectònica es formaren conques subsidents davant les primeres estructures encavalcants, tant a la banda N com a la banda S dels Pirineus (Muñoz i Puigdefàbregas 1992). Així, en aquest estadi inicial, la tectònica compressiva responsable de l'orogènia pirinenca va dividir la conca d'avantpaís Sud Pirinenca en diverses unitats o depocentres (López-Martínez et al. 1999; Ardèvol et al. 2000), que actualment es troben separats per una sèrie progressiva d'encavalcaments amb un desplaçament vers el sud de desenes de kilòmetres i apilats sobre materials autòctons del Paleogen de la Conca de l'Ebre (Muñoz 1989). Les subconques més orientals en què es va dividir la conca Sud Pirinenca corresponen a les estudiades en la present tesi i són la Conca de Vallcebre, la Conca de Coll de Nargó, la Conca de Tremp i la Conca d'Àger. Les primeres es troben a la làmina encavalcant del Montsec-Pedraforca mentre que la darrera pertany a la làmina de les Serres Marginals (Fig. 1).

Marc estratigràfic

El registre estratigràfic del Cretaci superior de cada zona estudiada va estar condicionat per la geometria i el tipus de seqüència d'encavalcaments, junt a altres factors com els canvis eustàtics globals i el clima (Muñoz i Puigdefàbregas 1992). Per altra banda, el tipus de sediment i la distribució dels seus gruixos, així com les morfologies heretades de la fase rift del Cretaci inferior, van tenir una influència important en la seqüència, la forma i la velocitat d'emplaçament dels encavalcaments (Muñoz i Puigdefàbregas 1992).

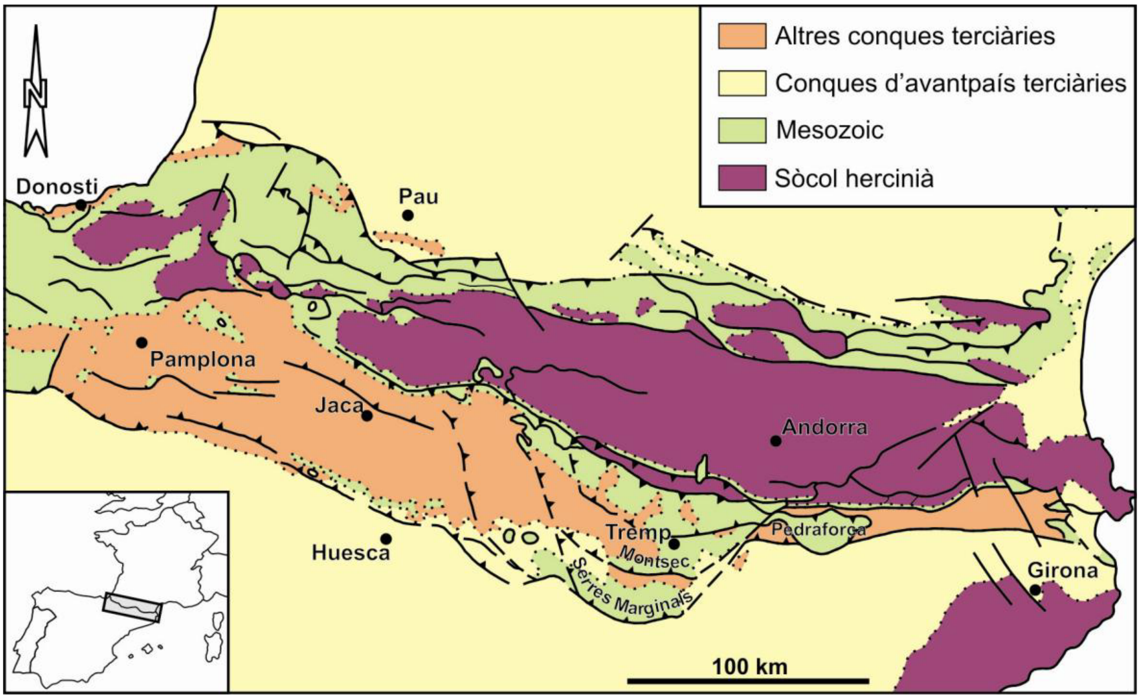


Figura 1. Mapa geològic dels Pirineus amb la localització de les làmines encavalcants del Montsec-Pedraforca i de les Serres Marginals.

Figure 1. *Geologic map of the Pyrenees with situation of the Montsec-Pedraforca and Serres Marginals thrust sheets.*

- Conca de Vallcebre

La Conca de Vallcebre forma un sinclinal situat a la làmina encavalcant inferior del Pedraforca (Fig. 2). Està oberta cap al sector nord-oest i té petits encavalcaments decamètrics a hectomètrics al seu nucli (Vergés et al. 1994). Durant el Cretaci superior el rebliment de la conca va ser pràcticament continu des del Santonià al Tanetià i segons Vergés et al. (1994) hi ha tres unitats sedimentàries principals, estratigràficament concordants. La unitat inferior és d'edat Santonià superior – Campanià inferior i consta de turbidites (Formació Vallcarga, Mey et al. 1968). La segona unitat és d'edat Campanià superior i està formada per calcàries i calcarenites marines (Formació Terradets, Pons 1977). La unitat superior, d'edat Campanià terminal – Tanetià, està formada principalment per capes roges (*red beds*) fluvials i subsidiàriament carbons, calcàries lacustres i margues transicionals de la Formació Tremp (Mey et al. 1968), regionalment anomenada Garumnià (Leymerie 1862). En aquesta conca, la Fm. Tremp té una potència màxima de 850 m (Vergès et al. 1994) i va ser dividida per Rosell et al. (2001) en quatres unitats, una de les quals va ser objecte d'estudi en aquesta tesi, la unitat transicional basal o Garumnià Gris.

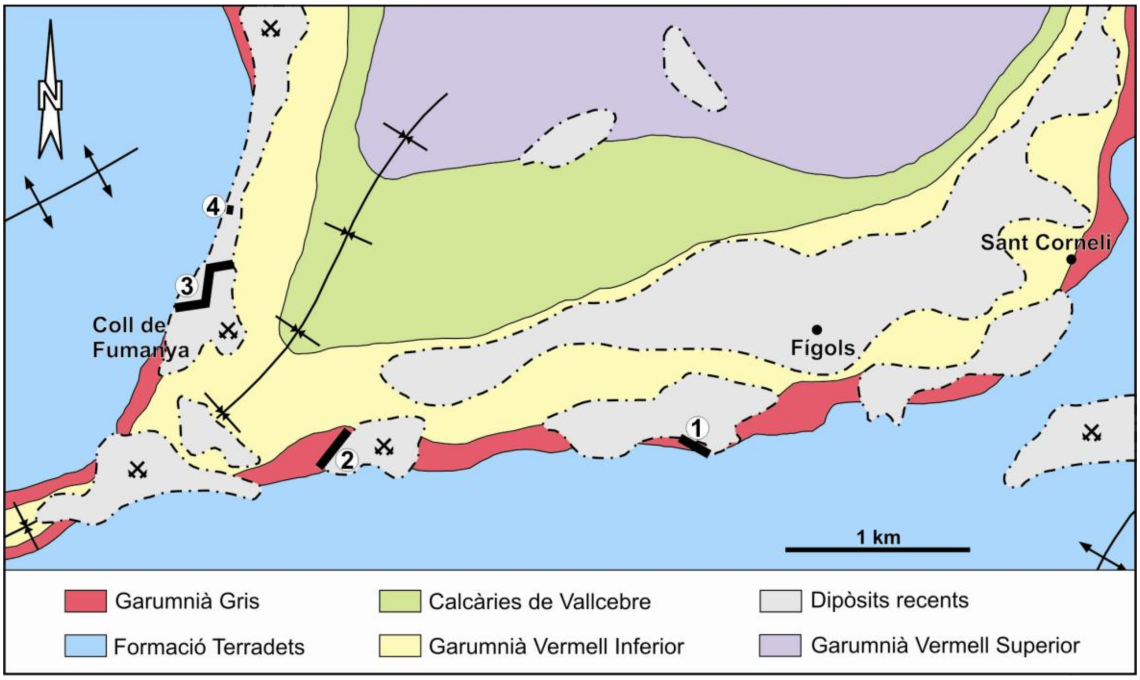


Figura 2. Mapa geològic de la Conca de Vallcebre amb la localització de les columnes estratigràfiques estudiades (1-4). Geologia adaptada d'Institut Cartogràfic de Catalunya (2006).

Figure 2. *Geologic map of the Vallcebre Basin with location of the stratigraphic sections studied (1-4). Geology adapted from Institut Cartogràfic de Catalunya (2006).*

El Garumnià Gris està format per una successió heterolítica de fins 100 m de potència, constituïda per lutites grises i margues amb intercalacions de lignit, calcàries amb caròfits i gresos (Fig. 3). A la base d'aquesta sèrie la litologia dominant són margocalcàries micrítiques amb abundants petjades de dinosaures a sostre. Aquestes icnites són properes al límit Campanià – Maastrichtià segons indiquen les dades paleomagnètiques d'Oms et al. (2007). Per sobre de les margocalcàries hi ha una successió de margues riques en matèria orgànica alternant amb lignits i calcàries amb caròfits, les qual van proporcionar les flores de plantes i caròfits estudiades. Una sèrie de limolites bigarrades amb ous de dinosaure correspon al sostre del Garumnià Gris. Aquesta successió es va dipositar en un ambient inter i supramareal, des de *lagoons* salabrosos a la base, seguits per torberes amb aiguamolls salabrosos i llacs d'aigua dolça, i finalment en planes d'inundació al sostre (Rosell et al. 2001).

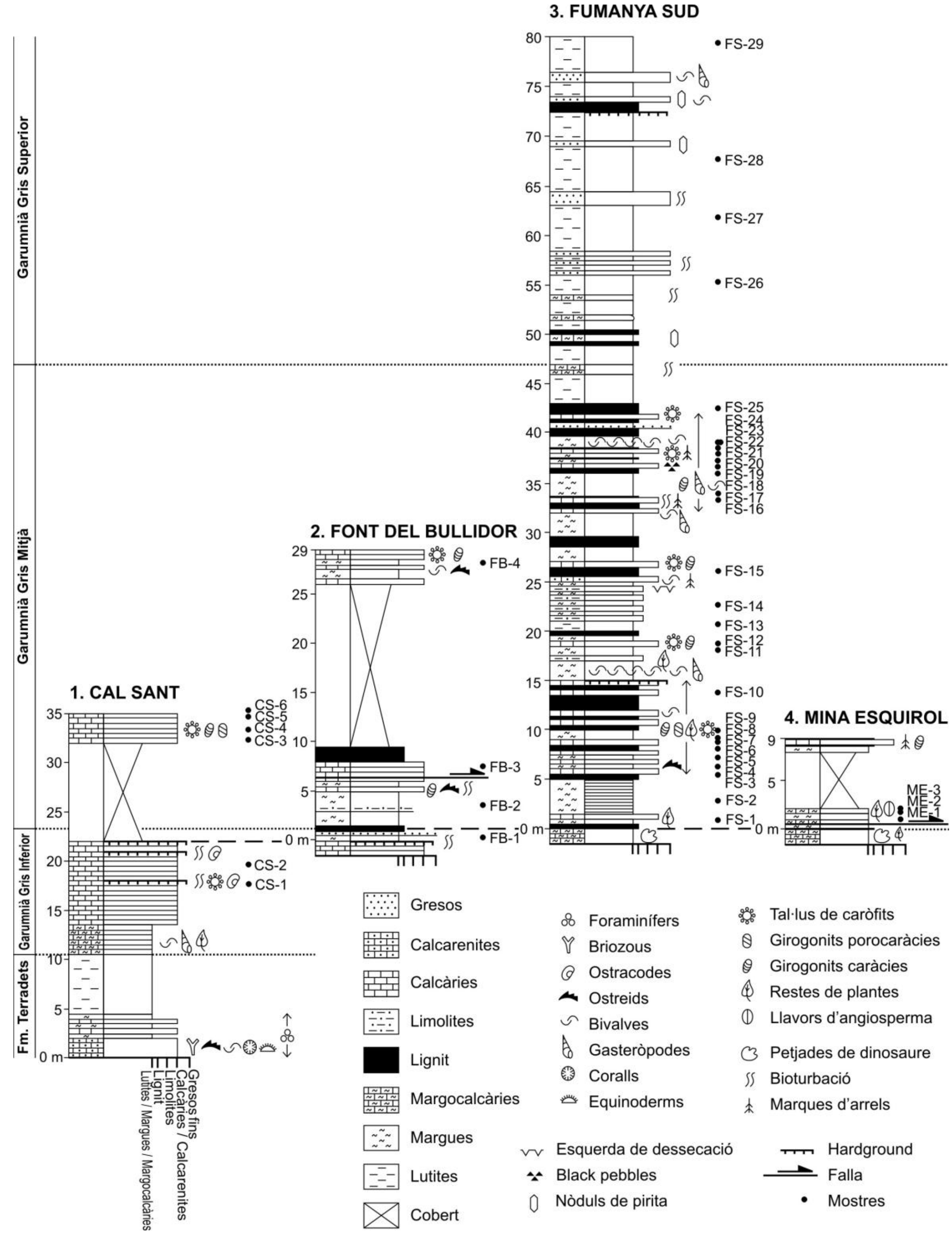


Figura 3. Columnes estratigràfiques estudiades al Garumnià Gris a la Conca de Vallcebre amb la situació de les mostres estudiades. Veure Figura 2 per a la situació de les columnes.

Figure 3. *Stratigraphic sections of the Grey Garumnian studied in the Vallcebre Basin with location of samples studied. See Figure 2 for the location of these logs.*

- Conca de Coll de Nargó

La Conca de Coll de Nargó forma un petit sinclinal situat a la làmina encavalcant del Montsec (Fig. 4). El rebliment de la conca durant el Cretaci superior es pot dividir en quatre unitats litostratigràfiques segons Willems (1985). La unitat inferior correspon a margues i margocalcàries alternants amb turbidites de la Formació Vallcarga (Mey et al. 1968) d'edat Coniacià – Santonià. Per sobre, discordant, es va dipositar una sèrie de margues sorrenques i calcarenites d'edat Campanià corresponent a la unitat inferior de la Formació Gresos d'Areny (Nagtegaal 1972). Els materials suprajacents corresponen als Gresos d'Areny *sensu stricto* definits segons Nagtegaal (1972), d'edat Campanià superior. Les calcarenites costaneres passen lateralment a les fàcies del Garumnià o Formació Tremp (Mey et al. 1968) d'edat Maastrichtià – Tanetià. Willems (1985) divideix la Fm. Tremp en tres membres, dels quals el basal, anomenat Garumnià Inferior, ha sigut objecte d'estudi en aquesta tesi.

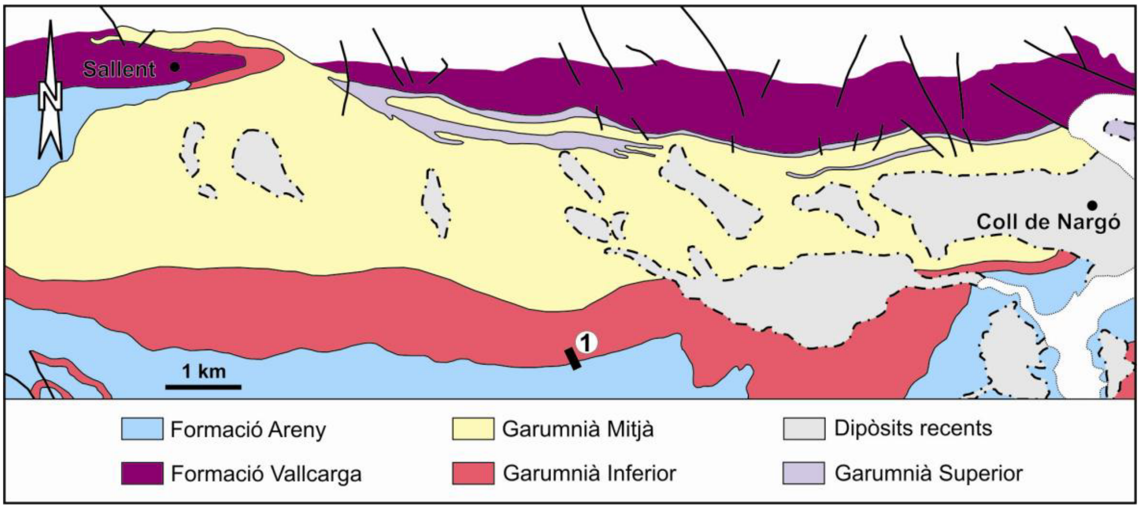


Figura 4. Mapa geològic de la Conca de Coll de Nargó amb la localització de la columna estratigràfica estudiada (1). Geologia adaptada de Vila et al. (2009).

Figure 4. *Geologic map of the Coll de Nargó Basin with location of the stratigraphic section studied (1). Geology adapted from Vila et al. (2009).*

El Garumnià inferior té una potència d'uns 60 m i petrològicament és equivalent a la Fm. La Posa definida per Liebau (1973) a la Conca de Tremp, formada per margues amb ostracodes, intercalacions de lignits i calcàries amb caròfits, les quals van proporcionar la flora de caròfits estudiada en la tesi (Fig. 5). Aquesta successió s'ha atribuït a una transició des de fàcies de *lagoon* a condicions lacustres d'aigua dolça (Willems 1985).

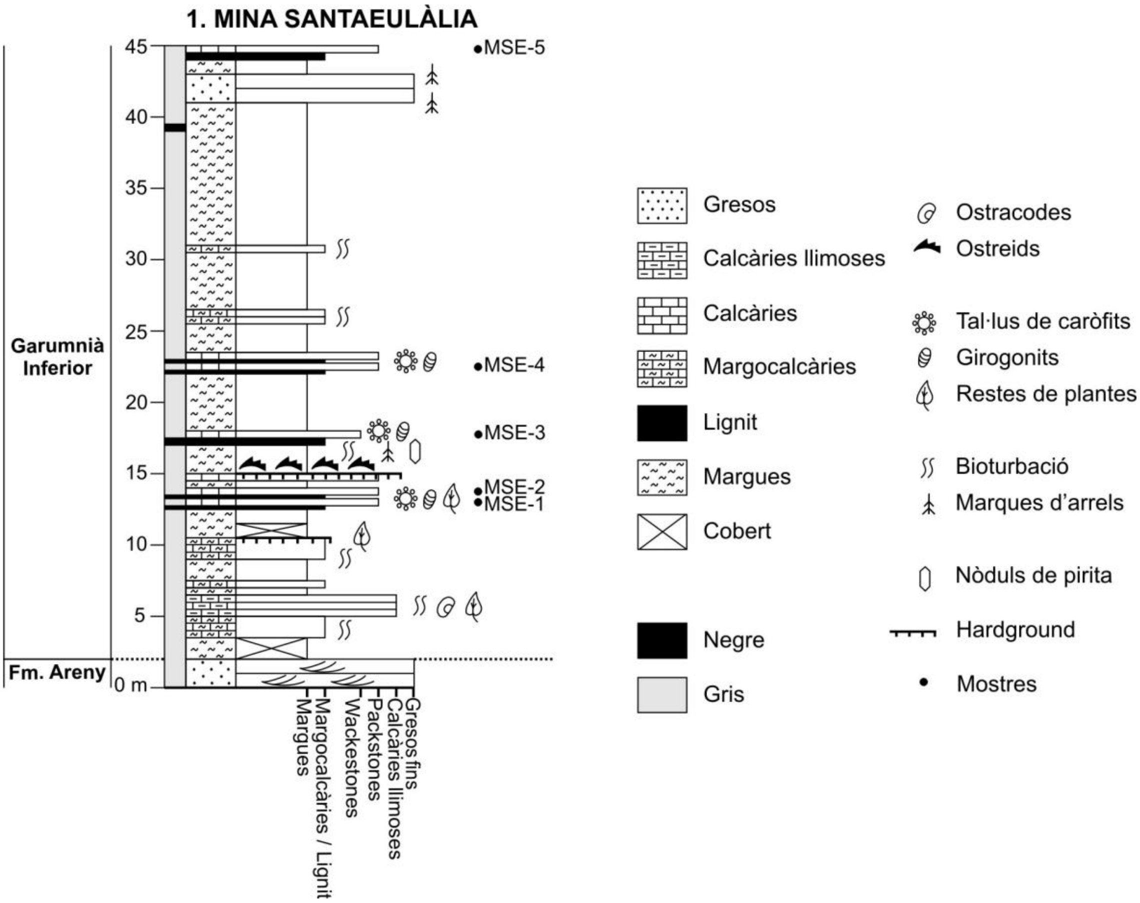


Figura 5. Columna estratigràfica estudiada al Garumnià Inferior a la Conca de Coll de Nargó amb la situació de les mostres estudiades. Veure Figura 4 per a la situació de la columna.

Figure 5. *Stratigraphic section of the Lower Garumnian studied in the Coll de Nargó Basin with location of samples studied. See Figure 4 for the location of this log.*

- Conca de Tremp

La Conca de Tremp forma un ampli sinclinal situat a la làmina d'encavalcament del Montsec (Fig. 6). Segons Caus i Gómez-Garrido (1989), el rebliment de la conca durant el Cretaci superior es divideix en set unitats litostratigràfiques, que van des de calcàries lacustres a margues de fàcies marines profundes. A partir del Campanià la seqüència deposicional comença a ser regressiva seguint una tendència d'est a oest. A la base dominen les calcarenites nerítiques somes i costaneres amb laminació encreuada de la Formació Gresos d'Areny (Mey et al. 1968), que contenen cap al sostre el rudista *Radiolites pulchellus*. Aquestes roques marines somes passen lateralment a margues i calcàries lacunars i lacustres intercalades a vegades amb lignits, els quals són coberts per capes roges fluvio-lacustres del Grup Tremp, anomenat regionalment Garumnià. La successió completa té un rang d'edat del Campanià superior al Tanetià. La base del Grup Tremp, formada majoritàriament per carbonats no marins va ser descrita per

Liebau (1973) i posteriorment per Cuevas (1992) com la Formació La Posa i ha sigut objecte d'estudi a la tesi.

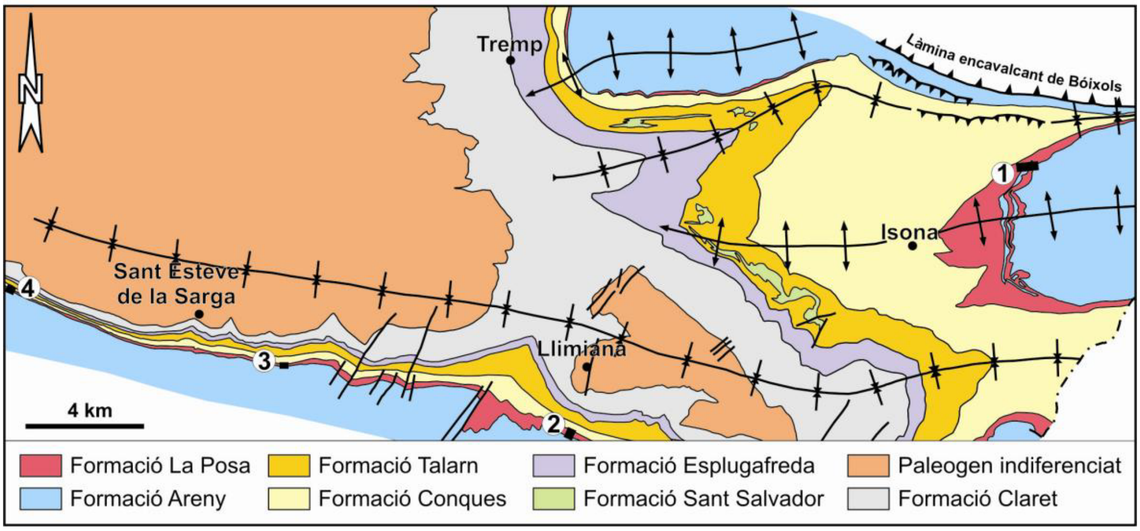


Figura 6. Mapa geològic de la Conca de Tremp amb la localització de les columnes estratigràfiques estudiades (1-4). Geologia adaptada de Cuevas (1992).

Figure 6. *Geologic map of the Tremp Basin with location of the stratigraphic sections studied (1-4). Geology adapted from Cuevas (1992).*

La base de la Fm. La Posa mostra dues intercalacions de gresos marins de la Fm. Areny, relacionades a la deposició en barres costaneres (Mey et al. 1968; Nagtegaal 1972). La sèrie suprajacent té 130 m de potència i està formada per una alternança de margues riques en matèria orgànica, lignits, calcàries amb caròfits i diverses intercalacions de margocalcàries, limolites i gresos. Cap al sostre de la formació hi ha una altra intercalació de gres marí amb abundants rudistes *Hippuritella castroi* (Fig. 7). Aquesta successió s'ha atribuït a la deposició en un ambient de pantà costaner connectat a llacs soms d'aigua dolça (Nagtegaal 1972).

- Conca d'Àger

La Conca d'Àger se situa a la làmina encavalcant de les Serres Marginals (Fig. 8), concretament a la unitat tectònica d'Àger-Montroig (Saula i Samsó 1996). El registre sedimentari durant el Cretaci superior a la conca va ser pràcticament continu des del Campanià al Tanetià i es diferencien tres unitats sedimentàries principals (Caus i Gómez-Garrido 1989). La unitat inferior és d'edat Campanià inferior – mitjà i correspon a la Formació Calcàries de Les Serres (Souquet 1967), formada per calcàries bioclàstiques marines. La segona unitat, d'edat Campanià mitjà – superior, consisteix en calcàries detrítiques alternants amb gresos (Formació Bona, Mey et al. 1968), corresponents a un sistema d'illa barrera (Mey et al. 1968; Lopez-Martínez et al. 1996), que conté dos horitzons de rudistes (*Hippurites radiosus* i *Radiolites pulchellus*).

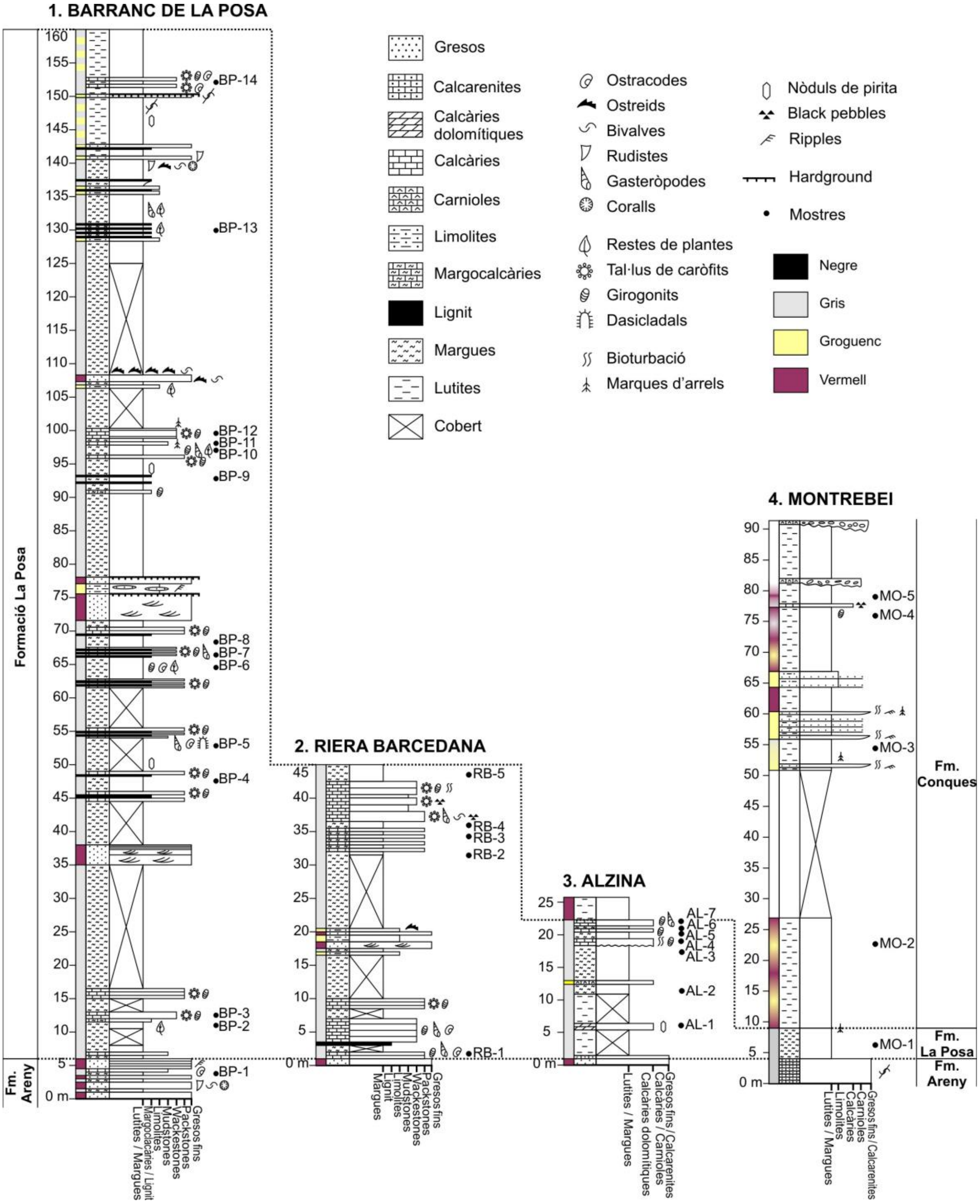


Figura 7. Columnes estratigràfiques estudiades de la Fm. La Posa a la Conca de Tremp amb la situació de les mostres estudiades. Veure Figura 6 per a la situació de les columnes.

Figure 7. *Stratigraphic sections of the La Posa Fm studied in the Tremp Basin with location of samples studied. See Figure 6 for the location of these logs.*

La unitat superior (Garumnià) és d'edat Campanià superior – Tanetià i està formada principalment per calcàries lacustres i capes roges fluvials. Colombo i Cuevas (1993) van descriure aquesta unitat com Grup Fontllonga, el qual van dividir en les formacions: La Maçana, Figuerola i Millà i el Complex Perauba, sent la primera formació, La Maçana, objecte d'estudi d'aquesta tesi.

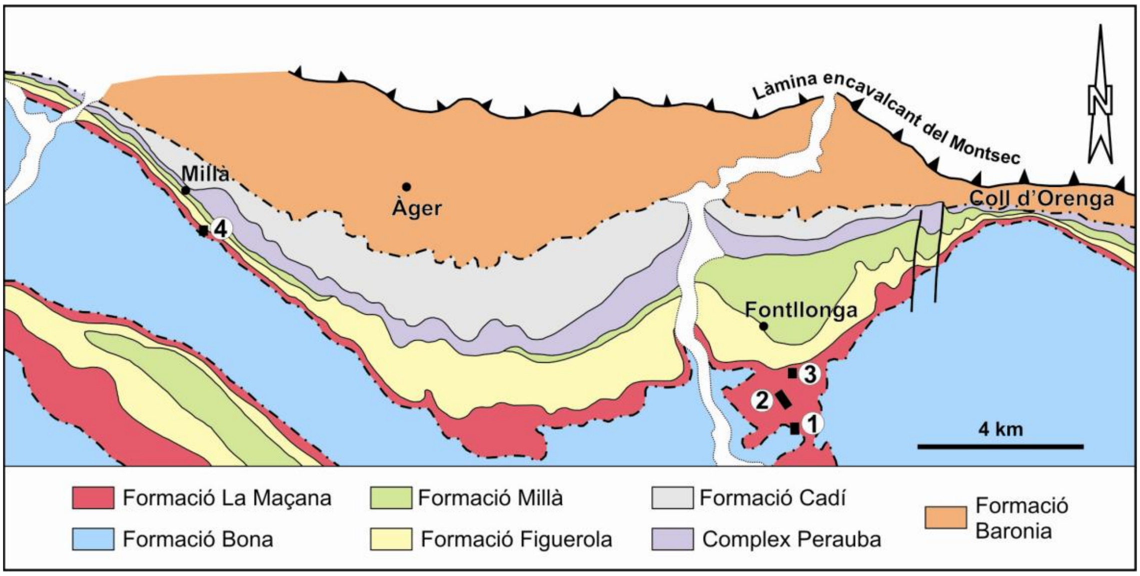


Figura 8. Mapa geològic de la Conca d'Àger amb la localització de les columnes estratigràfiques estudiades (1-4). Geologia adaptada de Colombo i Cuevas (1993).

Figure 8. *Geologic map of the Àger Basin with location of the stratigraphic sections studied (1-4). Geology adapted from Colombo and Cuevas (1993).*

La Fm. La Maçana té una potència d'uns 100 m i està constituïda per margues i intercalacions de calcàries amb caròfits amb un característic bandejat de wackestones blancs i packstones grisos, corresponents a cicles lacustres de baix ordre que van proporcionar la flora de caròfits estudiada (Fig. 9). Cap al sostre de la sèrie, les margues s'intercalen amb wackestones grisos amb bretxificació, crostes ferruginoses i petjades de dinosaure al sostre de les capes. Aquesta successió ha sigut atribuïda a la deposició en un ambient lacustre-palustre , amb zones protegides on es produïa la conservació de matèria orgànica sota condicions anòxiques (Colombo i Cuevas 1993). La bretxificació observada cap al sostre de la formació és de tipus edàfic i suggeriria la presència de vegetació en períodes de retracció lacustre o fluctuacions del nivell freàtic.

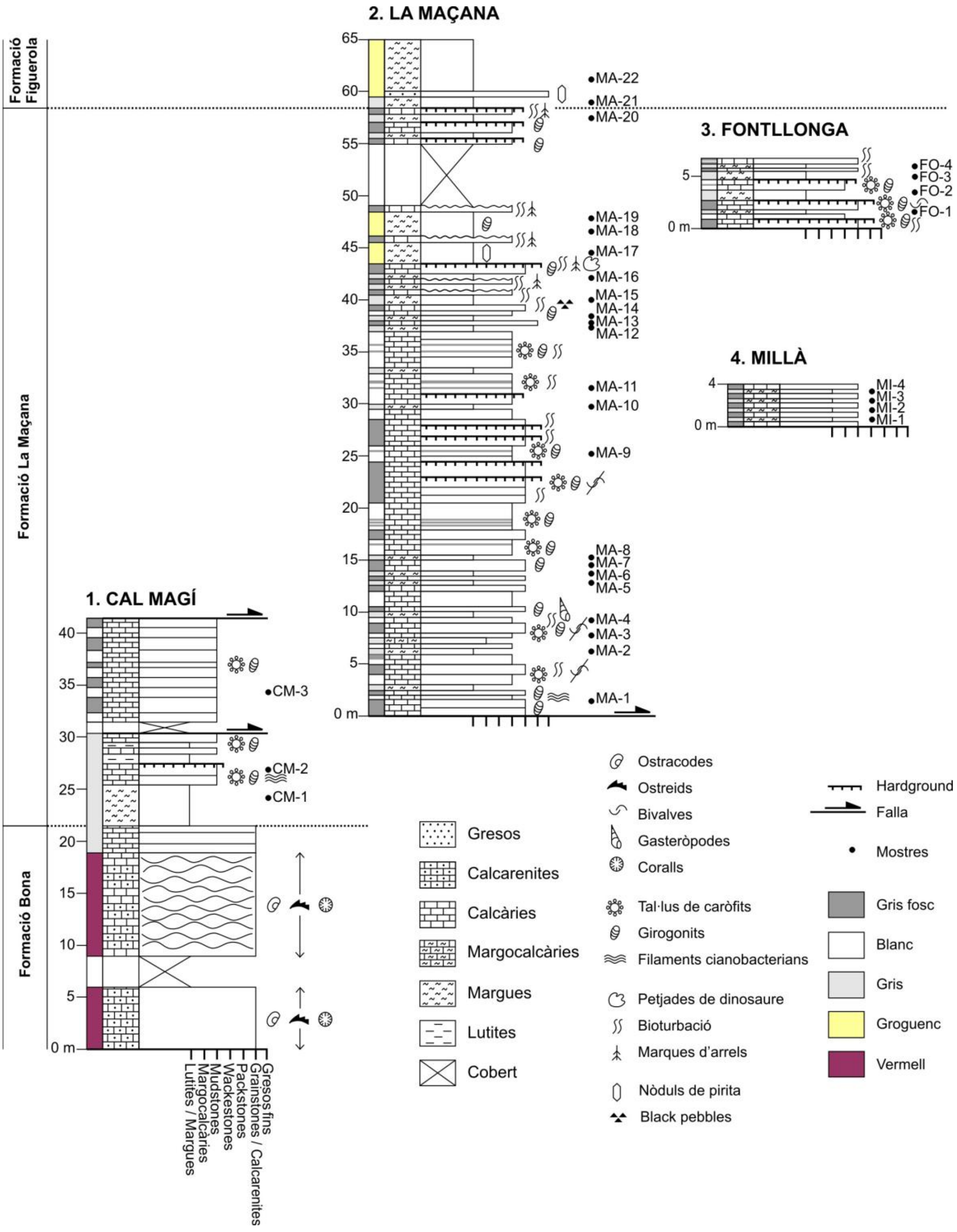


Figura 9. Columnes estratigràfiques estudiades de la Fm. La Maçana a la Conca d'Àger amb la situació de les mostres estudiades. Veure Figura 8 per a la situació de les columnes.

Figure 9. *Stratigraphic sections of the La Maçana Fm studied in the Àger Basin with location of samples studied. See Figure 8 for the location of these logs.*

METODOLOGIA

Treball de camp

Es van estudiar diverses columnes estratigràfiques representatives del depocentres de les quatres conques estudiades: Cal Sant, Font del Bullidor, Fumanya Sud i Mina Esquirol a la Conca de Vallcebre; Mina de Santaeulàlia a la Conca de Coll de Nargó; Barranc de la Posa, Riera Barcedana, Alzina i Montrebei a la Conca de Tremp; Cal Magí, La Maçana, Fontllonga i Millà a la Conca d'Àger. Aquestes columnes van ser analitzades des d'un punt de vista estratigràfic, sedimentològic, de microfàcies de carbonats i de la paleontologia i biostratigrafia de caròfits. Per aquest darrer motiu es va realitzar un mostreig sistemàtic en tots els nivells margosos d'una certa entitat, o quan aquests mancaven en els interbancs margosos. A més a més, es mostrejaren els nivells calcaris on s'observaren caròfits de *visu*, sota la lupa de camp (15×). Addicionalment, a la Conca de Vallcebre es van mostrejar diversos nivells de lignits, margues riques en matèria orgànica i margocalcàries per obtenir macro- i mesorestes de plantes vasculars i pol·len i es van descriure les tafofàcies amb plantes fòssils per determinar el paleoambient i la paleoecologia de les restes de plantes vasculars. En total es recolliren més de 100 mostres.

També es va participar en la co-direcció d'una excavació paleobotànica en col·laboració amb l'equip de Mesozoic de l'Institut Català de Paleontologia (Dr. Josep Marmi) durant el mes de juliol de 2010. L'excavació va tenir lloc en el Garumnià basal dels voltants de la població d'Isona. La intervenció paleontològica consistí en: neteja i habilitació de l'aflorament, aixecament de la columna estratigràfica d'Isona Sud, excavació de les restes fòssils per a la seva posterior documentació i protecció de l'aflorament. Provisionalment es van dipositar les restes fòssils trobades al Museu d'Isona i Conca Dellà, per al seu posterior estudi a la Universitat de Barcelona (caròfits), a l'Institut Català de Paleontologia i a l'Université de Lyon 1 (plantes vasculars).

Treball de laboratori

Es van rentar unes 70 mostres de marga amb garbells sobreposats d'1 mm, 0.5 mm i 0.2 mm de llum, després de deixar que el material es desfés en una solució d'aigua, peròxid d'hidrogen i carbonat sòdic durant 24-72 hores. Els garbellats es triaren sota la lupa binocular. La quantitat de sediment triada fou funció en cada mostra de l'abundància de material. Durant el triatge ja es feu una separació preliminar dels gèneres. La preparació del material comportà la separació provisional de les espècies determinades preliminarment i el seu posterior rentatge, si s'esqueia, amb el vibrador d'ultrasons. Es van tallar unes 30 mostres de roca paral·lela i perpendicularment a l'estratificació per preparar desenes de làmines primes, de 2.5 x 5 cm i unes 30 μm de gruix, per al seu posterior estudi de microfàcies. Les mostres de caròfits es troben dipositades a la col·lecció de caròfits del Departament d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona, i al Museu Geològic del Seminari Conciliar de Barcelona (MGSCB).

Les mostres per l'estudi de cutícules foliars i mesorestes de plantes (llavors i fruits) de la Conca de Vallcebre van ser preparades pel Dr. Bernard Gomez i el Dr. Josep Marmi a l'Université Lyon 1, seguint els procediments metodològics explicats a Marmi et al (2010, 2012) i Villalba-Breva et al. (2012). Les mostres de plantes vasculars es troben dipositades a la col·lecció de l'Institut Català de Paleontologia. També es van preparar 6 mostres de la Conca de Vallcebre per anàlisis palinològiques al Laboratori de Paleontologia de la Universitat de Barcelona per part del Sr. Alejandro Gallardo. Primer es van triturar les mostres, i després es va fer un tractament amb àcid clorhídric (HCl) i àcid fluorhídric (HF) tal com s'explica a Villalba-Breva et al. (2012). Posteriorment aquestes mostres palinològiques van ser estudiades per la Dra. María Teresa Fernández-Marrón a la Universidad Complutense de Madrid i es troben dipositades a la UEI de Paleontología, Instituto de Geología Económica de Madrid (CSIC-UCM).

Treball de gabinet

Les fructificacions de caròfits es van estudiar i mesurar sota un binocular Wild M5A, amb un micròmetre acoblat a l'ocular. Posteriorment es va emprar el microscopi electrònic de rastreig Quanta 200 dels Serveis Cientificotècnics de la Universitat de Barcelona per fotografiar el material. Finalment, es va treballar amb la bibliografia especialitzada i les col·leccions de referència de caròfits pertanyents al Dept. Estratigrafia, Paleontologia i Geociències Marines per determinar i descriure les espècies reconegudes. També es van realitzar dues estades a l'Institut des Sciences de l'Évolution de l'Université Montpellier II (juny de 2009 i octubre-novembre de 2010, finançada per AGAUR, Generalitat de Catalunya). Durant aquestes dues estades les determinacions taxonòmiques van ser revisades per la Dra. Monique Feist, especialista en caròfits del Cretaci superior,. D'una altra banda, les làmines primes es van estudiar amb un microscopi òptic Motic B3-220ASC. En un cas, es va poder reconstruir la planta sencera tridimensionalment. En altres casos, només es van obtenir dades dels tal·lus sense les fructificacions en connexió anatòmica. Aquestes restes es van fer servir amb finalitats paleoecològiques en combinació amb anàlisis tafonòmiques i sedimentològiques.

També es va realitzar una estada a l'Université de Lyon 1 (juny de 2011, finançada parcialment per la Facultat de Geologia, Universitat de Barcelona) supervisada pel Dr. B. Gomez i on es van estudiar les restes fòssils trobades a l'excavació paleobotànica d'Isona. Durant aquesta estada es van aprendre mètodes de preparació de cutícules foliars fòssils (descrits per Kerp i Krings 1999) i altres tipus de preservacions de restes vegetals (llavors). Les roques amb mesorestes de plantes fòssils es van macerar amb àcid clorhídric (HCl) i peròxid d'hidrogen (H_2O_2) per dissoldre la matriu de roca. Després les mostres en van rentar en aigua amb garbells sobreposats de 0.7 mm i 0.4 mm de llum. Els garbellats es triaren sota una lupa binocular i se separaren cutícules i llavors. Les cutícules triades es van macerar amb el reactiu Schulze (la durada del tractament va dependre del grau de la carbonització i la preservació dels fòssils). Posteriorment les cutícules es van separar en dues parts, separant la cara adaxial de l'abaxial amb un escalpel. Finalment, les cutícules i les llavors es van muntar en portaobjectes de vidre amb glicerina per al seu posterior estudi al microscopi. També es van descriure morfològicament les macrorestes vegetals a partir de representacions gràfiques dels caràcters foliars, realitzades amb cambra clara.

Biostratigrafia

Les associacions de caròfits estudiades es van assignar a les biozones definides per M. Feist a Riveline et al. (1996) i Hardenbol et al. (1998). Posteriorment es van calibrar amb les magnetozones definides per Oms et al. (2007) i Galbrun et al. (1993) a les conques de Vallcebre i Àger respectivament, i amb fòssils marins soms amb interès biostratigràfic, especialment foraminífers bentònics (Willems 1985; Hottinger i Caus 2009), a les conques de Coll de Nargó i Tremp. A més a més, la presència de nivells marins amb rudistes a les conques de Tremp i Àger (Pons 1977, 1982; Gallemí et al. 1983; Vicens et al. 2004), ha permès correlar les biozones de caròfits amb els horitzons de rudistes definits per J. Philip a Hardenbol et al. (1998).

Tafonomia i paleoecologia

Les associacions de caròfits del Garumnià basal del Pirineu Oriental es van caracteritzar paleoecològicament, en fàcies transicionals i estrictament d'aigua dolça, a partir de l'anàlisi deposicional, l'estudi de la tafonomia en microfàcies i la comparació amb altres indicadors paleobiològics (foraminífers, ostracodes i mol·luscs). A més a més, es va caracteritzar la paleoecologia de les plantes vasculars del Garumnià basal de la Conca de Vallcebre i la seva relació amb la resta de la biota (invertebrats e icnites de dinosaure).

RESULTATS

Sistemàtica

- Caròfits

a) Fructificacions

Les mostres de margues estudiades a la Conca d'Àger ha proporcionat la flora de caròfits més rica i diversa del Garumnià basal de la Conca Sud Pirinenca (Villalba-Breva i Martín-Closas en revisió), formada per un número important de girogonits i utricles (Figs. 10 i 11): *Feistiella malladae* (BATALLER 1945) nov. comb. VILLALBA-BREVA ET MARTÍN-CLOSAS, *Microchara cristata* GRAMBAST 1971, *M. parazensis* MASSIEUX 1987, *Dughiella obtusa* GRAMBAST ET GUTIÉRREZ 1977, *Peckichara cancellata* GRAMBAST 1971, *P. sertulata* GRAMBAST 1971, *Platychara caudata* GRAMBAST 1971 i *P. turbinata* GRAMBAST ET GUTIÉRREZ 1977, i *Clavator brachycerus* (GRAMBAST 1962) MARTÍN-CLOSAS 1996 (=*Septorella brachycera*).

A les altres conques d'estudi la flora de caròfits trobada és menys abundant. Així, a Vallcebre i Tremp està constituïda per girogonits de *Feistiella malladae*, *Microchara cristata*, *Peckichara cancellata*, *P. sertulata* i utricles de *Clavator brachycerus* (Villalba-Breva et al. 2012; Villalba-Breva i Martín-Closas en revisió) (Figs. 10 i 11). En molts casos, les associacions de caròfits obtingudes són monoespecífiques, formades per la porocaràcia *Feistiella malladae*.

b) Tal·lus

L'estudi de microfàcies de les mostres de roca de les conques de Vallcebre, Coll de Nargó, Tremp i Àger ha permès diferenciar tres tipus de tal·lus de caròfits. El primer correspon a *Munieria grambastii* BYSTRICKÝ 1976. Els tal·lus *Munieria* es caracteritzen en làmina prima per calcificar només a l'espai intercel·lular entre la cèl·lula nodal i les corticals. Com a resultat, les seccions tranversals dels entrenusos tenen forma de roda dentada amb crenulacions corresponents a la cara interna de les cèl·lules corticals i la cèl·lula nodal visible dins. Es per això que alguns autors, com Feist et al. (2003, 2005) han relacionat el gènere *Munieria* amb les dasicladals, basant-se en l'aspecte general de la planta, però altres autors, com Schudack (1993) i Martín-Closas (2000) l'atribueixen als caròfits basant-se en les característiques de la corticació. A banda, en totes les mostres estudiades, els tal·lus de l'espècie *M. grambastii* es troben recristal·litzats en calcita espàtica, suggerint que la mineralogia original era aragonita en lloc de calcita pobra en magnesi. A més a més, les seccions transversals en làmina prima d'aquest tal·lus presenten una forma irregular, generalment triangular, amb la cèl·lula internodal, no deformada, al mig del tal·lus o desplaçada a un costat del triangle. Aquesta peculiar preservació probablement es deguda a una deformació diagenètica.

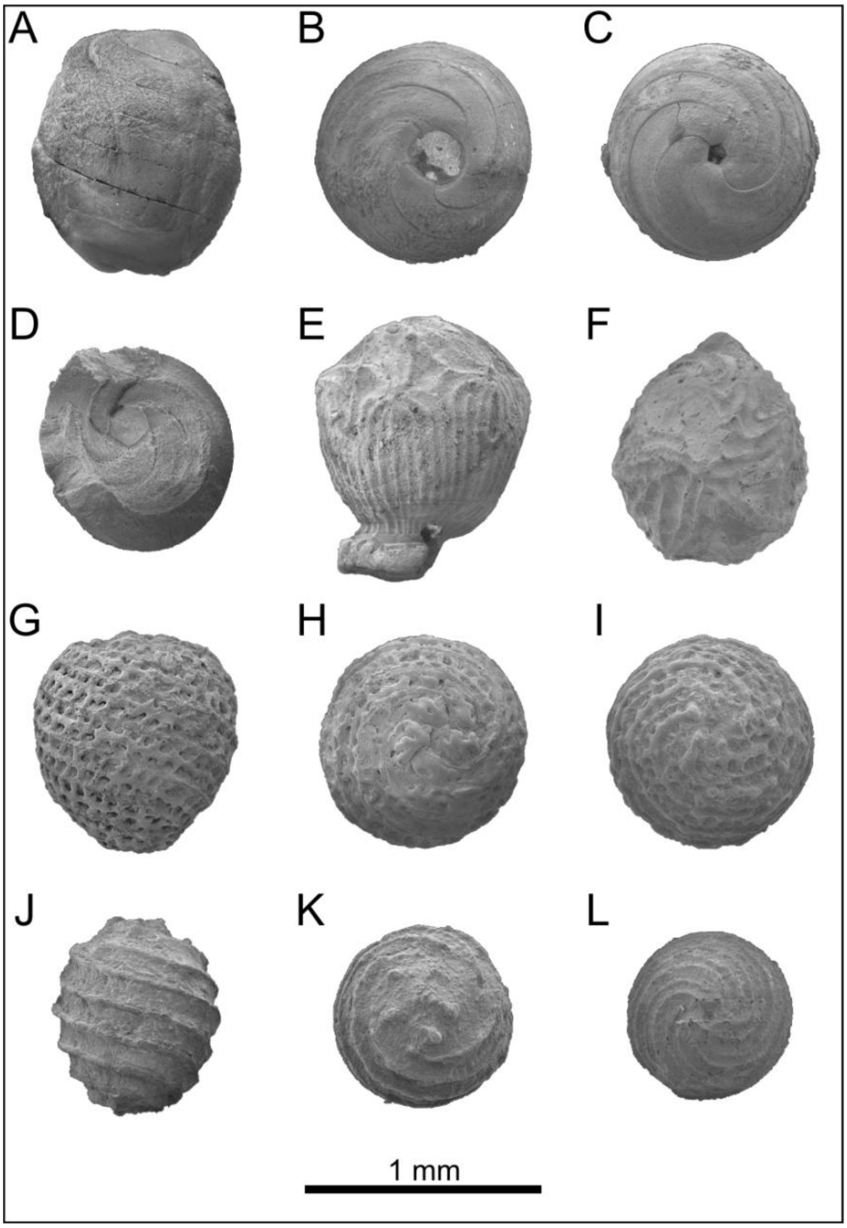


Figura 10. Caròfits del Cretaci superior de les Fms. La Maçana i La Posa. **(A)** a **(D)** *Feistiella malladae*, mostra BP-8, sèrie Barranc de la Posa; **(A)** vista lateral, **(B)** àpex, **(C)** base, **(D)** base amb la placa basal vista des de dins. **(E)** i **(F)** *Clavator brachycerus*, mostra AL-3, sèrie Alzina; **(E)** vista lateral, **(F)** àpex. **(G)** a **(I)** *Peckichara cancellata*, mostra MA-2, sèrie La Maçana; **(G)** vista lateral, **(H)** àpex, **(I)** base. **(J)** a **(L)** *Peckichara sertulata*, mostra AL-2, sèrie Alzina; **(J)** vista lateral, **(K)** àpex, **(L)** base.

Figure 10. *Charophytes from the Late Cretaceous of La Maçana and La Posa Fms* ***a*** *to* ***d*** Feistiella malladae*, sample BP-8, Barranc de la Posa section;* ***(A)*** *lateral view,* ***(B)*** *apex,* ***(C)*** *base,* ***(D)*** *base with basal plate as seen from inside.* ***(E)*** *and* ***(F)*** Clavator brachycerus*, sample AL-3, Alzina section;* ***(E)*** *lateral view,* ***(F)*** *apex.* ***(G)*** *to* ***(I)*** Peckichara cancellata*, sample MA-2, La Maçana section;* ***(G)*** *lateral view,* ***(H)*** *apex,* ***(I)*** *base.* ***(J)*** *to* ***(L)*** Peckichara sertulata*, sample AL-2, Alzina section;* ***(J)*** *lateral view,* ***(K)*** *apex,* ***(L)*** *base.*

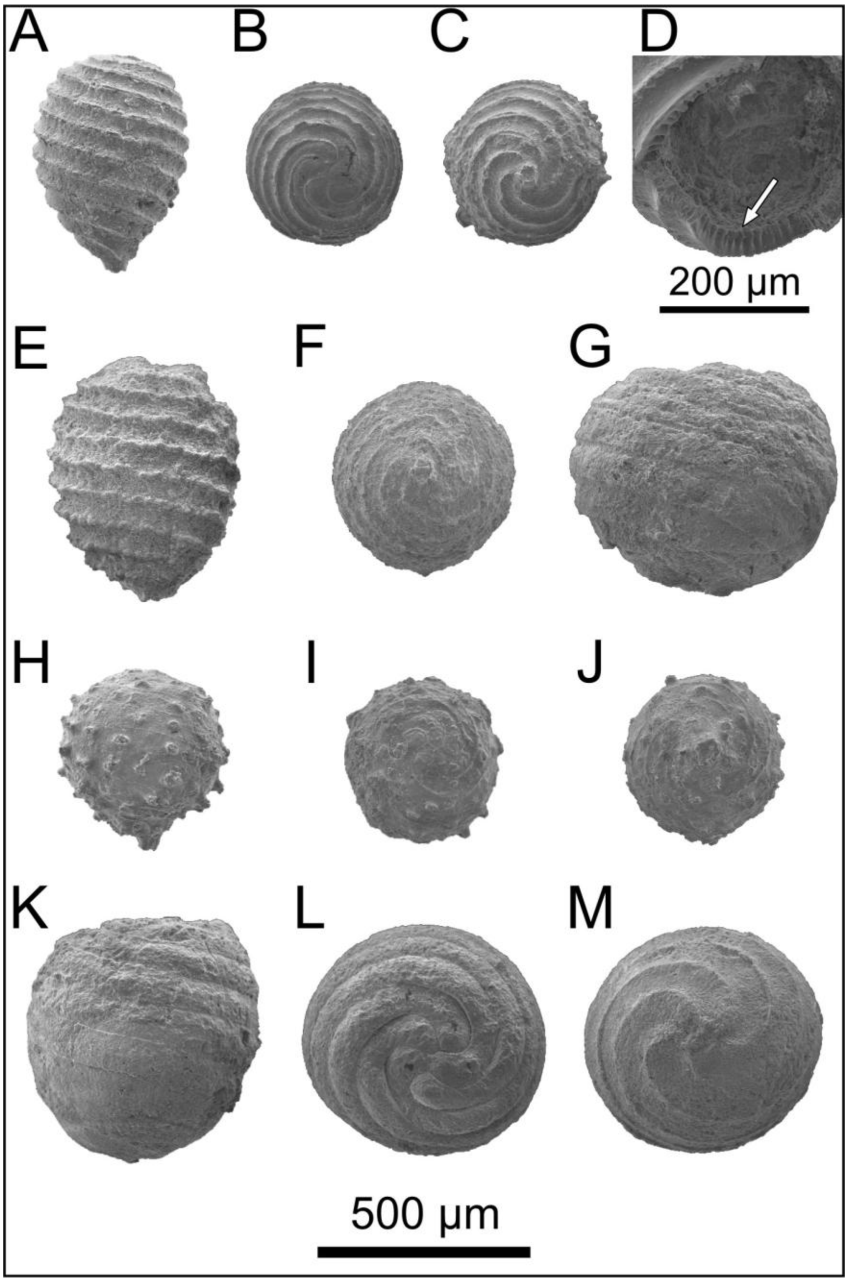


Figura 11. Caròfits del Cretaci superior de les Fms. La Maçana i La Posa (continuació). **(A)** a **(D)** *Microchara parazensis*, mostra MA-2, sèrie La Maçana; **(A)** vista lateral, **(B)** àpex, **(C)** base, **(D)** detall de la sutura de les cèl·lules amb ondulacions (*fletxa*). **(E)** i **(F)** *Microchara cristata*, mostra MA-16, sèrie La Maçana; **(E)** vista lateral, **(F)** base. **(G)** vista lateral de *Platychara turbinata*, mostra MA-2, sèrie La Maçana. **(H)** a **(J)** *Platychara caudata*, mostra MA-2, sèrie La Maçana; **(H)** vista lateral, **(I)** àpex, **(J)** base. **(K)** a **(M)** *Dughiella obtusa*, mostra MA-2, sèrie La Maçana; **(K)** vista lateral, **(L)** àpex, **(M)** base.

Figure 11. *Charophytes from the Late Cretaceous of La Maçana and La Posa Fms (continued).* ***(A)*** *to* ***(D)*** Microchara parazensis*, sample MA-2, La Maçana section;* ***(A)*** *lateral view,* ***(B)*** *apex,* ***(C)*** *base,* ***(D)*** *detail of cell-sutures with undulations (arrow).* ***(E)*** *and* ***(F)*** Microchara cristata*, sample MA-16, La Maçana section;* ***(E)*** *lateral view,* ***(F)*** *base.* ***(G)*** *lateral view of* Platychara turbinata*, sample MA-2, La Maçana section.* ***(H)*** *to* ***(J)*** Platychara caudata*, sample MA-2, La Maçana section;* ***(H)*** *lateral view,* ***(I)*** *apex,* ***(J)*** *base.* ***(K)*** *to* ***(M)*** Dughiella obtusa*, sample MA-2, La Maçana section;* ***(K)*** *lateral view,* ***(L)*** *apex,* ***(M)*** *base.*

El segon tal·lus observat pertany al morfogènere *Charaxis* Harris 1939. Aquests tal·lus tenen una corticació isòstica, són molt grans (de diversos centímetres de llarg i fins a 3 mm d'ample) i es reconeixen al camp fàcilment, inclús sense lupa, degut a la gran mida de les seves restes. No obstant el grau d'articulació de les restes és baix i en cap cas s'ha pogut identificar nusos ni verticils. Els entrenusos estan calcificats només a l'àrea intercel·lular entre la cèl·lula nodal i les corticals, i en làmina prima sovint es troben acumulacions d'aquests fragments intercel·lulars, de forma triangular, corresponents a tal·lus col·lapsats.

El tercer tipus de tal·lus correspon al morfogènere *Clavatoraxis* Martín-Closas et Diéguez 1998, caracteritzat per presentar rosetes aciculars en les cèl·lules corticals. La conservació excepcional d'aquests tal·lus va permetre descriure una nova espècie, *Clavatoraxis microcharophorus* Villalba-Breva et Martín-Closas 2011 (Fig. 12). Aquest resultat representa el primer cop que es pot reconstruir la planta sencera d'una caràcia fòssil a partir de diferents seccions en làmina prima (Villalba-Breva i Martín-Closas 2011) (Fig. 13). La nova espècie es caracteritzava per presentar tal·lus isòstics relativament petits amb coixinets aciculars en les cèl·lules corticals i coixinets bracteals a les branques, els quals portaven girogonits de *Microchara* sp. (Figs. 12A i 13). Cada girogonit estava embolcallat per una bràctea expandida, formant una veritable túnica estructural (Figs. 12B i 13).

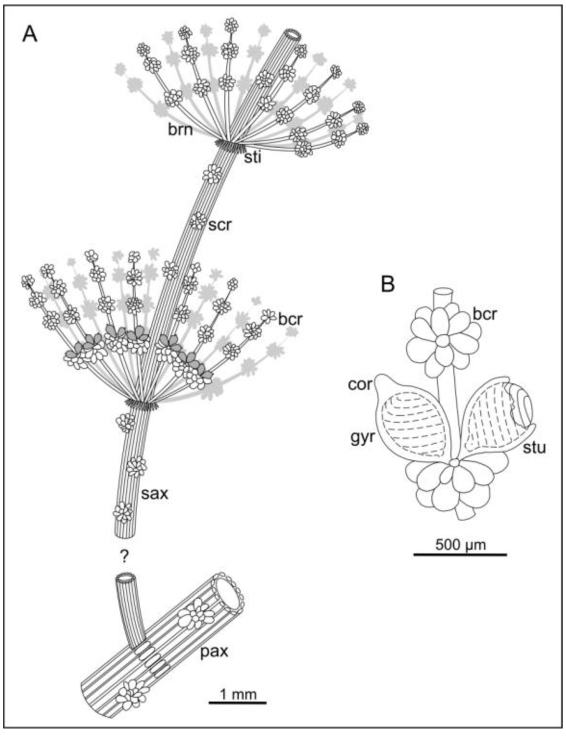


Figura 12. *Clavatoraxis microcharophorus* sp. nov. **(A)** Reconstrucció de la planta fòssil sencera. **(B)** Detall d'una branca amb dos girogonits en un coixinet o roseta bracteal, un d'ells amb una corónula (no observada). bcr, roseta bracteal; brn, branca; cor, corónula; gyr, girogonit; pax, eix primari; sax, eix secundari; scr, roseta acicular; sti, estipuloids; stu, túnica estructural.

Figure 12. Clavatoraxis microcharophorus *sp. nov.* ***(A)*** *Reconstruction o f the whole fossil plant.* ***(B)*** *Detail of a branchlet with insertion of two gyrogonites in a bract-cell rosette, one of them with coronula (not observed). bcr, bract-cell rosette; brn, branchlet; cor, coronula; gyr, gyrogonite; pax, primary axis; sax secondary axis; scr, spine-cell rosette; sti, stipulodes; stu, structural tunica.*

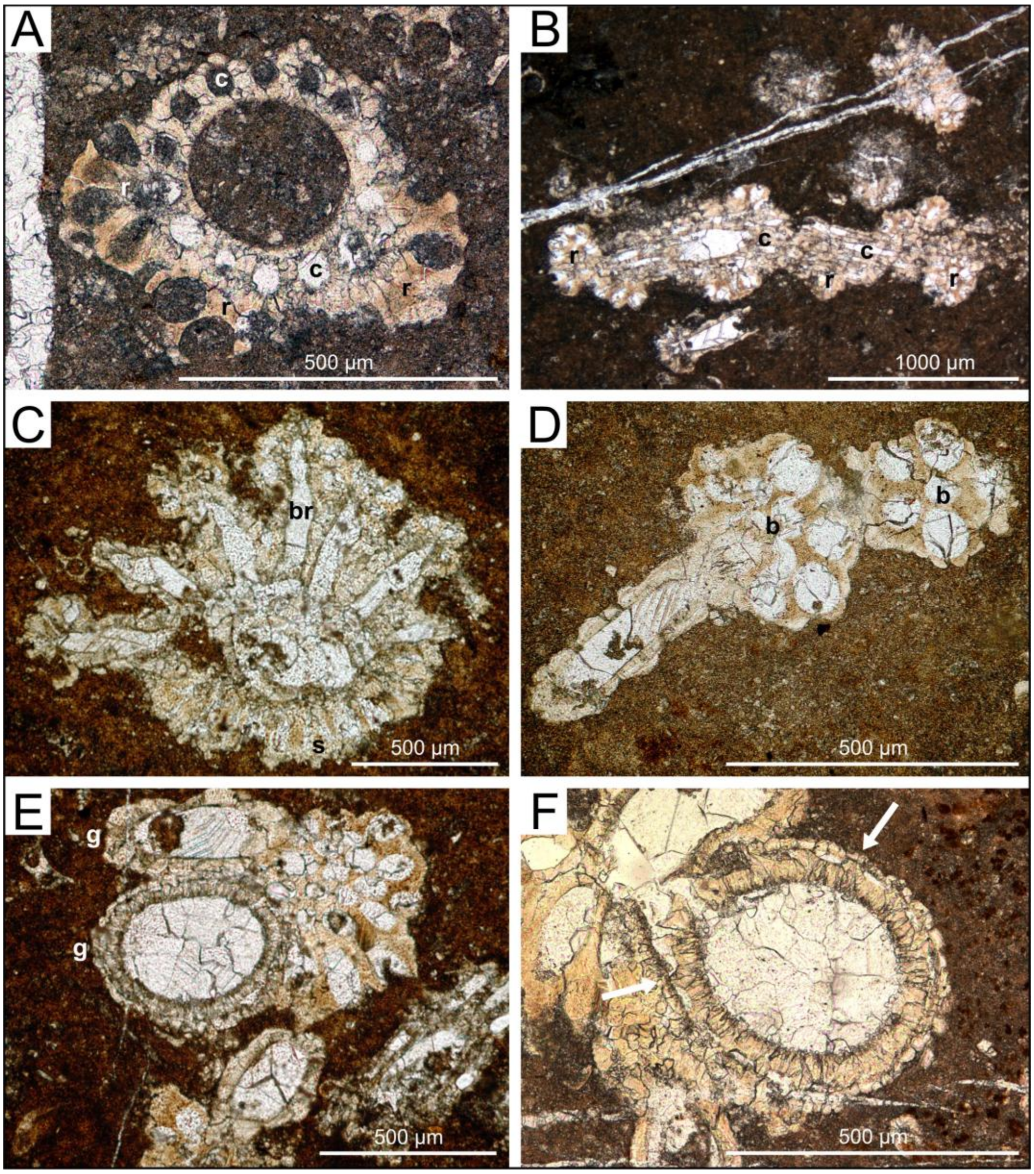


Figura 13. *Clavatoraxis microcharophorus* sp. nov. **(A)** Secció transversal d'un eix secundari mostrant les cèl·lules corticals (c) i les rosetes aciculars (r); làmina prima 76960. **(B)** Secció tangencial d'un eix secundari mostrant les cèl·lules corticals (c) recobert per rosetes aciculars (r); làmina prima 76961. **(C)** Secció quasi transversal d'un nus mostrant la disposició dels estipuloids (s) i les branques (br); làmina prima 76959. **(D)** Secció longitudinal d'una branca mostrant la disposició de dues rosetes bracteals (b); làmina prima 76962. **(E)** Secció tangencial d'una roseta bracteal amb dos girogonits (g); làmina prima 76962. **(F)** Secció longitudinal d'un girogonit ornamentat amb una cresta intercel·lular (*fletxes*) en una roseta bracteal i embolcallat per una túnica; làmina prima 76961. Totes les làmines primes pertanyen a la mostra FS-8.

Figure 13. *Clavatoraxis microcharophorus* sp. nov. **(A)** Transversal section through secondary axis showing cortical cells (c) and spine-cell rosettes (r); thin section 76960. **(B)** Tangential section through secondary axis showing cortical cells (c) covered by spine-cell rosettes (r); thin section 76961. **(C)** Near-transversal section though a node showing arrangement of stipulodes (s) and branchlets (br); thin section 76959. **(D)** Longitudinal section of a branchlet showing arrangement of two bract-cell rosettes (b); thin section 76962. **(E)** Tangential section through a bract-cell rosette bearing two gyrogonites (g); thin section 76962. **(F)** Longitudinal section through a gyrogonite ornamented with a mid-cellular crest (*arrows*) attached to a bract-cell rosette and covered by a tunica; thin section 76961. All thin sections belong to sample FS-8.

- Plantes vasculars

L'associació de macrorestes de plantes vasculars del Garumnià basal de Vallcebre i Coll de Nargó presenten característiques molt semblants. Ambdues estan formades majoritàriament per les tiges desarticulades de la conífera queirolepidiàcia *Frenelopsis* (SCHENK 1869) WATSON 1977. Les anàlisis tafonòmiques indiquen que aquesta planta és la precursora de la torba que va donar lloc a la major part dels lignits explotats fins fa poc temps a les mines de les conques de Vallcebre i Coll de Nargó (Villalba-Breva et al. 2012). A part d'aquestes coníferes, també són importants les restes de la palmera *Sabalites longirhachis* (UNGER) J. KVAČEK ET HERMAN, que ha pogut ser reconstruïda tridimensionalment gràcies a la conservació *in situ* de les seves soques amb aparells radiculars en connexió anatòmica, associades a restes parautòctones dels seus troncs i fulles (Marmi et al 2010) (Fig. 14). A la Conca de Vallcebre, també s'han trobat altres macrorestes de plantes menys abundants, com una fronda de falguera, una fulla de cicadal i diversos fragments de fulles de monocotiledònia amb nervadura paral·lela, similars a fulles de Pandanàcies (Villalba-Breva et al. 2012) (Figs. 15A-D). Així mateix, també es va descriure la nova llavor d'angiosperma *Bergacarpon viladricii* MARMI, GOMEZ, VILLALBA-BREVA ET MARTÍN-CLOSAS 2012 a la Conca de Vallcebre (Marmi et al. 2012) (Fig. 15E i F). La presència d'una llavor amb micròpil portador d'opercle i amb un desenvolupament ortòtrop (àtrop) suggereixen que aquestes llavors podrien haver sigut produïdes per una monocotiledònia, probablement un commelínid.

D'altra banda, a la conca de Tremp la flora és més diversa que la flora de Vallcebre i Coll de Nargó. Tot i que hi ha taxons que apareixen en les tres conques, com les coníferes *Frenelopsis* sp.i les palmeres *Sabalites longirhachis*, la flora d'Isona inclou altres coníferes i una gran varietat en angiospermes, especialment en fulles de dicotiledònies (Fig. 16). Les macrorestes de plantes trobades corresponen majoritàriament a fulles, generalment molt fragmentades, amb una mida normalment de 2 a 3 cm, i preservades com a compressions i impressions, amb disposició aleatòria en el gruix de la capa. També s'han trobat llavors d'angiosperma que presenten similituds amb la llavor *Bergacarpon viladricii* determinada a Vallcebre, però són necessaris estudis més detallats per arribar a uns resultats més concloents.

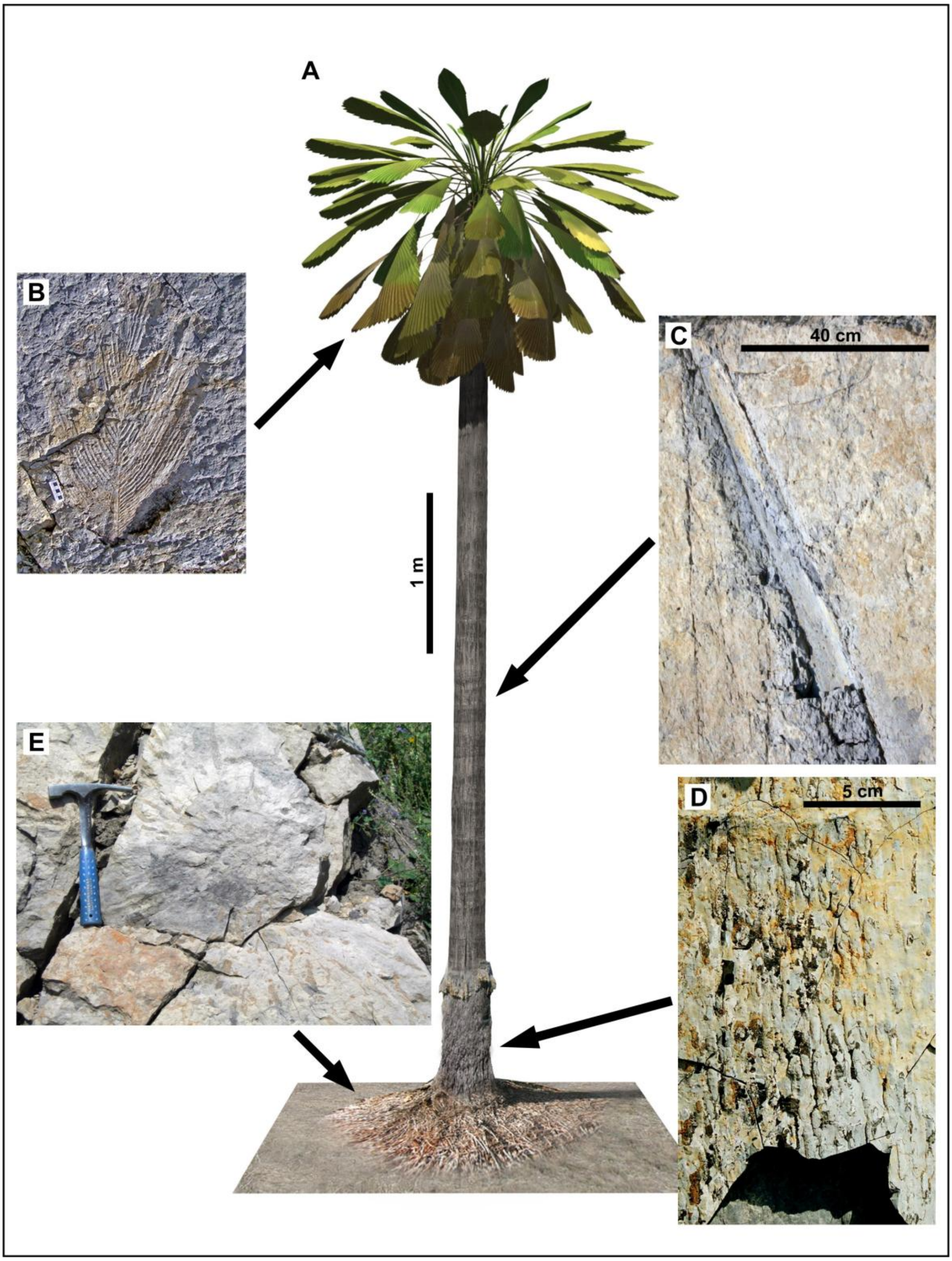


Figura 14. *Sabalites longirhachis*. **(A)** Reconstrucció hipotètica de la palmera. **(B)** Fulla completa. Escala gràfica = 5 cm. **(C)** Impressió d'un tronc. **(D)** Motlle extern d'un tros de tronc amb marques d'arrels adventícies. **(E)** Estructura d'arrelament de tipus escombra.

Figure 14. Sabalites longirhachis. ***(A)*** *Hypothetical reconstruction of the palm tree.* ***(B)*** *Complete leaf lamina. Scale bar = 5 cm.* ***(C)*** *Impression of a log.* ***(D)*** *External cast of a log portion showing marks of adventitious roots.* ***(E)*** *Brush-like rooting structure.*

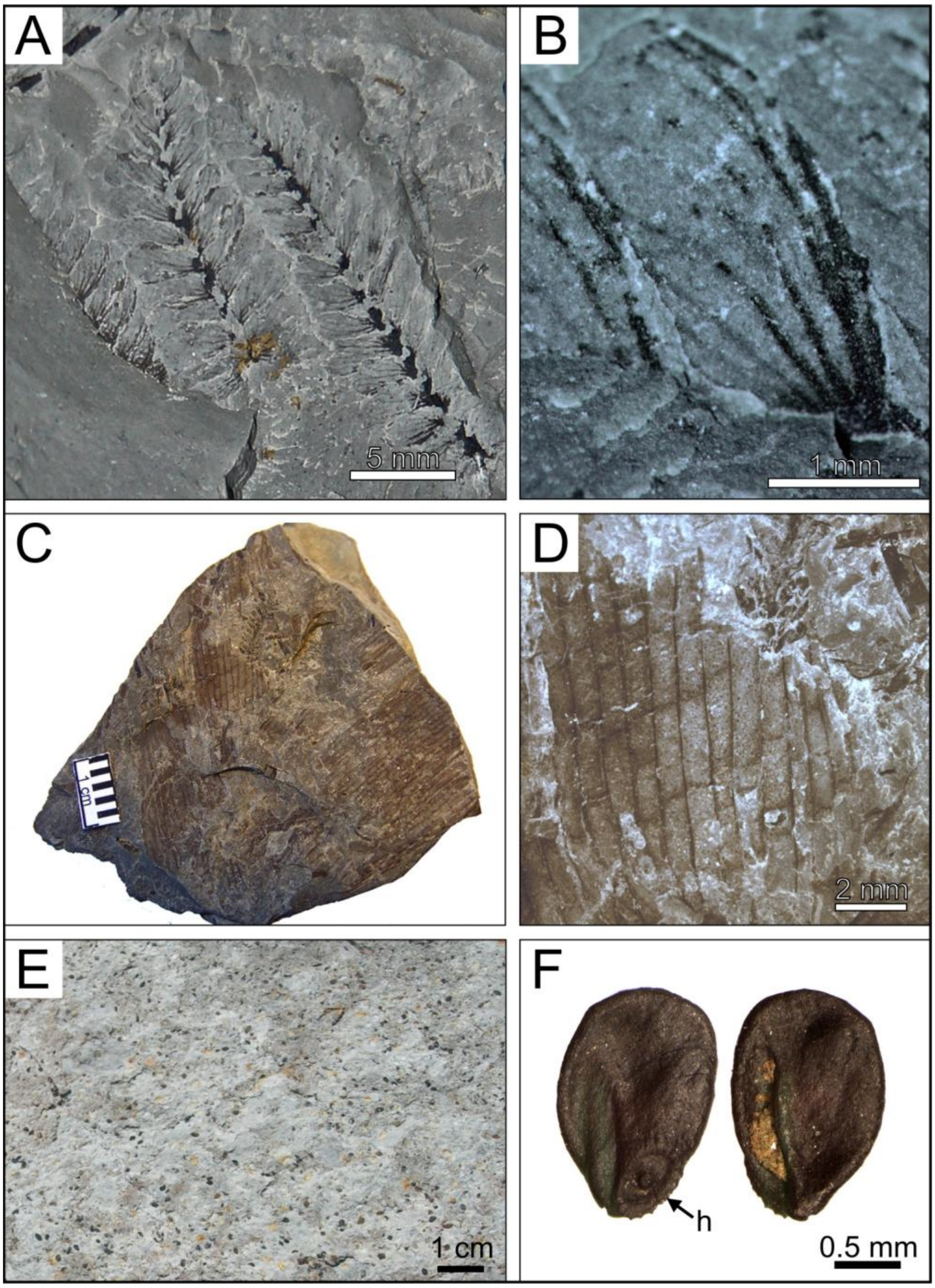


Figura 15. Plantes vasculars del Maastrichtià inferior de la Conca de Vallcebre. **(A)** i **(B)** Fulla de cicadal; **(A)** vista general d'un exemplar amb tres pinnes, **(B)** detall d'una pínnula mostrant la nervadura. **(C)** i **(D)** Fulles de monocotiledònies; **(C)** fragments de fulles, **(D)** detall de **(C)** mostrant la nervadura. **(E)** i **(F)** Llavors d'angiosperma; **(E)** detall de la superfície de la roca amb l'acumulació de llavors, **(F)** holotipus de *Bergacarpon viladricii* gen. et sp. nov. fotografiat pels dos costats (h = hílum).

Figure 15. *Vascular plants from the Early Maastrichtian of the Vallcebre Basin.* ***(A)*** *and* ***(B)*** *Cycadalean foliage;* ***(A)*** *general view of specimen showing three pinnae,* ***(B)*** *detail of a pinnule showing venation.* ***(C)*** *and* ***(D)*** *Monocot foliage;* ***(C)*** *fragments of leaves,* ***(D)*** *detail of* ***(C)*** *showing venation.* ***(E)*** *and* ***(F)*** *Angiosperm seeds;* ***(E)*** *detail of the rock surface showing the accumulation of seeds,* ***(F)*** *holotype of* Bergacarpon viladricii *gen. et sp. nov. photographed on both sides (h = hilum).*

Finalment, l'anàlisi palinològica duta a terme al Garumnià basal de la Conca de Vallcebre mostra que tres de les mostres estudiades van ser molt productives i representen tres fàcies diferents (Villalba-Breva et al. 2012) (Figs. 17 i 18). La primera mostra (ME-1) prové d'una margocalcària amb llavors d'angiosperma just per sota del primer nivell de carbó i estava formada majoritàriament per bialats (93%). Les espores de licòfits i falgueres eren minoritaris (5%). Finalment, el pol·len d'angiosperma només representava el 2%. L'associació d'una mostra provinent d'una marga orgànica (FS-17) és la més diversa. Contenia abundants espores (56%) de briòfits, licòfits i falgueres, sent les espècies de *Cyathidites*, *Chomotriletes*, *Klukisporites* i *Leiotriletes* dominants. El pol·len de coníferes (bialats) i cicadals era minoritari (7%). El pol·len d'angiosperma només representava el 4% i incloïa dos taxons atribuïts a palmera, un d'ells relacionat amb la palmera de manglar *Nypa*. Finalment el 33% de l'associació corresponia a oòspores d'algues verdes (*Oedogonium cretaceum* and *Ovoidites spriggi*). La tercera mostra (FS-23) provenia d'un nivell de lignit amb marques d'arrels i era molt poc diversa. Aquesta consistia quasi exclusivament (95%) en bialats, especialment *Pinuspollenites ruginosa*. Les espores de falgueres comprenien el 3% i la resta de l'associació eren oòspores d'algues d'aigua dolça. Altres mostres també van proporcionar palinomorfs, però eren molts escassos i estaven mal preservats per poder fer una determinació.

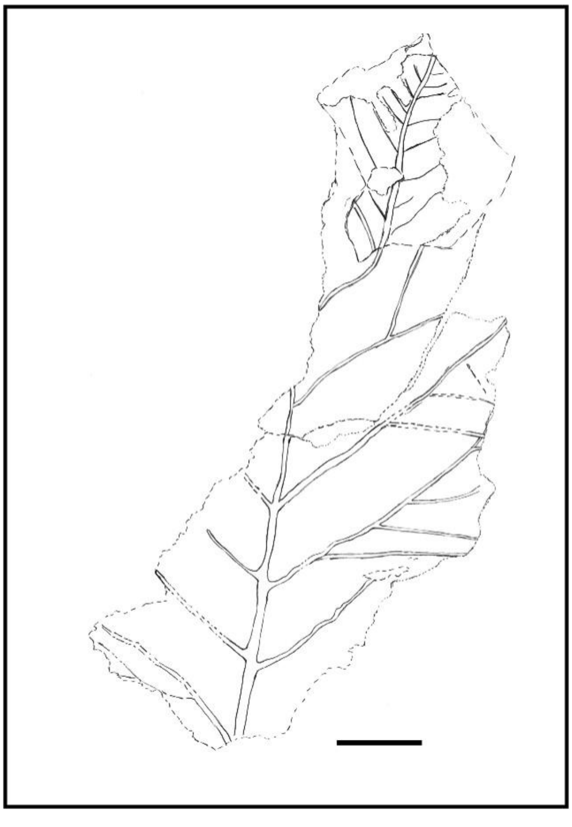


Figura 16. Dibuix amb cambra clara d'un morfotipus de fulla del Garumnià basal d'Isona (Conca de Tremp). Escala gràfica = 1 cm.

Figure 16. *Line drawing of a morphotype of leave from the basal Garumnian of Isona (Tremp Basin). Scale bar = 1 cm.*

Biostratigrafia

L'estudi dels caròfits del Garumnià basal (Fm. La Maçana) de la Conca d'Àger proporciona les primeres dades sobre la biostratigrafia d'aquesta conca. Les datacions realitzades anteriorment a les conques de Vallcebre, Coll de Nargó i Tremp s'han revisat a partir de dades pròpies i calibrat amb dades magnetostratigràfiques d'altres autors (Villalba-Breva et al. 2012; Villalba-Breva i Martín-Closas en revisió). L'associació de caròfits trobada a Àger està dominada per *Clavator brachycerus* i *Peckichara cancellata*. L'espècie *P. cancellata* és important biostratigràficament i representa l'espècie índex de la biozona de caròfits homònima. D'acord amb Riveline et al. (1996), aquesta biozona està calibrada a Àger amb els magnetocrons C32r a C32n (part mitja i superior del Campanià superior). Aquests resultats són compatibles amb l'edat inferida per la Fm. La Maçana en base a l'edat de la formació infrajacent segons Caus i Gómez-Garrido (1989) i Vicens et al. (2004) en base a foraminífers (*C. lecalvezae* i *I. decussatus*) i rudistes (*Hippurites radiosus* i *Radiolites pulchellus*) respectivament.

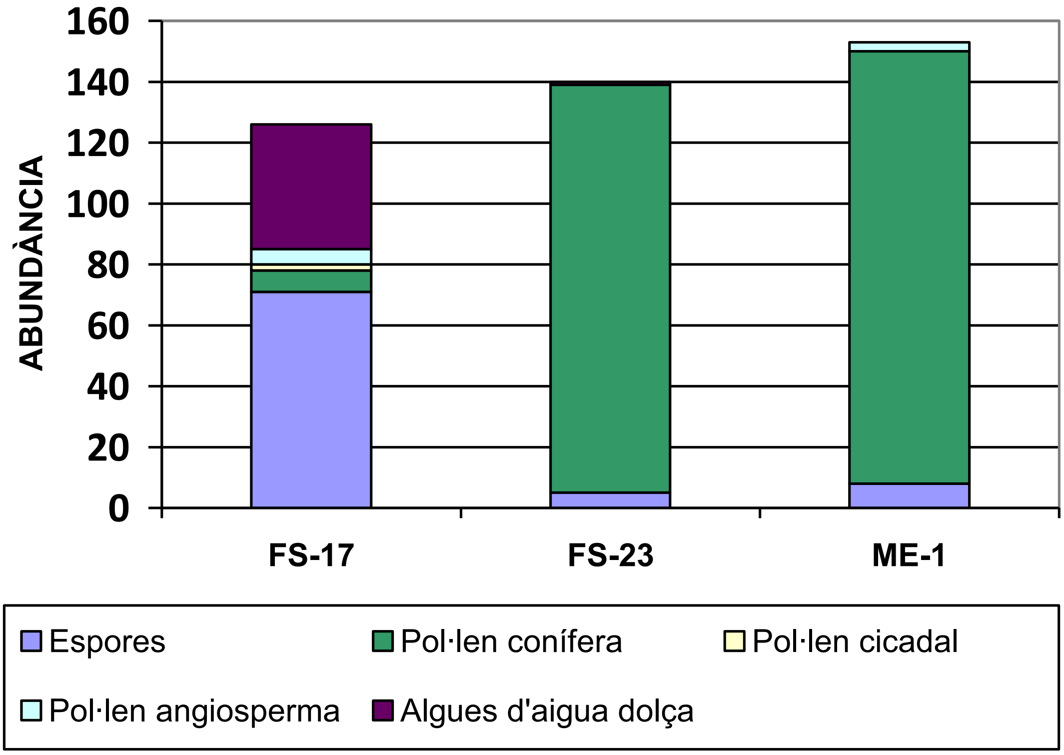


Figura 17. Diagrama que mosta l'abundància dels grups morfològics de palinomorfs més representatius de les mostres estudiades.

***Figure 17.** Diagram showing the abundance of the most representative morphological groups of palynomorphs in the studied samples.*

L'associació de caròfits del Garumnià basal (Garumnià Gris) de la Conca de Vallcebre està formada per girogonits de *Feistiella malladae*, *Peckichara cancellata* i *Microchara cristata*. Des d'un punt de vista biostratigràfic, l'associació està dominada per *P. cancellata*. Com a la Conca d'Àger, aquesta associació correspon a la biozona Peckichara cancellata. Noves dades magnetostratigràfiques a Vallcebre, obtingudes per Oms et al. (2007) permeten ampliar el sostre de la biozona fins al menys el magnetocron C31r, d'edat Maastrichtià inferior basal (Villalba-Breva et al. 2012). Aquests resultats són compatibles amb les dades biostratigràfiques obtingudes per Feist i Colombo (1983).

A la Conca de Tremp l'associació de caròfits del Garumnià basal (Fm. La Posa) està formada per girogonits de *Feistiella malladae*, *Peckichara sertulata* i *Microchara cristata*, i utricles de *Clavator brachycerus*. Les dues espècies *M. cristata* i *C. brachycerus* tenen un rang d'edat ampli, del Campanià mitjà al Maastrichtià superior, que comprèn les biozones Peckichara pectinata, Peckichara cancellata, Septorella ultima i Microchara cristata de Riveline et al. (1996). Tanmateix, aquest rang es pot limitar al Maastrichtià per l'aparició d'associacions homogènies de *P. sertulata* (Villalba-Breva i Martín-Closas en revisió), les quals es desenvolupen únicament a la biozona Septorella ultima, d'edat Maastrichtià inferior – mitjà (Riveline et al. 1996). A la sèrie del Barranc de la Posa, aquesta biozona es pot correlacionar amb la primera aparició del rudista *Hippuritella castroi* d'edat Maastrichtià inferior, definida per J. Philip a Hardenbol et al. (1998). Aquests resultats són compatibles amb dades biostratigràfiques obtingudes per Feist i Colombo (1983), Gallemí et al. (1983) i Caus i Gómez-Garrido (1989). No obstant això, els resultats presentats no concorden amb l'edat obtinguda a partir d'interpretacions d'estratigrafia seqüencial per Ardèvol et al. (2000) i Vicens et al. (2004).

Finalment, les mostres del Garumnià basal estudiades a la Conca de Coll de Nargó (Mina Santaeulàlia) han proporcionat una associació de caròfits formada únicament per girogonits de *Feistiella malladae*. Aquesta espècie és important des d'un punt de vista paleoecològic, malauradament el seu rang d'edat és massa ampli (Campanià superior – Maastrichtià superior) per poder precisar la cronostratigrafia del Garumnià basal a Coll de Nargó. Tanmateix, Feist i Colombo (1983) van trobar associacions monoespecífiques de *Peckichara sertulata* en nivells equivalents als estudiats aquí (secció de l'Estació d'Aforament de Coll de Nargó).

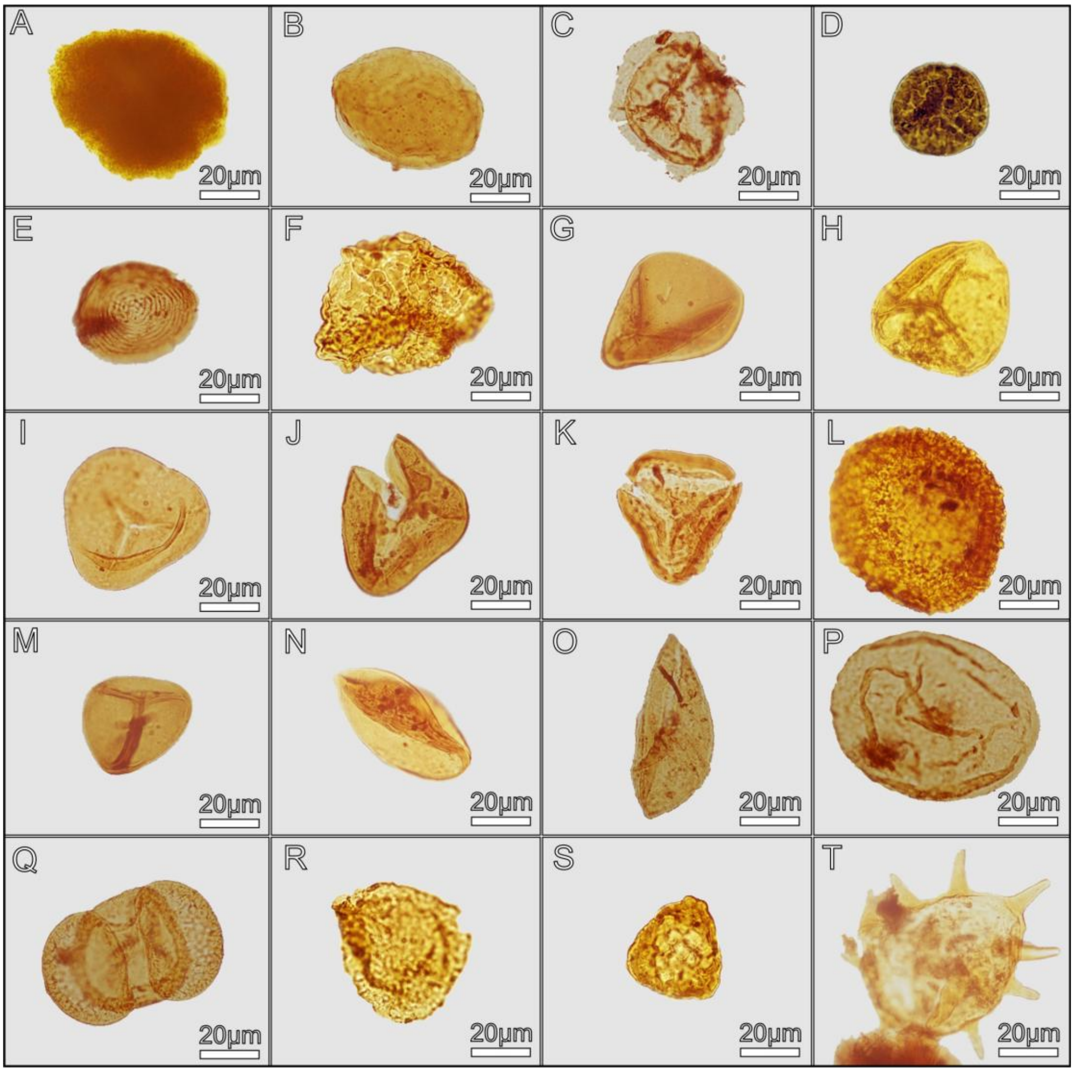
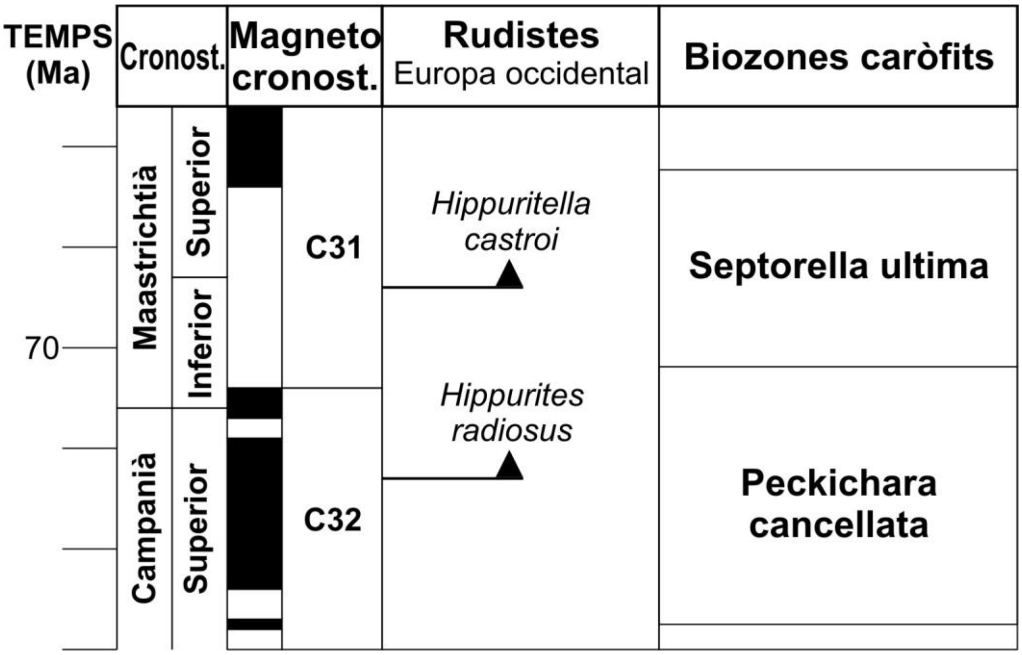


Figura 18. Palinomorfs del Garumnià Gris de la Conca de Vallcebre. **(A)** *Oedogonium cretaceum* Zippi, mostra FS-23. **(B)** *Ovoidites spriggi* (Cookson & Dettmann) Zippi, mostra FS-17. **(C)** *Zlivisporis blanensis* Pacltova, mostra FS-17. **(D)** *Hamulatisporis* sp., mostra ME-1. **(E)** *Chomotriletes fragilis* Pocock, mostra FS-17. **(F)** *Klukisporites* (*Ischyosporites*) *scaberis* (Cookson & Dettmann) Dettmann, mostra ME-1. **(G)** *Leiotriletes balinkaense* Kedves, mostra FS-17. **(H)** *Leiotriletes* sp., mostra ME-1. **(I)** *Cyathidites australis* Couper, mostra FS-17. **(J)** *Cyathidites* sp., mostra FS-17. **(K)** *Polypodiaceoisporites* sp., mostra FS-17. **(L)** *Gabonisporis vigourouxii* Boltenhagen, mostra FS-23. **(M)** *Triplanosporites* sp., mostra FS-17. **(N)** *Cycadopites minor* (Kedves) Kedves, mostra FS-17. **(O)** *Cycadopites* sp., mostra FS-15. **(P)** *Araucariacites australis* Cookson, mostra FS-15. **(Q)** *Pinuspollenites ruginosa* (Stanley) Oltz, mostra FS-15. **(R)** *Rugulitriporites pflugi* Kedves, mostra ME-1. **(S)** *Megatriopollis* sp., mostra ME-1. **(T)** *Spinizonocolpites* cf. *baculatus* Müller, mostra FS-17.

Figure 18. Palynomorphs from the Grey Garumnian of Vallcebre Basin. **(A)** *Oedogonium cretaceum* Zippi, sample FS-23. **(B)** *Ovoidites spriggi* (Cookson & 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 & 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.

Seguint el mateix raonament que per la Conca de Tremp, es pot considerar que l'edat del Garumnià basal a Coll de Nargó és també Maastrichtià inferior – mitjà (biozona Septorella ultima). Aquesta edat és compatible amb dades biostratigràfiques obtingudes per Willems (1985) a partir de foraminífers.

En resum, les biozones de caròfits definides a les conques sud pirinenques, Peckichara cancellata i Septorella ultima es poden correlar amb les primeres aparicions dels rudistes *Hippurites radiosus* i *Hippuritella castroi*, i calibrar amb les magnetozones C32r, C32n i C31r, tal i com es mostra a la Taula 1.



Taula 1. Biozones de caròfits correlades amb horitzons de rudistes i calibrades amb magnetozones. Les dades de rudites s'han obtingut de Hardenbol et al. (1998). Cronostratigrafia i magnetostratigrafia basades en Gradstein et al. (2004).

Table 1. *Charophyte biozones correlated with rudist horizons and calibrated with magnetozones. Rudist data were obtained from Hardenbol et al. (1998). Chronostratigraphy and magnetostratigraphy are taken from Gradstein et al. (2004).*

Sedimentologia, tafonomia i paleoecologia

A partir de les anàlisis sedimentològiques i de microfàcies s'han determinat les condicions paleoambientals que van marcar l'inici de la continentalització en el Cretaci superior de la Conca Sud Pirinenca (Villalba-Breva i Martín-Closas 2011; Villalba-Breva et al. 2012; Villalba-Breva i Martín-Closas en revisió) (Fig. 19). Hom pot distingir dues situacions ben diferenciades, corresponents a les conques de les dues làmines encavalcants estudiades.

- Làmina encavalcant de les Serres Marginals (Conca d'Àger)

El Garumnià basal de la Conca d'Àger (Fm. La Maçana) està organitzat en centenars de cicles de somització lacustre. Aquests cicles tenen una potència que generalment no supera el metre. De la base al sostre, estan formats per margues amb gasteròpodes, ostracodes i restes de caròfits, seguides per calcàries blanques de fàbrica wackestone i abundants tal·lus i girogonits de caròfits, i un últim terme de calcàries de color gris fosc de fàbrica packstone riques en matèria orgànica i restes de caròfits (Villalba-Breva i Martín-Closas en revisió). Des d'un punt de vista paleoecològic, s'observa que les associacions de caròfits estan dominades per *Peckichara cancellata*. L'estudi de microfàcies ha permès diferenciar diversos cinturons de fàcies a l'ambient lacustre de la Fm. La Maçana (Villalba-Breva i Martín-Closas en revisió) (Fig. 19A). El cinturó de vegetació de vora de llac està representat per fàcies de restes fragmentades de caròfits i altres bioclasts. La part soma del llac està representada per tres tipus diferents d'herbeis de caròfits; els quals estaven dominats respectivament per: (1) tal·lus de *Munieria grambastii* associats a utricles de *Clavator brachycerus*, (2) tal·lus de *Charaxis* sp. i girogonits de *Peckichara* sp. associats a plantes vasculars submergides, probablement angiospermes, i (3) tal·lus de *Clavatoraxis microcharophorus* associats a girogonits de *Microchara* sp. La repetició de cicles de somització, formats per wackestones blancs amb *Charaxis – Peckichara* i *Clavatoraxis – Microchara* a base i packstones grisos amb *Munieria – Clavator* a sostre, suggereix que, en termes paleoecològics, aquests darrer herbei creixia a les parts més somes. En canvi, els herbeis *Charaxis – Peckichara* i *Clavatoraxis – Microchara* es trobaven a les parts relativament més profundes del llac. Cal destacar el fet que les clavatoràcies creixessin al cinturó de vegetació més som i millor il·luminat, doncs *Clavator brachycerus* es una de les últimes clavatoràcies, poc abans de l'extinció de la família durant el Maastrichtià.

- Làmina encavalcant del Montsec-Pedraforca (conques de Tremp, Coll de Nargó i Vallcebre)

Els primers dipòsits continentals de les conques de Vallcebre, Coll de Nargó i Tremp, estan organitzats en desenes de cicles de varis metres de potència formats, de base a sostre, per (1) margues amb gasteròpodes, bivalves i fructificacions de caròfits, (2) capes de carbó (lignit) i (3) calcàries grises amb fàbrica wackestone-packstone i abundants restes de caròfits (Villalba-Breva et al. 2012; Villalba-Breva i Martín-Closas en revisió). L'estudi de microfàcies ha permès diferenciar un tipus d'herbei de caròfits de fàcies salabroses dominat per *Feistiella malladae* i tres tipus d'herbeis de fàcies lacustres, els quals estaven dominats respectivament per: (1) tal·lus de *Munieria grambastii*, (2) tal·lus de *Charaxis* sp. i girogonits de *Peckichara*, i (3) tal·lus de *Clavatoraxis microcharophorus* i girogonits de *Microchara.* Les relacions laterals entre aquests herbeis i la seva relativa abundància varien segons l'àrea d'estudi.

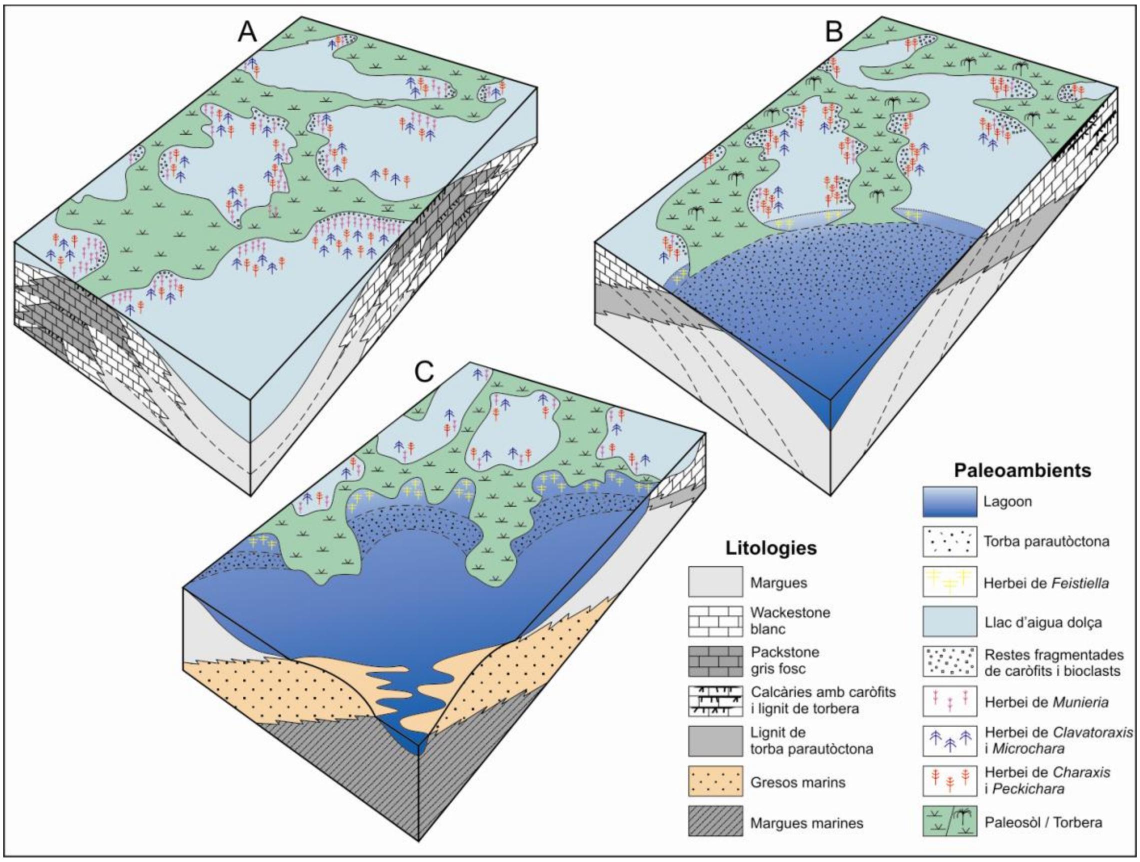


Figura 19. Reconstruccions paleoambientals del Garumnià basal a les Conques Sud Pirinenques amb la zonació proposada d'herbeis de caròfits. **(A)** Al Campanià superior de la Conca d'Àger. **(B)** Al Maastrichtià basal de la Conca de Vallcebre. **(C)** Al Maastrichtià inferior de la Conca de Tremp.

Figure 19. *Palaeoenvironmentals reconstructions in the basal Garumnian of the Southern Pyrenean Basins with the proposed zonation of charophyte meadows.* ***(A)*** *In the Late Campanian of the Àger Basin.* ***(B)*** *In the Earliest Maastrichtian of the Vallcebre Basin.* ***(C)*** *In the Early Maastrichtian of the Tremp Basin.*

A la Conca de Vallcebre hi havia associacions de caròfits de fàcies salabroses dominades per associacions de *Feistiella malladae* amb altres espècies menys abundants com *Platychara* sp. En canvi, els medis lacustres presentaven una gran varietat de plantes hidrofítiques, des de les parts més somes dominades per *Munieria grambastii* i *Charaxis* sp. associat a *Peckichara* sp. fins a les zones més profundes dominades per *Clavatoraxis microcharophorus* associat a *Microchara* sp. L'herbei més abundant era el dominat per *Peckichara* mentre que els altres dos només creixien sota condicions particulars (Villalba-Breva et al. 2012) (Fig. 19B). En canvi, a les conques de Coll de Nargó i Tremp l'herbei més abundant estava dominat per *Feistiella malladae* i creixia en ambients salabrosos de *lagoon*. Als llacs d'aigua dolça, els altres tres tipus d'herbeis de caròfits només creixien localment i les relacions laterals entre ells és desconeguda (Villalba-Breva i Martín-Closas en revisió) (Fig. 19C).

Paleogeografia

Durant el Cretaci superior els primers dipòsits no marins (Garumnià) de les conques sud pirinenques d'Àger, Vallcebre, Coll de Nargó i Tremp mostren característiques contrastades en quant a la seva cronostratigrafia, sedimentologia i paleoecologia. Aquestes diferències són importants des d'un punt de vista paleogeogràfic doncs suggereixen que la Conca Sud Pirinenca presentava una polaritat de fàcies sud-nord durant el límit Campanià – Maastrichtià (Fig. 20). Les fàcies més proximals, estrictament lacustres, d'edat més antiga es van dipositar al Campanià superior (biozona Peckichara cancellata, magnetocrons C32r i C32n) i estaven situades al sud (Fm. La Maçana, Conca d'Àger) mentre que al nord tenien lloc al mateix temps una sedimentació en fàcies més distals, marines, corresponents a la Fm. Terradets a Vallcebre i a la Fm. Areny a Coll de Nargó i Tremp (Fig. 20A). Just al límit Campanià – Maastrichtià (biozona Peckichara cancellata, magnetocron C31r) continuava la mateixa polaritat de fàcies sud-nord però s'observa que també existia una polaritat de fàcies est-oest. En aquest moment les fàcies eren fluvials a la Conca d'Àger (Fm. Figuerola), mentre que a les conques situades més al nord (làmina del Montsec-Pedraforca) la sedimentació variava des de fàcies transicionals de *lagoons* salabrosos amb acumulacions detrítiques de matèria orgànica i fàcies lacustres a la Conca de Vallcebre, fins a fàcies netament marines (Fm. Areny) a les conques de Coll de Nargó i Tremp (Fig. 20B). Finalment, durant el Maastrichtià inferior (biozona Septorella ultima) es mantenen les dues polaritats de fàcies: sud-nord i est-oest. A les conques de Coll de Nargó i Tremp comencen a dipositar-se fàcies transicionals de pantà costaner connectat a petits llacs d'aigua dolça (Fm. La Posa), mentre que a les conques d'Àger i Vallcebre tingué lloc una sedimentació fluvial (Fm. Figuerola, Garumnià Vermell Inferior) (Fig. 20C).

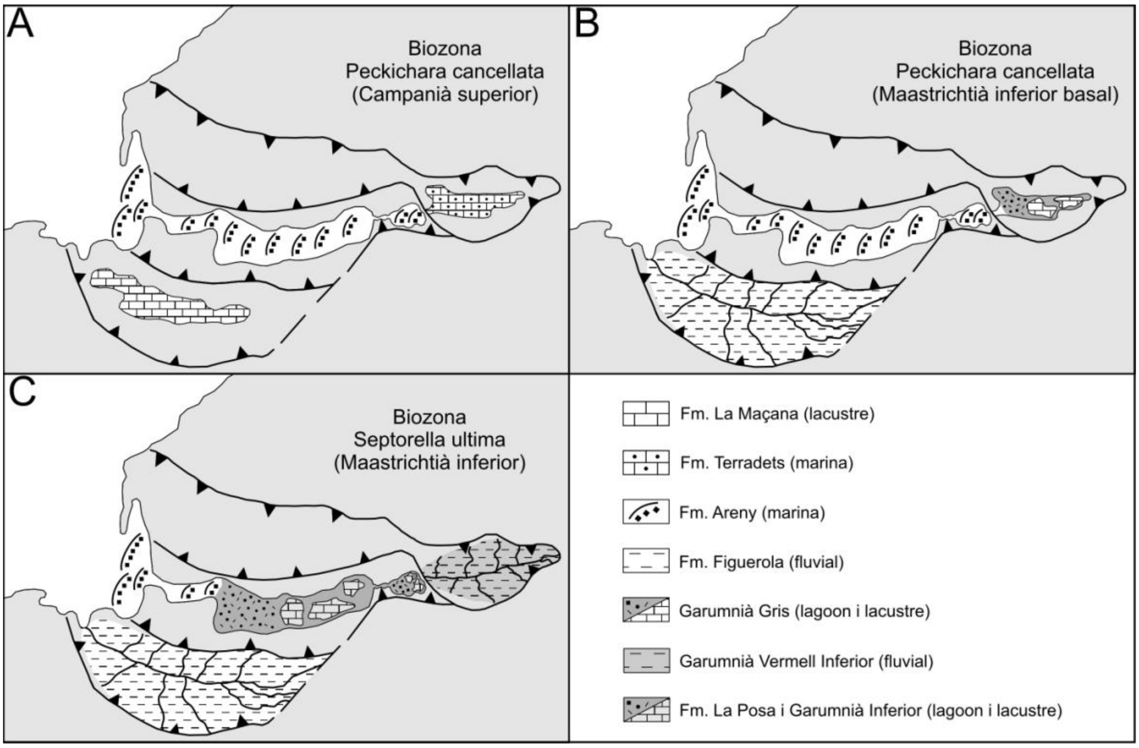


Figura 20. Evolució paleogeogràfica de les Conques Sud Pirinenques durant **(A)** el Campanià superior (correlat amb la part inferior de la biozona Peckichara cancellata), **(B)** el Maastrichtià basal (correlat amb la part superior de la biozona Peckichara cancellata) i **(C)** el Maastrichtià inferior (correlat am la biozona Septorella ultima), amb dues polaritats de fàcies ben marcades: sud-nord i est-oest.

Figure 20. *Palaeogeographical evolution of the Southern Pyrenean Basins during* ***(A)*** *the Late Campanian (correlated with the lower part of the Peckichara cancellata biozone),* ***(B)*** *the Earliest Maastrichtian (correlated with the upper part of the Peckichara cancellata biozone) and* ***(C)*** *the Early Maastrichtian (correlated to the Septorella ultima biozone), showing two well-marked facies distribution: S-N and E-W.*

DISCUSSIÓ

Sistemàtica

- Caròfits

a) Fructificacions

En aquesta tesi s'ha adoptat la sistemàtica dels caròfits del Cretaci superior preexistent, definida sobretot per Grambast (1971). No obstant, des del punt de vista taxonòmic, cal destacar dos aspectes rellevants, referents a les espècies *Clavator brachycerus* i *Feistiella malladae* (Villalba-Breva i Martín-Closas en revisió):

- La distinció entre *Clavator brachycerus* i *Clavator ultimus* (GRAMBAST 1971) MARTÍN-CLOSAS 1996, que són les dues darreres espècies de la família de les Clavatoràcies, es fonamentava segons Grambast (1971, 1974) en la presència/absència d'un porus apical. De fet, l'absència d'aquest porus germinatiu a *C. ultimus* havia estat proposada com la raó de l'extinció de l'espècie, i, en conseqüència, de la família. Posteriorment Massieux et al. (1979) havien assenyalat que el porus apical de *C. brachycerus* tenia una forma molt variable i irregular, i corresponia en realitat a una fractura de l'utricle. De fet, quan l'àpex de *C. brachycerus* era sencer, es trobava tancat com a *C. ultimus*. Les nostres observacions corroboren les de Massieux et al. (1979), i s'ha observat que la distinció entre *Clavator brachycerus* i *C. ultimus* està limitada a la mida de l'utricle i especialment al nombre de cèl·lules bracteals, que a *C. brachycerus* és de 5-7 cèl·lules bracteals enfront a 8-9 a *C. ultimus*.
- Feist i Colombo (1983), Massieux et al. (1985, 1987) i Masriera i Ullastre (1988) havien identificat una única espècie de porocaràcia al Cretaci superior dels Pirineus, *Porochara malladae*. A partir de l'estudi taxonòmic dels girogonits de porocaràcies de les mostres estudiades de la Conca Sud Pirinenca, s'ha provat que aquestes fructificacions han de ser assignades al gènere *Feistiella* i no al gènere *Porochara*, seguint el criteri proposat per Schudack (1986). En efecte totes les mostres en les que s'ha obtingut la placa basal, aquesta és simple. Les altres dues espècies de porocaràcies descrites en el Cretaci superior d'Espanya (Cadena Ibèrica), *Porochara oblonga* GRAMBAST 1975 i *Porochara globosa* GRAMBAST ET GUTIÉRREZ 1977, presenten caràcters externs similars a *Feistiella malladae*, però

per ara no es poden sinonimitzar, donat que es desconeix quina era la seva placa basal.

La distribució paleobiogeogràfica de les espècies trobades a les conques sud pirinenques és en general similar a la que ja havia estat descrita per altres autors. En el moment actual del coneixement la majoria d'espècies serien endèmiques del sud-est d'Europa. Com a noves aportacions cal assenyalar que *Microchara parazensis* només s'havia trobat al Maastrichtià del Minervés (Llenguadoc) per Massieux et al. (1987). Aquí es documenta per primera vegada la seva aparició al Campanià superior de la Conca Sud Pirinenca. *Dughiella obtusa* i *Platychara turbinata* semblen ser espècies endèmiques d'Ibèria, que només es coneixien del límit Campanià – Maastrichtià de la Cadena Ibèrica per Grambast i Gutièrrez (1977) i al Maastrichtià de les conques de Tremp i Coll de Nargó per Feist i Colombo (1983). Ara es documenten al Campanià superior de la Conca d'Àger.

b) Tal·lus

Aquesta és la primera vegada que s'ha reconstruït la planta sencera d'un caròfit fòssil a partir de làmines primes de calcàries lacustres. A diferència d'altres plantes fòssils que biocalcifiquen, aquest mètode no havia estat utilitzat prèviament amb caròfits fòssils. Es considerava que les plantes senceres de caròfits fòssils eren rares i només podien ser reconstruïdes si es trobaven preservades sota condicions excepcionals de fossilització, com per exemple silicificades o en calcàries litogràfiques. En aquesta tesi (Villalba-Breva i Martín-Closas 2011) s'ha comprovat que existeix un potencial important per reconstruir caròfits fòssils a partir de làmines primes de calcàries riques en caròfits, les quals són extremadament abundants al registre fòssil del domini de la Tetis.

La reconstrucció de *Clavatoraxis microcharophorus* sp. nov. ha permès obtenir dos resultats importants: 1) la connexió anatòmica entre fructificacions de caràcies i un tal·lus de *Clavatoraxis* mostra clarament que aquest tipus de tal·lus no és exclusiu de les clavatoràcies com és pensava prèviament, i 2) la relació entre tal·lus i girogonits proporciona nous caràcters molt significatius per a una millor distinció entre *Microchara* i *Chara*. Fins ara, aquests dos gèneres només es distingien per la mida del girogonit. Ara se sap que estaven units a diferents tal·lus, *Microchara* a *Clavatoraxis* i *Chara* a *Charaxis*.

D'una altra banda, els tal·lus de *Munieria grambastii* s'han trobat localment associats a utricles de clavatoràcia relacionats a *Clavator brachycerus*, i encara que no s'han observat en connexió anatòmica, és molt probable que *Munieria grambastii* pertanyi a aquesta fructificació de caròfit, tal com ja havia suggerit Fabre-Taxy i Chatelet (1971). De forma similar, el fet de trobar de forma constant molts girogonits dispersos del gènere *Peckichara* associats a tal·lus grans de *Charaxis* suggereix que pertanyien a la mateixa planta, tot i que no s'han trobat en connexió anatòmica.

- Plantes vasculars

a) *Frenelopsis* sp.

Les restes de coníferes estudiades a la Conca de Vallcebre pertanyen a *Frenelopsis* perquè presenten els caràcters diagnòstics proporcionats per Gomez et al. (2002): estomes més o menys disposats en fileres paral·leles (11-14 fileres per mm^2), amb 4-6 papil·les massives, cadascuna amb una cèl·lula subsidiària, i cèl·lules epidèrmiques de forma quadrada, rectangular o poligonal (31-40 de llarg i 16-19 d'ample).

b) *Sabalites longirhachis*

Les fulles de palmera de la Conca de Vallcebre s'han identificat com *Sabalites longirhachis* en base a la seva morfologia general i les característiques de la nervadura. Les fulles estudiades mostren tots els caràcters macroscòpics indicats per Kvaček and Herman (2004) en la diagnosis de *S. longirhachis* del Campanià inferior de la Formació Grünbach (Àustria), així com un patró de nervadura similar: fulles costapalmades, lanceolades; amb una costa llarga i gruixuda; segments de les fulles fusionats, netament lineals, lleugerament més amples a l'àpex, amb forma de V en secció transversal i disposats en angle agut des de la costa; un nervi principal i quatre ordres de nervis paral·lels per segment. Pel que fa als troncs associats a aquestes fulles, aquests presenten característiques típiques de les palmeres actuals: són rectes, d'amplada més o menys uniforme, llisos sense evidències d'espines i amb només estructures el·lipsoides i forats atribuïbles a marques d'arrels adventícies a la part basal del tronc. Les arrels atribuïdes a l'arbre portador de fulles de *S. longirhachis* estan conservades com adpressions i motlles interns. Tanmateix, es poden interpretar com sistemes d'arrelament de palmera en base a la seva gran similitud en forma i mida amb les palmeres actuals. La marca circular central pot correspondre a la soca de la palmera i té el mateix diàmetre que els troncs de palmera estudiats, mentre que les estructures radials tenen una amplada similar a les arrels de palmeres actuals. A més a més, els sistemes d'arrelament de les altres plantes vasculars identificades a Vallcebre són diferents als de les palmeres en diversos aspectes: les coníferes i la majoria d'angiospermes presenten arrels axonomòrfiques, les cicadals presenten una arrel principal amb dues fileres d'arrels més petites ramificades,i les pandanals tenen arrels molts gruixudes a prop de la base del tronc.

c) *Bergacarpon viladricii*

Totes les llavors estudiades a la Conca de Vallcebre tenen una forma, mida i estructura similars, fet que indica que pertanyen a una única espècie: *Bergacarpon viladricii*. Aquestes llavors presenten un desenvolupament àtrop i un micròpil amb opercle, caràcter típic de les monocotiledònies, especialment en membres dels commelínids, però també de nimfeals i algunes eudicotiledònies. Les nimfeals tenen un desenvolupament anàtrop, més de dos òvuls per carpel i fruits carnosos; mentre que les begònies i les cactàcies tenen òvuls anàtrops i campilòtrops, respectivament, i probablement es van originar durant el Cenozoic. Per tant, és probable que aquestes llavors pertanyin a un commelínid.

d) Altres macrorestes de plantes vasculars

Un únic exemplar trobat a la Conca deVallcebre podria ser interpretat com un fragment de fulla bipinnada de cicadal. Malauradament, les característiques diagnòstiques de les cicadals i l'anatomia de la cutícula no són observables a l'exemplar estudiat. A més a més, les fulles de cicadals poden tenir una forma molt similar a les bennettitals, fet que dificulta la seva distinció sense dades cuticulars. No obstant això, les restes més modernes de bennettitals documentades són d'edat Campanià inferior.

Diversos fragments de fulles trobats també a la Conca de Vallcebre tenen similituds amb fulles de Pandanàcies. Per exemple, els exemplars comparteixen caràcters amb el gènere *Pandanites*, especialment pel que fa a la nervadura: nervis paral·lels de primer odre (de la mateixa amplada) i nervis més prims orientats obliqua o perpendicularment. El gruix dels nervis i la densitat d'aquests per centímetre són consistents amb les dades de Kvaček i Herman (2004) per *Panadanites trinervis* (ETTINGSHAUSEN) KVAČEK ET HERMAN. Tanmateix, és necessari més material i en millor estat de preservació per a una determinació més precisa.

Biostratigrafia

Pel que fa a la biozonació de caròfits establerta es realitzen dues aportacions, referents respectivament a les biozones de Peckichara cancellata i Septorella ultima.

- Biozona de Peckichara cancellata. Aquesta biozona definida per Feist a Riveline et al. (1996) comprenia la part mitja del Campanià superior i estava calibrada amb les magnetozones C32r a C32n (Galbrun et al. 1993) i possiblement el sostre del magnetocron C33n (Westphal i Durand 1990). No obstant, també s'havia correlat directament amb palinoflores del Maastrichtià inferior (Médus et al. 1988). Aquesta incongruència s'ha resolt a partir de noves dades a la Conca de Vallcebre, on s'ha definit la biozona Peckichara cancellata en materials datats com Maastrichtià inferior (magnetocron C31r) segons dades paleomagnètiques d'Oms et al. (2007). Per tant, es proposa modificar la biozona Peckichara cancellata, i ampliar el seu sostre fins al Maastrichtià inferior.
- Biozona de Septorella ultima. Les associacions de caròfits estudiades a la Conca de Tremp no contenen cap espècie índex de la biozonació de caròfits Segons Grambast (1971) i Riveline et al. (1996), l'espècie *Peckichara sertulata* forma poblacions homogènies només quan es troba associada a *Clavator ultimus*, espècie índex de la biozona Septorella ultima. Així doncs, tot i no trobar *C. ultimus*, potser per limitacions paleoecològiques d'aquesta espècie, la presència de la seva espècie acompanyant *P. sertulata* és suficient per a datar el Garumnià basal de Tremp com Maastrichtià inferior – mitjà.

Sedimentologia, tafonomia i paleoecologia

- Caròfits

L'anàlisi tafonòmica de les restes de *C. microcharophorus* combinada amb les anàlisis sedimentològiques i de microfàcies ha permès la descripció del hàbitat d'aquesta nova espècie en llacs d'aigua dolça i ha proporcionat la clau per reconèixer aquelles fàcies favorables per a la preservació de restes ben articulades de caròfits. Aquestes fàcies corresponen als fons dels llacs més profunds pobres en oxigen i habitats només per tapissos algals. Per contra, els herbeis de caròfits *in situ* donen lloc a acumulacions d'un gran número de tal·lus de caròfits col·lapsats amb només una petita fracció de sediment, formant calcàries packstone-grainstones on les estructures anatòmiques en detall i especialment la connexió anatòmica dels girogonits als tal·lus són difícils de reconèixer o absents.

D'alta banda, si es comparen les conques de Vallcebre, Coll de Nargó, Tremp i Àger observem que els llacs d'aquestes quatre conques tenien tres tipus semblants de fàcies riques en caròfits, dominades respectivament per tal·lus de *Clavatoraxis microcharophorus*, *Charaxis* sp. i *Munieria grambastii*, a vegades amb abundants restes d'altres macròfits submergits (angiospermes?). Tanmateix, hi havia importants diferències tant en la composició específica com en la riquesa de caròfits determinades a partir de les seves fructificacions. Així doncs, la riquesa d'espècies és molt més gran al Garumnià basal de la Conca d'Àger que a les conques de Vallcebre, Coll de Nargó i Tremp, com és d'esperar quan es comparen associacions de caròfits de llacs d'aigua dolça amb associacions d'aigua salabrosa (García 1999). No només la riquesa d'espècies entre aquests dos ambients era diferent, sinó també la composició específica, ja que a la formació lacustre de la Conca d'Àger les associacions estaven dominades per caràcies, especialment *Peckichara cancellata* als marges de llac i clavatoràcies (*Clavator brachycerus*) a les vores de llac, mentre a les altres conques l'espècie més abundant era la porocaràcia *Feistiella malladae*.

- Plantes vasculars

La combinació de les anàlisis sedimentològiques i tafonòmiques ha permès determinar l'hàbitat de les plantes vasculars. El lignit garumnià del Pirineu Oriental ha estat objecte de diversos estudis petrològics en el passat, els quals mostraven que aquest carbó contenia abundants restes de teixits llenyosos atribuïbles a boscos pantanosos de coníferes (García-Vallès et al. 1994). Aquests autors van relacionar provisionalment les restes de plantes a taxodiàcies, per comparació amb els pantans forestals de coníferes del Terciari i actuals. Tanmateix, les evidències taxonòmiques i tafonòmiques trobades en els lignits de Vallcebre suggereixen que les plantes que van proporcionar la matèria orgànica precursora de la majoria del lignit garumnià eren principalment coníferes queirolepidiàcies (*Frenelopsis* sp.) i, en menor proporció, angiospermes arecàcies (*Sabalites longirhachis*). Així mateix, l'absència d'arrels a la base de la majoria de capes de lignits sobre margues orgàniques d'ambients salabrosos suggereix que aquests horitzons de carbó es van formar per l'acumulació detrítica de restes de plantes, principalment eixos de *Frenelopsis*. El transport de la matèria orgànica podria haver estat efectuat per flotació, depenent de la seva densitat i flotabilitat. D'altra banda, les poques torberes que van créixer *in situ* ho van fer al costat dels llacs d'aigua dolça. La prova d'això són els dos tipus d'estructures d'arrelament trobades a sostre de calcàries lacustres riques en caròfits. El tipus d'arrel més abundant són petites arrels axonomòrfiques d'afinitat botànica incerta, mentre el segon tipus, en forma d'escombra, s'atribueix a la palmera *Sabalites longirhachis*. L'existència de oòspores d'algues verdes als nivells de lignits amb marques d'arrels, també suggereix condicions d'aigua dolça durant la deposició d'aquest carbó.

Respecte a les altres macrorestes trobades a la Conca de Vallcebre (fulles de cicadals i monocotiledònies), la seva poca abundància i gran fragmentació i l'absència de marques d'arrels pertanyents a aquestes plantes suggereixen que aquestes fulles són parautòctones o al·lòctones. Els hàbitats d'aquestes restes són difícils de determinar. Aquestes plantes podrien haver crescut en les mateixes torberes límniques que les palmeres, però en menys abundància, fet que dificultaria trobar les seves marques d'arrels, o, alternativament, podrien haver crescut fora de l'ambient deposicional, és a dir de les torberes i dels pantans salabrosos. En relació a les llavors *Bergacarpon viladricii*, estudiades a la Conca de Vallcebre, es pot dir que aquestes mesorestes (llavors i fruits) es van trobar concentrades en una sola capa de margocalcària. Aquests tipus d'acumulacions estan probablement influenciats tant per limitacions ecològiques com per processos tafonòmics. D'una banda, en ambients de *lagoons* costaners i maresmes intermareals com el de Vallcebre, les associacions carpològiques es caracteritzen per un baix nombre d'espècies (en aquest cas tan sols una) però una alta densitat de llavors (50000 llavors per m^2). D'una altra banda, en aquests mateixos ambients no hi ha gaire correspondència entre la flora local i les associacions de llavors transportades. Aquest transport probablement va ser més degut a flotació que a la tracció en el fons o a la suspensió en la columna d'aigua, fet que també explicaria perquè no s'ha trobat cap macroresta de planta associada a aquestes llavors. Finalment, és important assenyalar que es tracta d'una de les més antigues associacions monotípiques de llavors d'angiosperma del registre fòssil.

Pel que fa a la macroflora estudiada a la Conca de Tremp, les dades obtingudes fins ara són preliminars. Des d'un punt de vista tafonòmic, les macrorestes trobades en l'excavació d'Isona (principalment fulles d'angiospermes) pertanyen a medis transicionals i per tant han sofert un cert transport abans de dipositar-se. La gran fragmentació que presenten aquestes fulles indicaria que va existir col·lisió amb altres objectes existents, quan van ser transportades en suspensió o tracció dins un flux d'aigua.

A part de les restes trobades en l'excavació d'Isona, les fulles més ben preservades d'aquesta flora van ser trobades per Vicente (2002), qui en la seva monografia citava un total de sis jaciments als voltants del poble d'Isona amb abundants restes vegetals (Isona-Sud, Isona-Nord-Est, Isona-Est, Isona-Comiols, Isona-Oest, Isona-Sud-Oest). L'autor esmentat no va indicar la localització exacta d'aquests afloraments, per evitar possibles espolis, ni va fer una explicació detallada del context geològic. Així doncs, és difícil saber si tots els exemplars catalogats com provinents d'Isona pertanyen a la mateixa unitat litostratigràfica estudiada en aquesta tesi. No obstant, encara que de moment no hi ha prou dades per fer una reconstrucció d'aquesta comunitat vegetal del passat, la qualitat del material permet suposar que en el futur es podrà ampliar el coneixement sobre la flora del Cretaci superior del nord d'Ibèria a nivell regional i també inferir paràmetres paleoclimàtics.

Les associacions palinològiques obtingudes a la Conca de Vallcebre es poden comparar amb altres associacions mostrejades en dipòsits similars del Maastrichtià del Pirineu, com les de Coll de Nargó (Médus 1972; Ashraf i Erben 1986), les del Barranc de la Posa a la Conca de Tremp (Porta et al. 1985; Médus et al. 1988) i les de Fontllonga a la Conca d'Àger (López-Martínez et al. 1999; Fernández-Marrón et al. 2004b). En general les mostres de Vallcebre són diferents a les de la resta de localitats pirinenques del Maastrichtià al estar dominades per pol·lens bialats de pinàcia i presentar una menor proporció de monocolpats, encara que a vegades s'observen abundants espores triletes de falgueres, tal com succeeix en la majoria d'altres localitats del Pirineu. D'altra banda, la contradictòria absència del pol·len de queirolepidiàcia, *Classopollis*, en nivells rics en les restes vegetatives de la mateixa planta, *Frenelopsis*, es pot explicar en alguns casos per una selecció durant el transport i deposició. Taugourdeau-Lanz et al. (1982) va assenyalar que els bialats de pinàcies i els grans de pol·len més densos de queirolepidiàcies tenien comportaments tafonòmics oposats, sent el darrer difícilment transportable per l'aigua. Alternativament, l'absència de *Classopollis* pot ser atribuïda a una baixa producció de pol·len en la planta font, entre altres raons. Aquesta hipòtesi, de confirmar-se en el futur, seria molt significativa per explicar l'extinció de les coníferes queirolepidiàcies prop del límit K-T.

Paleogeografia

La polaritat de fàcies sud-nord que presentaven les conques de Vallcebre, Coll de Nargó, Tremp i Àger durant el límit Campanià – Maastrichtià s'assembla a la que presentaven les conques sud pirinenques durant el Cretaci inferior (Peybernès 1976). No obstant això, al Cretaci superior la polaritat sud-nord està superposada a la ja coneguda polaritat est-oest relacionada amb el rebliment de la Conca Pirinenca i la rotació de la placa Ibèrica (Capote et al. 2002). Aquesta distribució de fàcies mostra que des de l'inici de la sedimentació no marina del Cretaci superior, la làmina encavalcant del Montsec-Pedraforca va actuar com un alt sedimentari que separava un domini netament més continental situat al sud del llindar (Conca d'Àger), i un domini amb més influència marina al nord (conques de Vallcebre, Coll de Nargó i Tremp).

CONCLUSIONS

Les associacions de caròfits dels Garumnià basal de les conques de Vallcebre, Coll de Nargó, Tremp i Àger s'han estudiat des d'un punt de vista taxonòmic, biostratigràfic i paleoecològic. La flora de caròfits està formada per *Feistiella malladae* (BATALLER 1945) nov. comb. VILLALBA-BREVA ET MARTÍN-CLOSAS, *Microchara cristata* GRAMBAST 1971, *M. parazensis* MASSIEUX 1987, *Dughiella obtusa* GRAMBAST I GUTIÉRREZ 1977, *Peckichara cancellata* GRAMBAST 1971, *P. sertulata* GRAMBAST 1971, *Platychara caudata* GRAMBAST 1971 i *P. turbinata* GRAMBAST ET GUTIÉRREZ 1977, i *Clavator brachycerus* (GRAMBAST 1962) MARTÍN-CLOSAS 1996 (=*Septorella brachycera*). Des del punt de vista taxonòmic es confirma la distinció de les espècies *Clavator brachycerus* i *C. ultimus* en base a la seva mida i número de cèl·lules bracteals, i no per la presència/absència d'un porus apical. Dins les porocaràcies es corrobora l'existència únicament del gènere *Feistiella* en el Cretaci superior dels Pirineus. Des del punt de vista biogeogràfic la flora presenta moltes similituds amb les flores del sud-est d'Europa. Per primera vegada se citen les espècies *Microchara parazensis* i *Dughiella obtusa* a la Conca Sud Pirinenca, i s'identifica l'espècie *Platychara turbinata* a la Conca d'Àger. D'altra banda, s'han diferenciat tres tipus de tal·lus de caròfits a les calcàries lacustres del Garumnià basal de la Conca Sud Pirinenca: *Munieria grambastii* BYSTRICKÝ 1976, *Charaxis* sp. i *Clavatoraxis microcharophorus* VILLALBA-BREVA ET MARTÍN-CLOSAS 2011. Aquesta darrera espècie presenta caràcters desconeguts en les caràcies actuals, com rosetes aciculars en les cèl·lules corticals i girogonits embolcallats en bràctees, formant veritables túniques. A més a més, la reconstrucció d'aquesta nova espècie demostra que el tipus de tal·lus *Clavatoraxis* no és exclusiu de les clavatoràcies i permet una millor distinció entre els gèneres *Microchara* i *Chara* a partir de les seves restes vegetatives.

Es realitza un estudi biostratigràfic del Garumnià basal combinat amb dades magnetostratigràfiuques d'altres autors, fet que permet precisar el coneixement cronostratigràfic de l'inici del Garumnià a les conques sud pirinenques. Els resultats indiquen que el Garumnià basal (Formació La Maçana) a la Conca d'Àger és d'edat Campanià superior (biozona Peckichara cancellata, crons C32r i C32n). A la Conca de Vallcebre es corrobora la presència de la biozona de Peckichara cancellata en el Garumnià Gris, però els treballs magnetostratigràfics d'Oms et al. (2007) comporten estendre el sostre de la biozona fins el Maastrichtià basal. Finalment a les conques de

Coll de Nargó i Tremp es precisa l'edat del Garumnià basal, a partir de la presència de poblacions homogènies de *Peckichara sertulata*, que només existirien dins la biozona de Septorella ultima (Maastrichtià inferior-mitjà). En conseqüència, l'inici de la sedimentació no marina del Cretaci superior (Garumnià) va començar primer al sud, dins la làmina de les Serres Marginals, i després es va estendre al nord, dins la làmina del Montsec-Pedraforca. En aquesta làmina la continentalització va progressar d'est a oest. En resum aquests resultats mostren que la base del Garumnià basal és clarament diacrònica a les conques sud pirinenques de manera que la durada de la continentalització en aquest sector de la conca va ser d'uns 6-7 Ma.

La paleoecologia de les associacions de caròfits de les conques de Vallcebre, Coll de Nargó, Tremp i Àger s'ha estudiat a partir de la combinació de l'anàlisi sedimentològica i tafonòmica. Els resultats mostren que existí una polaritat de fàcies sud-nord a la Conca Sud Pirinenca central durant l'inici de la sedimentació continental del Cretaci superior. A la Conca d'Àger les associacions de caròfits són de medis lacustres, mentre que a les conques de Vallcebre, Coll de Nargó i Tremp les associacions lacustres es troben acompanyades per associacions monoespecífiques de porocaràcies, típiques de medis salabrosos. En aquestes conques amb influència marina, les calcàries de caròfits es troben generalment a sostre de cicles de somització que comencen amb margues salabroses i capes de lignit. La majoria dels nivells de lignit corresponen a matèria orgànica parautòctona, generalment formada per acumulacions de *Frenelopsis* sp., dipositats després d'un cert transport en les fàcies paràliques i salabroses de la conca. En canvi el carbó autòcton, dipositat en torberes d'aigua dolça, representa una part molt petita del volum total del carbó explotat. Les estructures d'arrelament associades a aquests carbons de torbera són de dos tipus. D'una banda trobem arrels axonomòrfiques d'afinitat biològica dubtosa i d'altra banda trobem arrels en forma d'escombra atribuïdes a *Sabalites longirhachis*. Altres plantes importants eren les llavors *Bergacarpon viladricii* MARMI, GOMEZ, VILLALBA-BREVA ET MARTÍN-CLOSAS, atribuïdes a un comelínid. En conclusió la comunitat vegetal dels aiguamolls del Maastrichtià inferior estava dominada per la conífera queirolepidiàcia *Frenelopsis* associada a la palmera *Sabalites longirhachis*, i en alguns casos amb més diversitat d'angiospermes. L'estudi del pol·len mostra, en canvi, una dominància de bialats, juntament amb espores de falgueres i oòspores d'algues d'aigua dolça menys abundants. Sorprenentment, el pol·len de *Frenelopsis*, *Classopolllis* és absent, tal i com passa a la majoria de conques sud pirinenques durant el Cretaci superior. Per tal d'explicar aquesta diferència entre el registre fòssil de macrorestes de plantes i de palinomorfs s'han de considerar possibles biaixos tafonòmics.

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ANNEXOS

Annex 1: Publicacions fonamentals de la tesi

Article 1

VILLALBA-BREVA, S., MARTÍN-CLOSAS, C., MARMI, J., GOMEZ, B., FERNÁNDEZ-MARRÓN, M. T. 2012. Peat-forming plants in the Maastrichtian coals of the Eastern Pyrenees. *Geologica Acta*, doi: 1133 101344/105000001711 (en premsa).

RESUM: El Maastrichtià inferior de Fumanya i de localitats veïnes del sinclinal de Vallcebre (Pirineu Oriental, Catalunya, Espanya) ha proporcionat la primera prova que les coníferes queirolepidiàcies van ser les principals precursores del carbó maastrichtià del Pirineu. La majoria de capes de lignit riques en *Frenelopsis* no presenten marques d'arrels, fet que suggereix que la torba original era detrítica. Altres dades sedimentològiques i tafonòmiques indiquen que les restes de queirolepidiàcies es van dipositar als marges d'un *lagoon* després de ser transportades per flotació. La mateixa associació parautòctona inclou impressions completes de fulles de *Sabalites longirhachis* i grans impressions de troncs atribuïts a la mateixa palmera. Altres macrorestes menys abundants parautòctones o al·lòctones de plantes inclouen fulles de cicadals i monocotiledònies i abundants llavors d'angiosperma. Algunes capes de lignit de poca potència presenten marques d'arrels a la base, fet que permet atribuir-les a l'acumulació de matèria orgànica autòctona, en torberes. Aquestes capes es troben al sostre de diverses calcàries amb caròfits. L'associació de caròfits, dominada per l'acumulació *in situ* de girogonits de *Peckichara* i *Microchara*, suggereix que aquestes calcàries es van dipositar en llacs d'aigua dolça, poc profunds i que les corresponents torberes eren límniques en lloc de paràliques. La morfologia de les arrels és axonomòrfica i no permet identificar amb seguretat quines van ser les plantes productores. Les anàlisis palinològiques presenten abundants bialats, amb espores de falguera i oòspores d'algues d'aigua dolça menys abundants. Localment, les marques d'arrels axonomòrfiques més abundants es troben associades amb grans estructures d'arrelament de tipus escombra atribuïdes a la palmera *Sabalites longirhachis*. Els resultats presentats mostren que, a l'inici del Maastrichtià, les restes de les coníferes queirolepidiàcies eren encara importants precursores de carbó, encara, que a diferència del seus anàlegs del Cretaci inferior, compartien aquest paper amb algunes angiospermes, com palmeres.

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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 in 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 (Gomez et al., 2001, 2002). However, the Lower Cretaceous coal-bearing beds studied up to now 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 Gomez 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 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 Geología Económica (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.

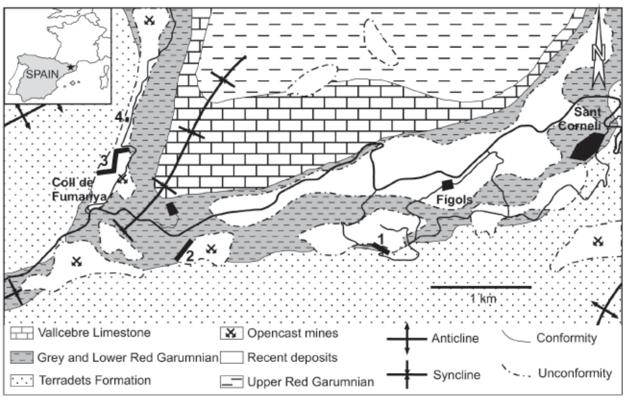

FIGURE 1 | **Geological map of the study area with location of the stratigraphic sections shown in Figure 2.**

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

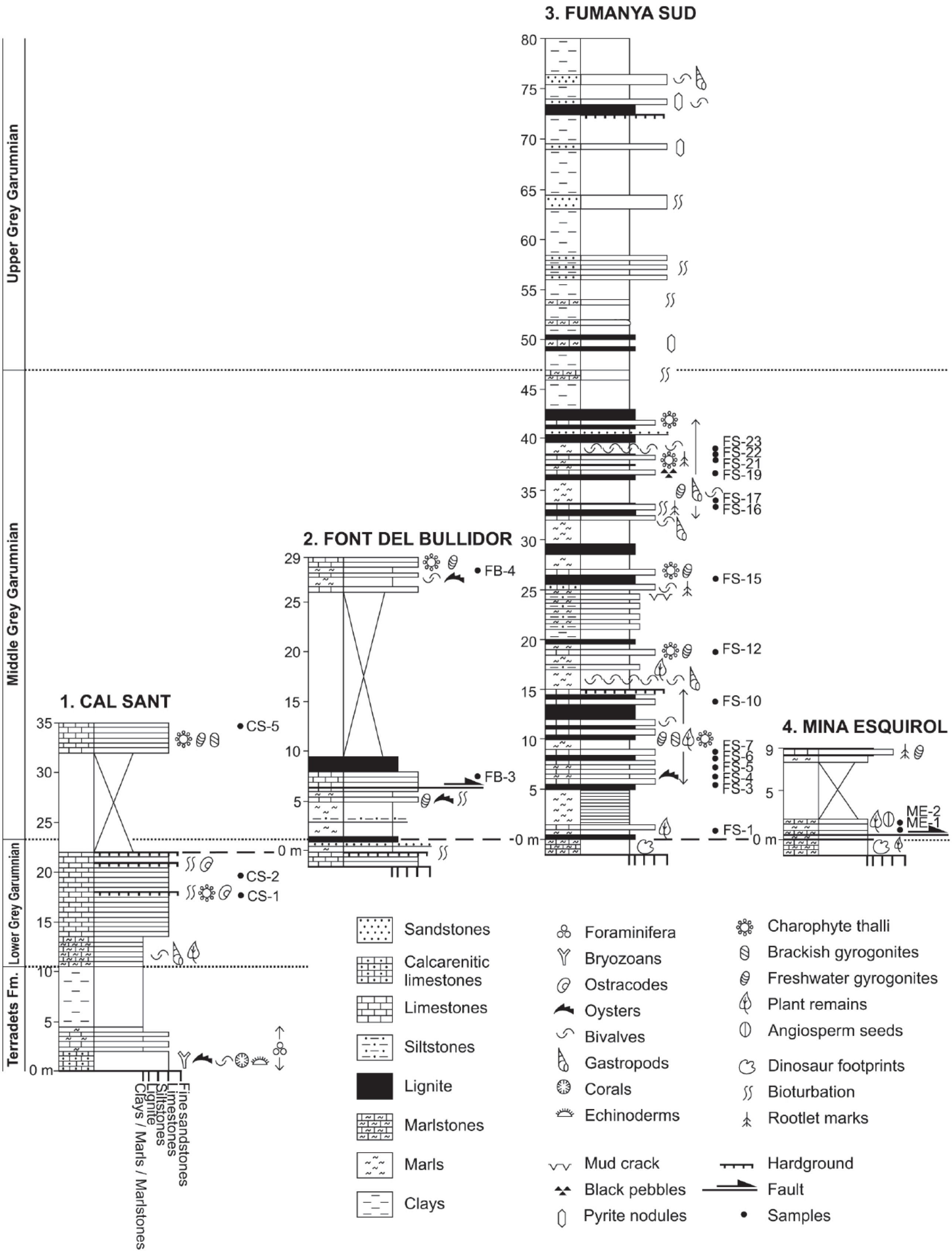

FIGURE 2 | **Stratigraphic sections studied in the Fígols-Vallcebre area. See Figure 1 for the situation of columns.**

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 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) Feist and Colombo 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 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

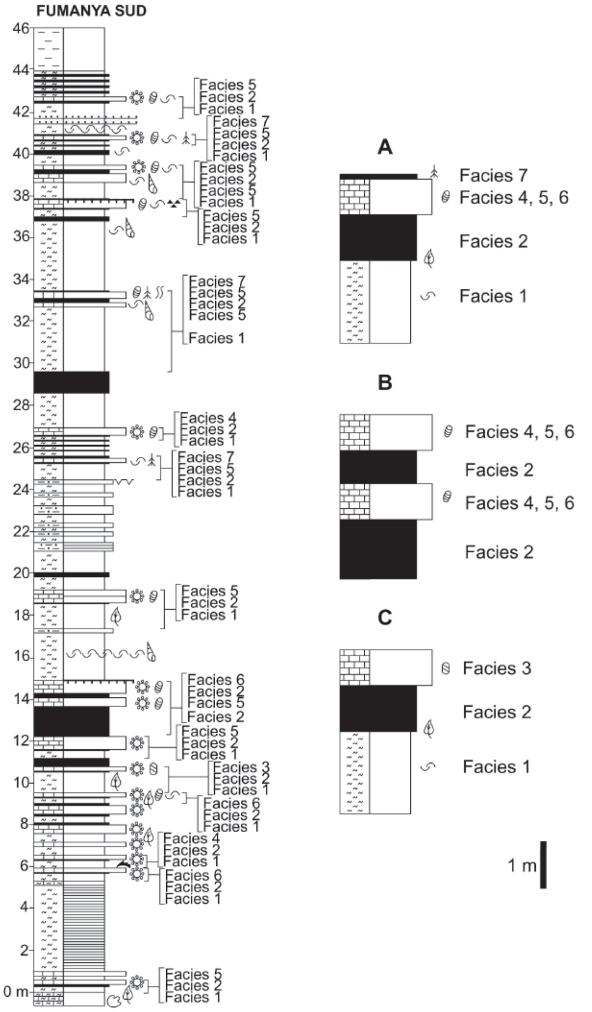

FIGURE 3 | **Detail of Fumanya Sud section with indication of the seven facies defined in the middle Grey Garumnian. Conceptual cycles resulting from the three facies associations (A-C) are shown on the left hand side. See legend of Figure 2.**

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 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) Feist and Colombo 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).

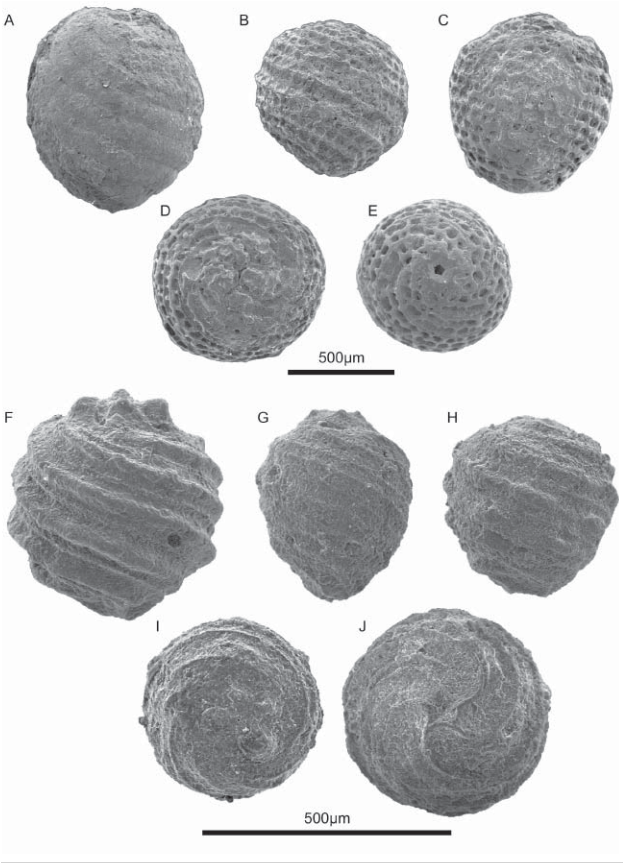

FIGURE 4 | **Charophytes from the Lower Maastrichtian of the Vallcebre syncline. A) *Feistiella malladae*, sample FS-5, lateral view. B to E) *Peckichara cancellata*, sample FS-7, B and C) lateral views, D) apex, E) base. F. to J) *Microchara cristata*, sample FB-4, F to H) lateral views, I) apex, J)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

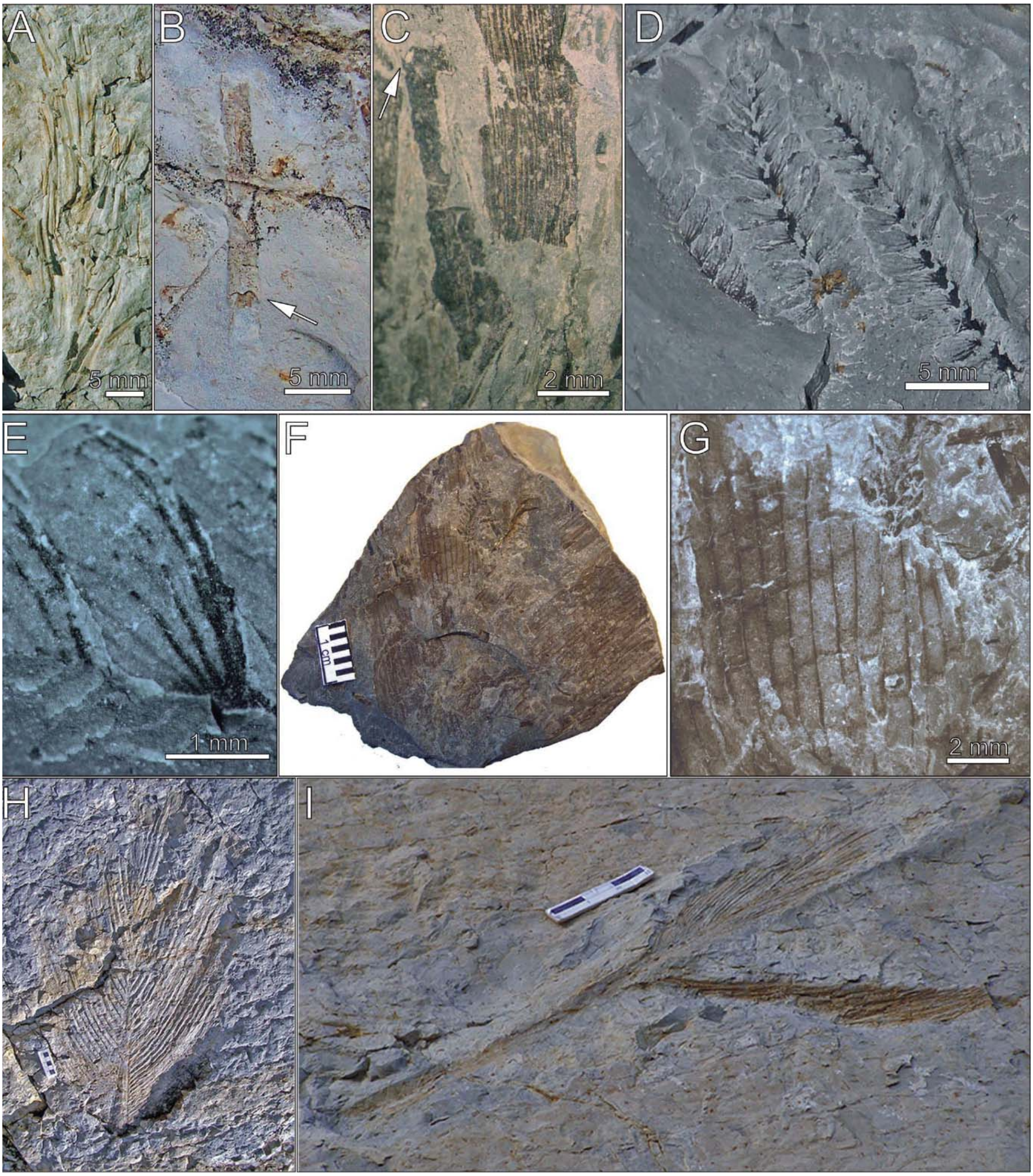

FIGURE 5 | **Vascular plants from the Lower Maastrichtian of the Vallcebre syncline. A to C) remains of *Frenelopsis* sp.; A) branched axes, B) two fragmented and connected internodes showing leaf tips (arrowed), C) branched internodes, two of them showing longitudinal parallel dotted lines. One leaf tip is marked with arrows. 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 young 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) Kvaček and Herman. 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 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.

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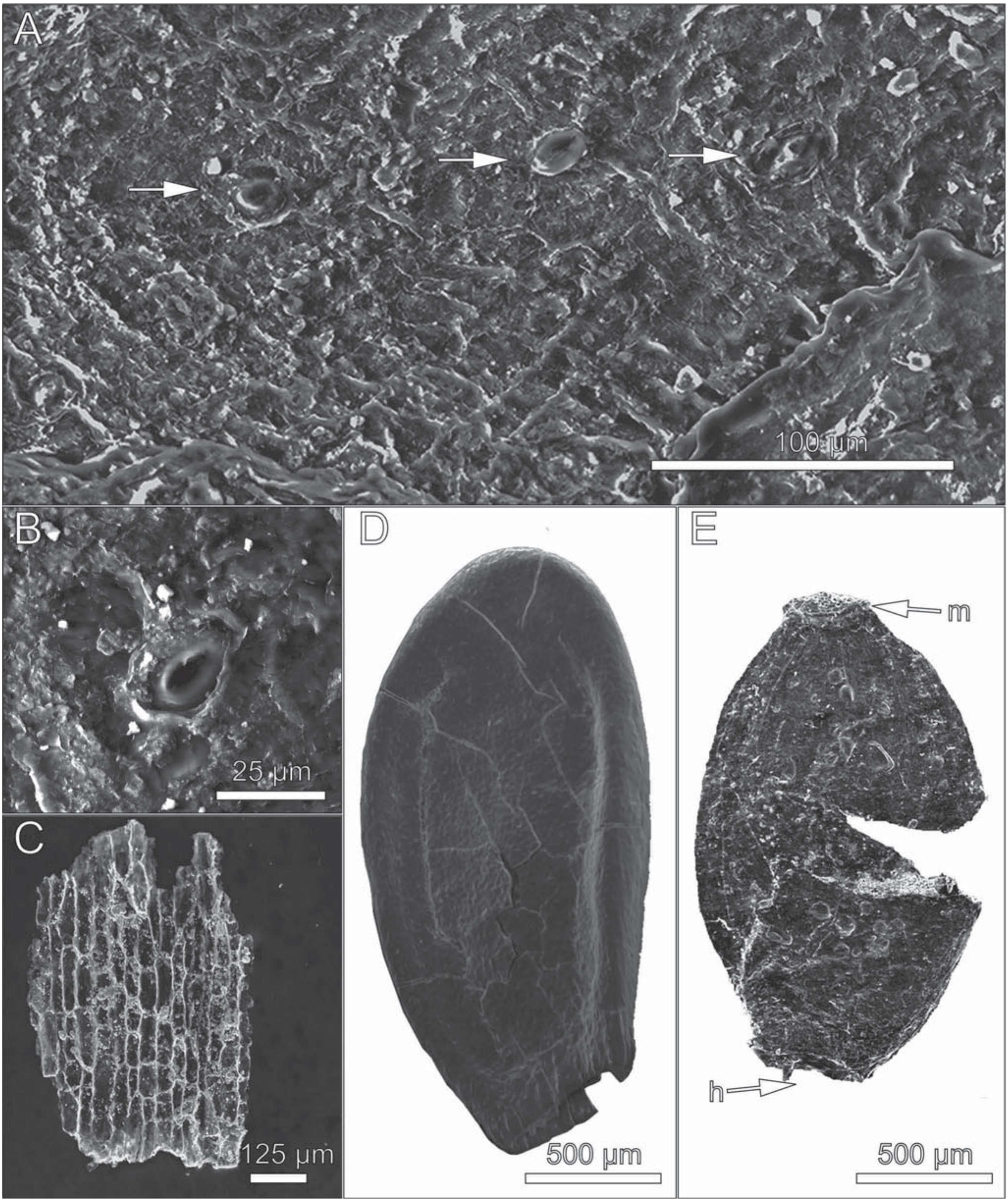

FIGURE 6 | **Vascular plants from the Lower Maastrichtian of the Vallcebre syncline (continued). A) external view of the cuticle showing three aligned stomata forming a row and stomatal pits. B) detail of stomatal pit around a ring with remains of at least four subsidiary cells. C) fragment of cuticle 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 PALAEO-ECOLOGY

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 the 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

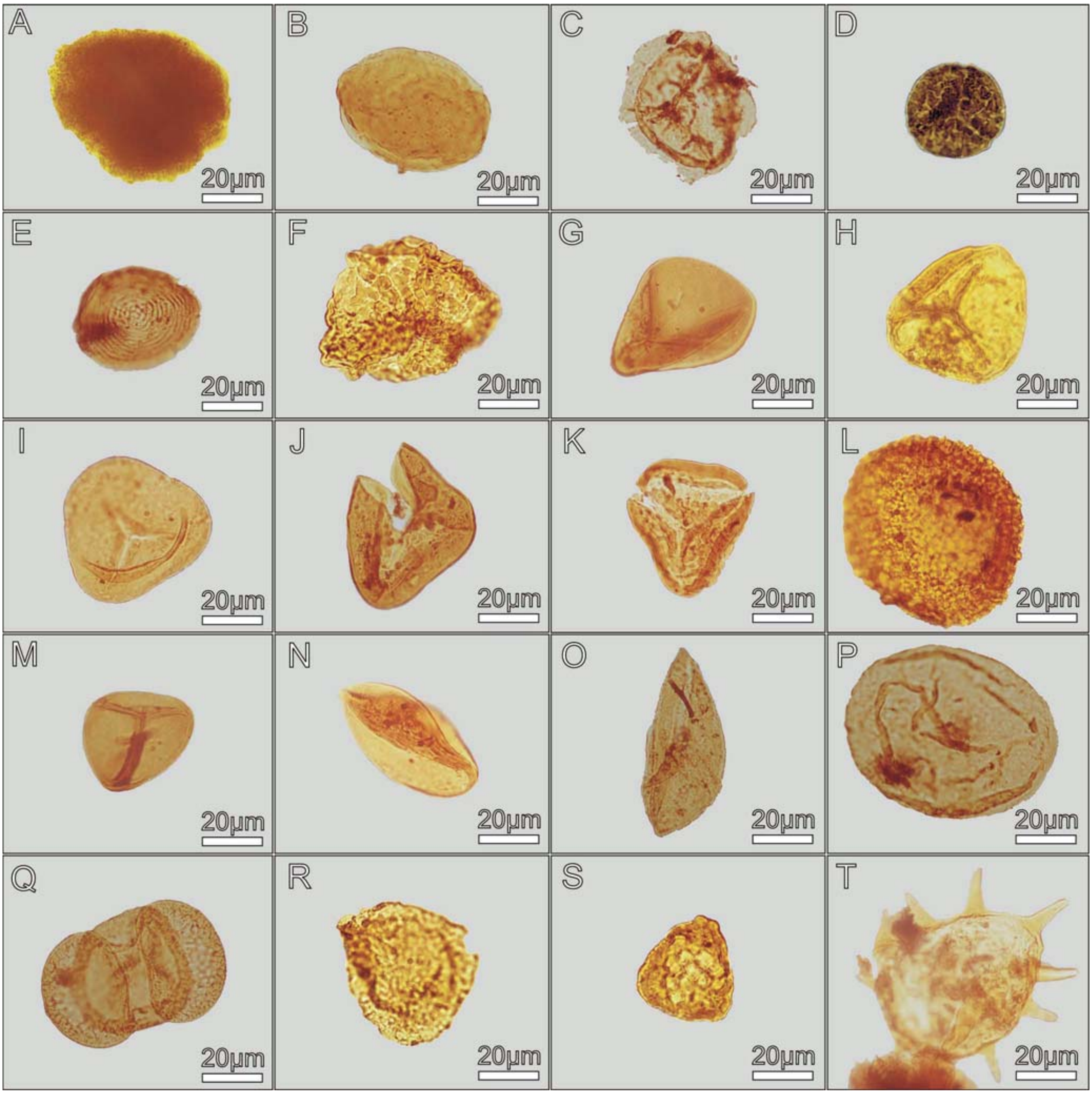

FIGURE 7 | **Palynomorphs from the middle Grey Garumnian of Vallcebre syncline. A) *Oedogonium cretaceum* Zippi, sample FS-23. B) *Ovoidites spriggi* (Cookson and Dettmann) Zippi, sample FS-17. C) *Zlivisporis blanensis* Pacltova, sample FS-17. D) *Hamulatisporis* sp., sample ME-1. E) *Chomotriletes 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.

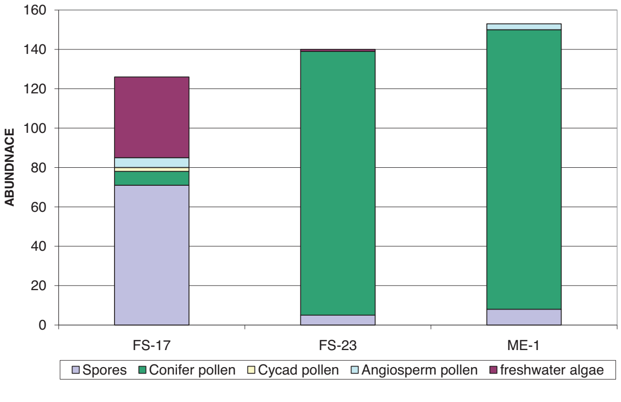

FIGURE 8 | **Diagram showing the abundance of the most representative morphological groups of palynomorphs in the studied samples.**

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 400-500rootlets/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.

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 Mina Esquirol. F) Large brush-like rooting structure attributed to a palm, upon a charophyte limestone at the Mina Esquirol coal mine. G) Monotonous accumulation of minute angiosperm seeds at the base of first coal at Mina Esquirol.**

Other less 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

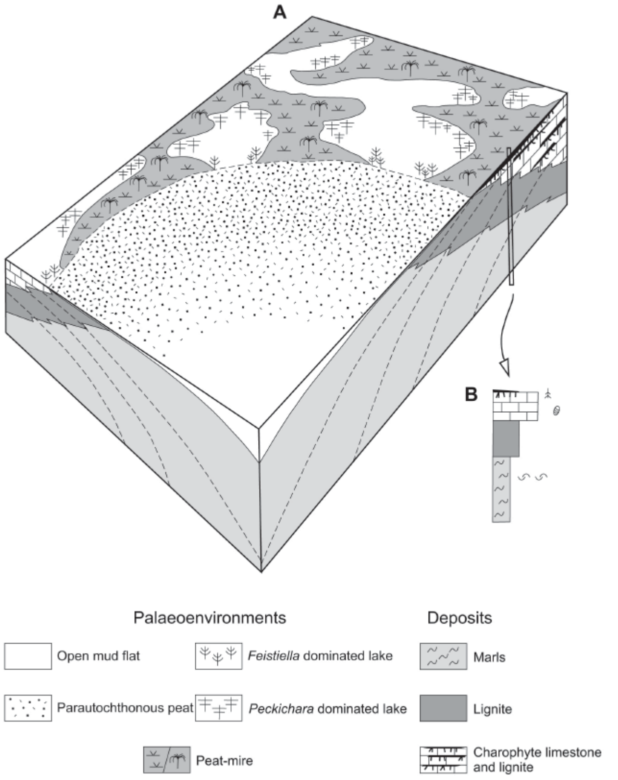

FIGURE 10 | **Palaeoenvironmental and taphonomic reconstruction from the Maastrichtian wetlands of the Vallcebre syncline. Not to scale. A) Palaeoenvironmental and taphonomic diagram showing transport and deposition of plant remains. B) Section showing the vertical development of a basic sedimentary 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 related provisionally 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 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 Early Cretaceous, the gymnosperms dominated in 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 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 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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Article 2

VILLALBA-BREVA, S., MARTÍN-CLOSAS, C. 2011. A characean thallus with attached gyrogonites and associated fossil charophytes from the Maastrichtian of the Eastern Pyrenees (Catalonia, Spain). *Journal of Phycology*, 47: 131-143.

RESUM: S'ha descrit la nova espècie *Clavatoraxis microcharophorus* al Maastrichtià inferior del Pirineu Oriental (Catalunya, Espanya). Els tal·lus presenten girogonits de *Microchara* sp. en connexió anatòmica. Els girogonits s'insereixen mitjançant una roseta bracteal i estan embolcallats en una túnica estructural, formada per una bràctea expandida. Aquesta característica és desconeguda a les caràcies actuals, les quals només presenten incrustacions de calcita semblants a túniques en medis extremadament alcalins i ben il·luminats. Aquesta és la primera vegada que es descriu un fòssil complet de caràcia. L'atribució de restes vegetatives de caràcies al gènere *Clavatoraxis* mostra que aquest gènere no és exclusiu de les clavatoràcies con es pensava prèviament. L'estudi tafonòmic de *C. microcharophorus* sp. nov. i dels altres caròfits fòssils associats, junt amb les anàlisis sedimentològiques i de microfàcies, ha permès caracteritzar l'hàbitat d'aquesta nova espècie dels llacs maastrichtians de Vallcebre. Aquestes algues creixien formant herbeis en les franges de vegetació relativament més profundes dels llacs, i les seves restes es dipositaven en el fons del llac poc oxigenat, on quedaven ben preservades. Un número important d'altres caràcies i porocaràcies vivien en cinturons algals més soms. Aquest és el cas de *Peckichara* sp. i *Munieria grambastii* en els llacs d'aigua dolça. L'altra espècie, *Feistiella malladae*, va ser trobada com parautòctona en llacs salabrosos.

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A CHARACEAN THALLUS WITH ATTACHED GYROGONITES AND ASSOCIATED FOSSIL CHAROPHYTES FROM THE MAASTRICHTIAN OF THE EASTERN PYRENEES (CATALONIA, SPAIN)[1]

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The new species *Clavatoraxis microcharophorus* is described from the Lower Maastrichtian of the Eastern Pyrenees (Catalonia, Spain). *Microchara* sp. gyrogonites were found in anatomical connection with this thallus, attached to bract-cell rosettes and coated by a structural tunica, formed by an expanded bract cell. This is a feature unknown in extant characeans, which only display lime incrustations similar to tunicae in extremely alkaline and well-illuminated environments. This is the first time that a complete fossil characean is described. The attribution of characean vegetative remains to the genus *Clavatoraxis* shows that this genus is not exclusive of clavatoraceans as previously thought. The taphonomic study of *C. microcharophorus* sp. nov. and associated fossil charophytes, along with sedimentological and microfacies analyses, has enabled us to characterize the habitat of this species in the Maastrichtian lake of Vallcebre. They grew forming meadows, and their remains were deposited in the poorly oxygenated lake bottom, where they were well preserved. A number of other characeans and porocharaceans were living in shallower belts. This was the case for *Peckichara* sp. and *Munieria grambasti* in the freshwater lacustrine meadows. Another species, *Feistiella malladae*, was found parautochthonous in brackish lakes.

Key index words: **Charophyta; lacustrine facies analysis; Maastrichtian; paleoecology; Pyrenees; taphonomy**

Abbreviation: **MGSCB, Museu Geològic del Seminari Conciliar de Barcelona**

The fossil record of charophytes is one of the most complete among fossil plants. It extends from the upper Silurian to the present and consists mainly of the calcified female fructifications, gyrogonites and utricles, and vegetative remains (Feist et al. 2005). Charophyte thalli are extremely abundant in lacustrine limestone, a type of rock that in some cases can be built up of charophyte thalli and is then called a ''characeite'' (Soulié-Märsche et al. 2010). In spite of this abundance, research on fossil charophytes has mainly been focused on the study of sieved disperse fructifications, which are extremely useful charophyte remains in geology, especially for biostratigraphic correlation.

The pioneering studies of Unger (1852) and Heer (1855) reported for the first time the occurrence of fossil vegetative remains of charophytes in the Tertiary of central Europe. Subsequently, only a few modern studies were devoted to charophyte thalli. Kidston and Lang (1921) were the first to describe a form taxon on the basis of a charophyte thallus. The subgenus, now the genus *Palaeonitella*, is an ecorticate thallus permineralized in the Early Devonian Rhynie chert from Scotland. The fructifications associated with, but not attached to, this thallus were not described until recently by Kelman et al. (2004). The first complete fossilized charophyte was described by Harris (1939) and consisted of Lower Cretaceous, exceptionally well-preserved silicified specimens from the English Purbeck. The attached fructifications enabled him to relate this plant to the extinct family Clavatoraceae, specifically to *Clavator reidii.* Harris (1939) also described a new form genus, *Charaxis*, for thalli similar to extant *Chara.* Other silicified clavatoracean plants include *Echinochara spinosa*, described by Peck (1957) in the Kimmeridgian of the Morrison Formation, United States, and *Diectochara andica*, described by Musacchio (1971) in the Barremian La Amarga Formation of Argentina. Another type of fossil thallus consists of vegetative remains without attached fructifications preserved as lime encrustations. To this type belong the Late Permian thallus of *Palaeonitella tarafiyensis*, from the Khuff Formation of Saudi Arabia (Hill and El-Khayal 1983), and a complete association of thalli described in the Barremian of La Huérguina Formation in Spain, composed of four species of genera *Palaeonitella*, *Charaxis*, and *Clavatoraxis* (Martín-Closas and Diéguez 1998). Less common are the thalli substituted by kaolinite and mica from genera *Octochara* and *Hexachara*, found in the Devonian Witteberg Group of South Africa (Gess and Hiller 1995).

As a result of this research scenario, phycologists generally believed that well-preserved charophyte

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thalli are extremely rare fossils, only occurring under exceptional preservation conditions. This would explain why most charophyte taxonomists paid little attention to the study of fossil thalli, leaving this discipline almost unexplored until today. However, our results indicate that whole charophyte plants can be reconstructed from fragments of calcified vegetative remains, which are abundant in lacustrine limestones. The different portions of the plant found dispersed in the sediment can be related to each other by the intermediary of common structures, very much in the same way as a jigsaw puzzle is constructed. The method of reconstructing tridimensional thalli from bidimensional thin sections is well known for other groups of biocalcified plants, such as dasicladalean and halimedacean chlorophytes (e.g., Barattolo 2006) but has not been used previously for charophytes. Through this procedure, we were able to reconstruct for the first time a whole fossil plant of a characean, the only living charophyte family, since the other whole-plant fossil charophytes known to date belong to the extinct family of clavatoraceans (*C. reidii*, *E. spinosa*, and *D. andica*) or to poorly known Paleozoic families (genera *Hexachara* and *Octochara*). Finally, taphonomic and microfacies analyses provided valuable information about the habitat of the new species and the associated charophytes.

MATERIALS AND METHODS

Three stratigraphic sections were raised to compile a 100 m composite section of the Grey Garumnian unit in the Vallcebre syncline (Figs. 1 and 2). They were measured along the mountain road of Cal Sant (base coordinates 42°10′29″ N, 01°49′44″ E; top coordinates 42°10′33″ N, 01°49′31″ E) and in the opencast coal mines of Font del Bullidor (base coordinates 42°10′30″ N, 01°49′7″ E; top coordinates 42°10′34″ N, 01°49′3″ E) and Fumanya Sud (base coordinates 42°10′50″ N, 01°47′42″ E; top coordinates 42°10′52″ N, 01°47′47″ E). These sites are located between the village of Fígols and the Fumanya pass, to the north of the town of Berga (Catalonia, Spain). Sedimentological analysis was carried out with field data, and 33 carbonate rock samples were selected after systematic sampling of the stratigraphic sections. Thin sections, ~30 μm thick, were prepared after the oriented samples had been cut parallel and perpendicular to the bedding surface. About a dozen 2.5 × 5 cm slides were prepared for each rock sample and studied using optical microscopy Motic B3-220ASC (Motic Group Co. Ltd., Xiamen, China) from these thin sections. Each charophyte portion was oriented with reference to the producing plant, and in one species, there were sufficient data to reconstruct the whole plant tridimensionally. In other cases, only fragmentary data on the thalli were obtained; in particular, data concerning the attachment of the associated fructifications were absent. These remains were only used for paleoecological purposes in combination with taphonomic and sedimentological analyses. Samples are deposited in the Museu Geològic del Seminari Conciliar de Barcelona (MGSCB).

Geological and paleontological setting. The Vallcebre Basin forms a syncline located in the Lower Pedraforca thrust sheet and has minor decametric to hectometric thrusts in its core (Vergés et al. 1994) (Fig. 1). The origin of the basin is related to the onset of successive thrust sheets, which during the Late Cretaceous and Cenozoic finally led to the formation of piggyback basins and the uplift of the whole Pyrenean range (Muñoz et al. 1986, Puigdefàbregas et al. 1986).

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 nearshore calcarenitic limestones (Terradets Formation; Vergés et al. 1994). 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 Basin is up to 850 m thick (Vergés et al. 1994) and was divided by

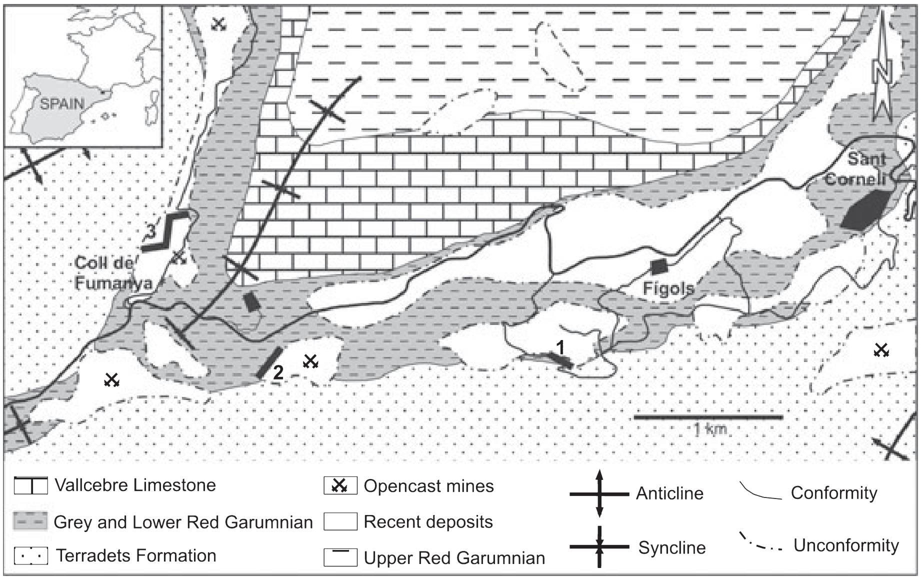

FIG. 1. Geological map of the study area with location of the stratigraphic sections represented in Figure 2.

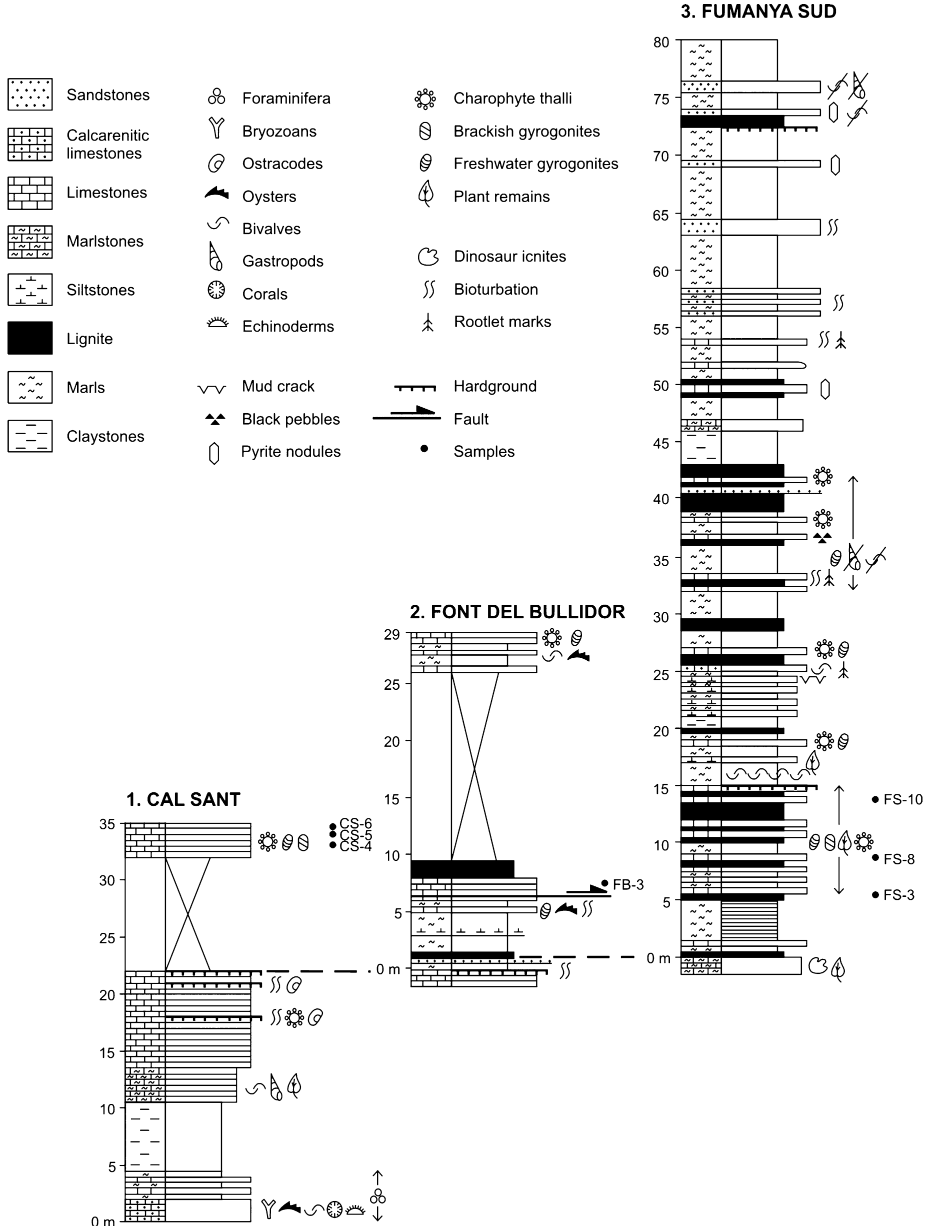

Fig. 2. Stratigraphic sections studied in the Fígols-Vallcebre area. See Figure 1 for the situation of columns.

Rosell et al. (2001) into four lithological units, of which the transitional basal unit (Grey Garumnian) was the subject of our study. The Fígols-Vallcebre composite section studied includes the whole Grey Garumnian unit and is formed by a heterolithic succession, up to 100 m thick (Fig. 2). Micritic marlstones comprise the dominating lithology at the base and contain frequent dinosaur trackways at the top. These trackways are close to the Campanian–Maastrichtian boundary as indicated by paleomagnetic data (Oms et al. 2007). Micritic marlstones are covered by a succession of alternating organic marl, lignite, and charophyte limestones, which supplied the charophyte samples studied. A succession of variegated siltstone with dinosaur eggshell fragments represents the top of the Grey Garumnian. This succession was deposited in peritidal to supratidal environments, including brackish lagoons at the base, followed by well-developed wetlands with brackish marshes and freshwater lakes and ending with flood plains to the top (Rosell et al. 2001).

The lower Grey Garumnian of Vallcebre yields a rich fauna, including ostracodes, mollusks, and vertebrates (Vila et al. 2009). The latter are represented by dinosaurs, crocodiles, chelonians, and batoid fishes (Schulp and Brokx 1999, Vila et al. 2005, 2009). Plant assemblages from the Vallcebre Basin have been poorly studied to date. Charophyte assemblages were analyzed with a biostratigraphic scope by Feist and Colombo (1983), Masriera and Ullastre (1983), Médus et al. (1988), and Ullastre and Masriera (1983). The gyrogonite assemblage documented in these studies is formed by *Microchara cristata* Grambast 1971 and *Peckichara cancellata* Grambast 1971 from the limestone, lignite, and organic marl terms, while the clavatoracean *Clavator brachycerus* (Grambast 1962) Martín-Closas 1996 (syn. *Septorella brachycera* Grambast 1962) and the characean *Peckichara sertulata* were found in variegated siltstones, at the top of the section. These assemblages indicate Lowermost Maastrichtian age for charophyte-bearing beds in the Vallcebre Basin, which is compatible with the occurrence of dinosaur fauna and recent paleomagnetic dating (Oms et al. 2007). The information on vascular plant assemblages in the basin was obtained from palynological and megafossil plant remains. Megaremains are dominated by the conifer *Frenelopsis* sp. together with rare cycad leafy remains and a number of angiosperm leaves (*Sabalites longirhachis* and *Pandanites* sp.) and seeds (Marmi et al. 2008, Riera et al. 2010). The palynological assemblage reported by Médus et al. (1988) from Vallcebre does not correspond to the limestone and lignite succession studied for charophytes but belongs instead to higher levels in the section, which were sampled to characterize the Cretaceous-Tertiary boundary. The palynoflora contains Normapolles pollen, such as *Trudopollis protrudens* and other triporate pollen along with abundant trilete fern spores. The latter are very frequent throughout the whole Maastrichtian in the Pyrenean basin (Fernández-Marrón et al. 2004).

RESULTS

Systematic paleontology.

Subkingdom: Viridaeplantae Cavalier-Smith 1981

Division: Charophyta Migula 1897

Class: Charophyceae Rabenhorst 1863

Order: Charales Dumortier 1829

Family: Characeae S. F. Gray 1821

Form genus: Clavatoraxis Martín-Closas and Diéguez 1998

Clavatoraxis microcharophorus Villalba-Breva et Martín-Closas **sp. nov.** (Figs. 3–5).

Diagnosis: Thallus of the *Clavatoraxis* type with spine-cell rosettes developing in each third cortical cell, principal cells (bearing the spines) similar in diameter to secondary cells; cortex is therefore triplostichous and isostichous. Stipulodes twice the number of branchlets, in one row (haplostephanous). Branchlets ecorticate, 14 in each whorl, with bract cells forming rosettes. Gyrogonites, 1–3, attached to a bract-cell rosette at the branchlet nodes. Each gyrogonite is completely covered by an expanded bract cell, which forms a structural tunica. Gyrogonites are attributed to the genus *Microchara*.

Holotype: Number 76961 of the MGSCB (Figs. 3F and 4).

Paratypes: Numbers 76959, 76960, and 76962 of the MGSCB (Fig. 3, A–E).

Type locality: Coal mine at Fumanya Sud, 9.5 km northwest of the town of Berga (Catalonia, Spain).

Type layer: Limestones, Grey Garumnian, 9 m above the structural surface with dinosaur trackways formed at top of the marlstone layer, named the ''concrete level'' by Oms et al. (2007).

Age: Lowermost Maastrichtian according to charophyte assemblage (Feist and Colombo 1983) and paleomagnetic data (Oms et al. 2007).

Derivation of name: From the Latin *Microchara*, referring to the name of a gyrogonite genus and from the Greek *phorus*, meaning ''which bears.''

Repository: Geological Museum of the Seminari Conciliar de Barcelona (MGSCB).

Description. Internodes: The longest internode measured is 3.6 mm long but is not in contact with a node at either end. Internodes range from 0.2 to 0.8 mm in diameter. They are corticated and covered by spine cells organized in rosettes. The central tube represents the internodal cell. Internodal cells are from 345 to 595 μm across on the main axis and 180 to 340 μm wide on secondary axes (Fig. 3A).

Cortical cells: Cortication is formed by a variable number of cortical cells. There were 14 near the only available transversal section of a node, but in transversal sections of internodes, their number varies from 9 to 18 (Fig. 3A). Cortical cells are similar in size (isostichous) at each specific level of the internode and are arranged longitudinally, without coiling. However, the size of cortical cells changes between internodes, ranging from 65 to 135 μm in diameter on main axes, while on secondary axes, it ranges from 35 to 90 μm in width. In some tangential sections, we observed two rows of bare cortical cells intercalated between the cortical cells bearing spine-cell rosettes. This finding suggests that the latter corresponds to primary cortical cells, which indicates that the cortication is triplostichous.

Spine-cell rosettes: Spine-cell rosettes are hemispherical structures, formed by up to 15 drop-shaped spine cells, visible in deep tangential sections. In superficial tangential sections, which are much more frequent, only about five to six cells are visible. On the main axis, spine-cell rosettes are 600 μm in diameter and ~170 μm high. They are inserted in the primary cortical cells at regular intervals of ~360 μm. On secondary axes, spine-cell rosettes are formed by the same number of spine cells as on the primary axis, but they are smaller, 200–300 μm in diameter and 60–135 μm high, and are inserted in the primary cortical cells at irregular intervals of 60–560 μm (Fig. 3B).

Nodes: Only one node was identified in near-transversal section. The node is 0.5 mm in diameter, bears whorls of ~14 branchlets (only seven visible in the half of the near-transversal section available, Fig. 3C), and has at least twice in number of stipulodes.

Stipulodes: Stipulodes are arranged in a single whorl, thus haplostephanous, directed downward, and cylindrical in shape. They are ~60 μm across, and the calcified portion is ~200 μm long. We observed 12 stipulodes in the half of the near-transversal section available (Fig. 3C), suggesting that the total number is probably close to double that of the branchlets (i.e., 28).

Branchlets: Branchlets are ecorticate. The incomplete longitudinal sections available show 1 mm long portions, suggesting that branchlets were short, about a few millimeters long. Branchlet internodal cells range from 100 to 190 μm in diameter, including the

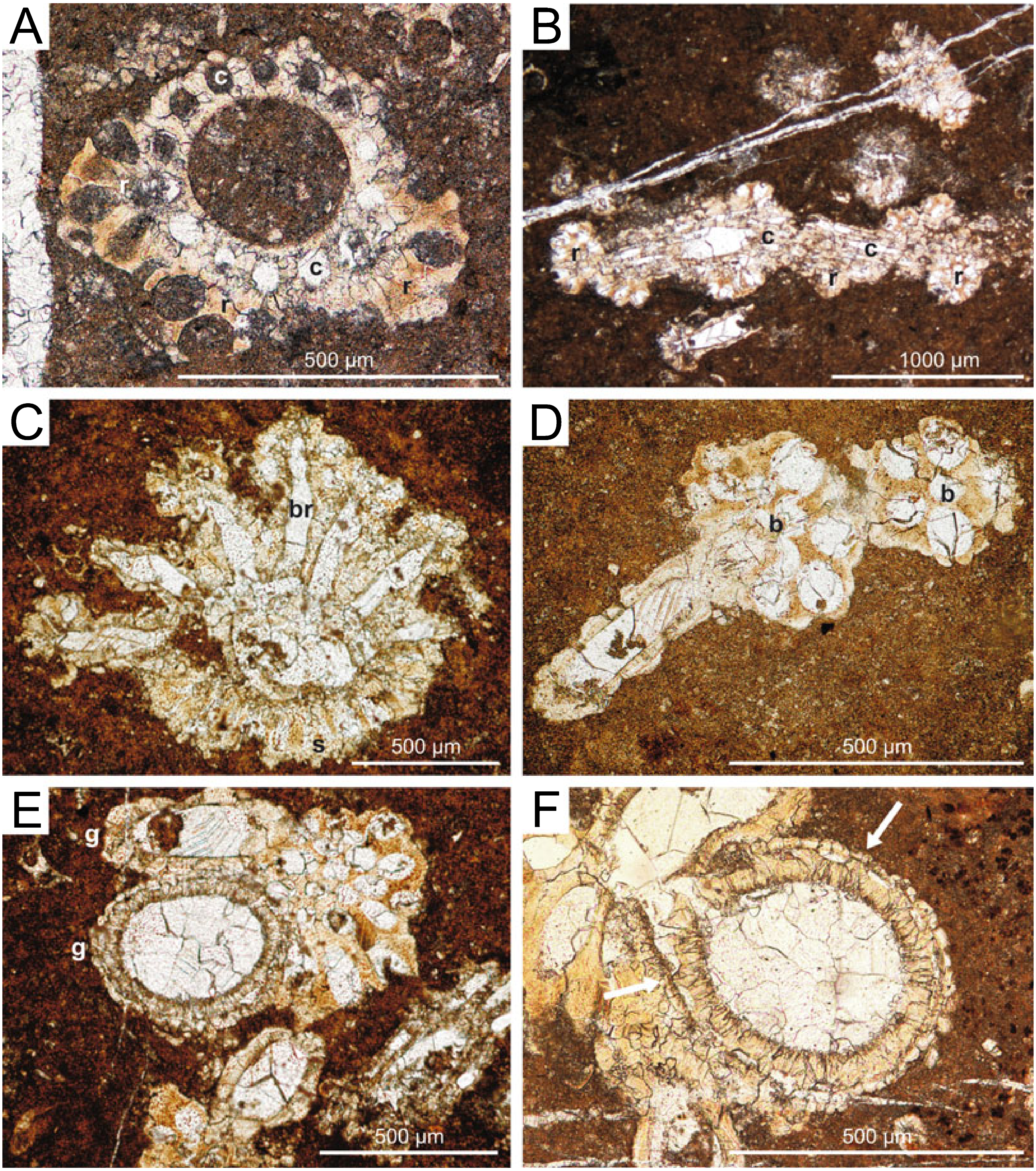

FIG. 3. *Clavatoraxis microcharophorus* sp. nov. (A) Transversal section through secondary axis showing cortical cells (c) and spine-cell rosettes (r); thin section 76960. (B) Tangential section through secondary axis showing cortical cells (c) covered by spine-cell rosettes (r); thin section 76961. (C) Near-transversal section through a node showing arrangement of stipulodes (s) and branchlets (br); thin section 76959. (D) Longitudinal section of a branchlet showing arrangement of two bract-cell rosettes (b); thin section 76962. (E) Tangential section through a bract-cell rosette bearing two gyrogonites (g); thin section 76962. (F) Longitudinal section through a gyrogonite ornamented with a midcellular crest (arrows) attached to a bract-cell rosette and covered by a tunica; thin section 76961. All thin sections belong to sample FS-8.

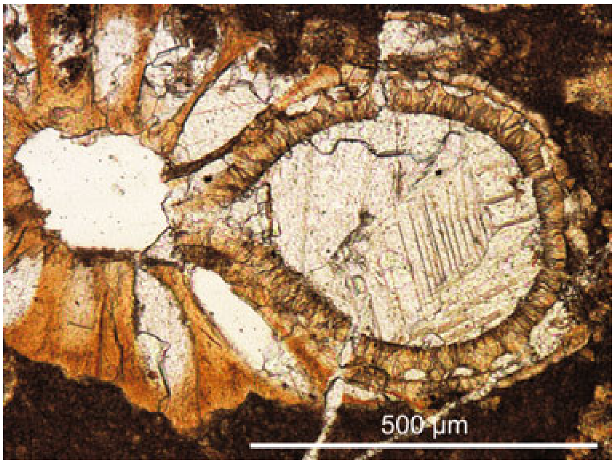

FIG. 4. Detail of longitudinal section through the holotype gyrogonite (thin section number 76961) showing its attachment to a bract-cell rosette and its coat formed by a tunica.

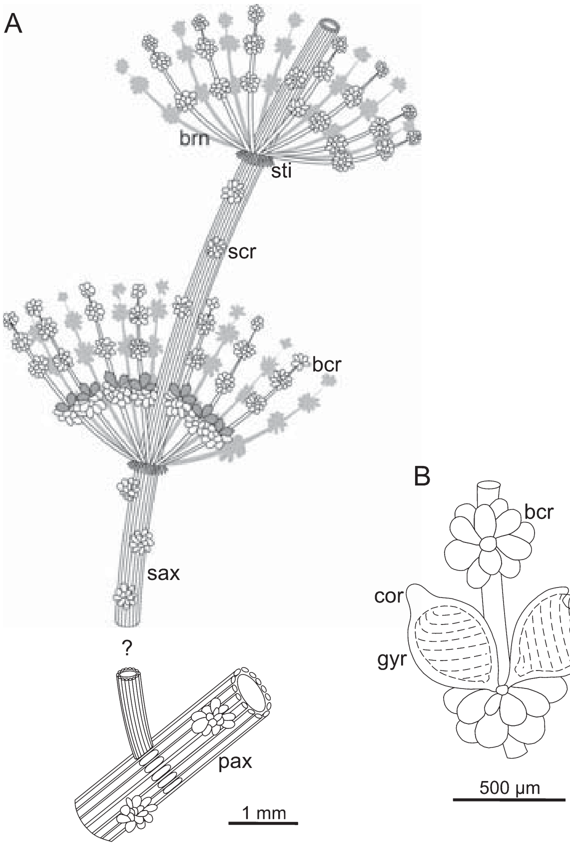

FIG. 5. *Clavatoraxis microcharophorus* sp. nov. (A) Reconstruction of the whole fossil plant. (B) Detail of a branchlet with insertion of two gyrogonites in a bract-cell rosette, one of them with coronula (not observed). bcr, bract-cell rosette; cor, coronula; gyr, gyrogonite; pax, primary axis; brn, branchlet; sax, secondary axis; scr, spine-cell rosette; sti, stipulodes; stu, structural tunica.

lime crust. They bear bract-cell rosettes organized in nodes. Bract-cell rosettes leave free intervals between them, allowing the bare internodal cell to crop out. These bare spaces are gradually shorter toward the apex of the branchlet (Fig. 3D).

Bract-cell rosettes: Bract-cell rosettes are ~200–300 µm in diameter and 55–135 µm high and are attached at the nodes of branchlets, forming spherical structures of wedge-shaped cells, ~200–300 µm in diameter and 55–135 µm high (Fig. 3D). The basal rosettes are larger, up to 550 µm in diameter and formed by up to 15 wedge-shaped bract cells, 160–280 µm high each. Some large bract-cell rosettes, probably basal in the branchlet, were fertile structures. They bear up to three gyrogonites per rosette (Fig. 3E). An expanded bract-cell coats the gyrogonite, forming a tunica (Figs. 3F and 4). The tunica was already known to occur in disperse gyrogonites of the genus *Microchara* (see *Microchara vestita* Castel 1969 and *Microchara tunicata* Grambast and Gutiérrez 1977), but it was interpreted as a physiological crust produced by enhanced calcification in highly alkaline water. The material studied shows that the tunica of *Microchara* is not a physiological feature but a structural element formed by an expanded calcified bract cell, which completely covers the gyrogonite. Gyrogonites of *Microchara laevigata* showing remains of vegetative elements that are similar to these expanded bract cells were shown by Grambast and Gutiérrez (1977, pl. 13, figs. 5 and 6).

Gyrogonites: Gyrogonites are ovoidal-spheroidal in shape and small in size, 470–560 µm high and 395–495 µm wide. Isopolarity index [value of (length/width) × 100] ranges from 112 to 130. Spiral cells are 66–78 µm wide and ornamented with a midcellular crest (Figs. 3F and 4). The apex is flat and shows a limited apical thinning in thin section. The base is pointed with a short basal column. While assignation of the attached gyrogonites to the genus *Microchara* would seem to be straightforward, more characters are needed to confirm the specific attribution. Hence, the gyrogonites are assigned to *Microchara* sp.

Comparison. The main character separating *Clavatoraxis* from other corticated organ genera, such as *Charaxis*, are the spine-cell rosettes. The new species *C. microcharophorus* is quite different from the two other species of *Clavatoraxis* described, both of which are from the Upper Barremian of Las Hoyas near Cuenca (Iberian Chain, Spain). It differs from *Clavatoraxis robustus* Martín-Closas and Diéguez 1998 in its slender appearance and because *C. robustus* bears closely distributed and spirally arranged spine-cell rosettes, with long, club-shaped spine cells completely covering the thallus, unlike the new species. The cortication of *C. robustus* is spiral, whereas it is uncoiled in *C. microcharophorus* sp. nov. Furthermore, six cortical cells occur near the nodes of *C. robustus*, instead of ~14 in the new species. The two species are similar in bearing ecorticate branchlets with bract-cell rosettes arranged in nodes. The new species does not correspond to *Clavatoraxis* *diaz-romerali* Martín-Closas and Diéguez 1998 either, since this species has a narrower internodal cell (<250 µm in diameter) and smaller spine-cell rosettes (<350 µm in diameter) and its cortication is formed by six cells near the nodes. Branchlets and bract-cell rosettes of *C. diaz-romerali* are again similar to other *Clavatoraxis* species.

Gyrogonites attached to basal bract-cell rosettes of *C. microcharophorus* sp. nov. have been attributed to *Microchara* sp. and show similitude to thin sections of *M. cristata* described by Grambast (1971, pl. 29, figs. 8–10). Disperse fructifications of this species were reported by Feist and Colombo (1983) in marls intercalated with the limestones studied. Both the available thin sections from Fumanya and the gyrogonites of the type population of *M. cristata* are ovoid in shape and small in size (450–625 µm high and 350–500 µm wide). Their isopolarity index (from 110 to 133) and the width of their spiral cells (50–78 µm) are similar. They are typically ornamented with a midcellular crest, but the details of the ornamentation are not visible in the thin sections available. The apex is rounded and the base is pointed, as in *M. cristata*, but, again, some details are not visible. Were the equivalence between gyrogonites in the thin sections and disperse gyrogonites of *M. cristata* to be established in future research, *C. microcharophorus* sp. nov. could be synonymized with *M. cristata*, and the latter species emended to include the vegetative characters.

Gyrogonites of the new species are quite different from other Upper Cretaceous *Microchara* species from which the thin sections were described. Thus, *Microchara leiocarpa* Grambast 1971, *M. tunicata* Grambast and Gutiérrez 1977, and *M. laevigata* Grambast and Gutiérrez 1977 are either not ornamented or do not show a midcellular crest. Other charophyte genera reported as disperse gyrogonites from the Pyrenean Upper Cretaceous are largely different in ornamentation, shape, or size.

The thin sections shed new light on the different origins of gyrogonite coats like tunicae in charophytes. The formation of such a coat by physiological precipitation of calcite crystals is a frequent phenomenon in several living species of the genus *Chara*, such as *Chara vulgaris* or *Chara hispida* (Soulié-Märsche 1989, pp. 72 and 144). According to Soulié-Märsche et al. (2008), the formation of calcite crusts upon gyrogonites in extant species is controlled by the water chemistry (alkaline lakes) and good illumination of the growth area.

Calcite incrustations on extant *Chara* and on some disperse *Microchara* fructifications (e.g., *M. vestita* in Feist-Castel 1975) comprise thick, very irregular, and nodular envelopes, which cover incompletely the upper half of the gyrogonite, frequently including the coronular cells. The base of the gyrogonite is often devoid of such a physiological coat, allowing the gyrogonite spiral cells to be seen from the outside. In the external part of these crusts, the imprints of vegetative elements, such as thalli or bract cells, may be preserved. In contrast, the structural tunica described here is formed by a smooth, regular, thin envelope, clearly attached to the base. Our results show that the structural tunica of *Microchara* sp. corresponds to an expanded bract cell, probably attached to the basal rosette of a branchlet.

In botany the term ''tunica'' has a wide meaning. Thus, Harris and Harris (1994) define tunica as an outer coating of seeds or bulbs without reference to its anatomy. In charophyte paleontology, this term has been used so far for lime incrustations upon gyrogonites, as proposed by Castel (1969) for genus *Microchara*. This use agrees with the definition given above; however, from all lime incrustations formed upon gyrogonites, only the incrustations based on a structural element can be called properly a tunica. In contrast, the exclusively physiological incrustations, such as those observed upon gyrogonites of extant *Chara*, should be better termed merely crusts. Also, as noted by Grambast (1962), a charophyte tunica differs from a utricle because the latter is a pluricellular structure that displays a well-established symmetry, as in the fossil order Sycidiales and family Clavatoraceae (Feist et al. 2005).

Discussion. Spine-cell rosettes are hemispherical structures unknown in extant charophytes. They were first reported to occur on internodes and branchlets of the clavatoracean species *C. reidii* by Harris (1939). Later on, Martín-Closas and Diéguez (1998) created the form genus *Clavatoraxis* to include sterile remains bearing spine-cell rosettes, and they assumed that this structure was unique to the thallus of the extinct family Clavatoraceae. Now, small characean gyrogonites attributed to *Microchara* sp. have been found attached to this type of thallus, clearly indicating that *Clavatoraxis* is not exclusive of clavatoraceans as previously thought.

The new species *C. microcharophorus* provides significant characters for a better understanding of the genus *Microchara*, which was difficult to distinguish from the genus *Chara* when only the information supplied by disperse gyrogonites was available. Whereas Grambast (1959) and Feist et al. (2005) noted that the most significant difference between the two gyrogonite genera was the size of the fructification, it is now clear that the two plants were clearly distinct in their vegetative organs, which belong to two different form genera, *Charaxis* for *Chara* and *Clavatoraxis* for *Microchara*.

The different portions of the plant found in thin sections can be related to each other, and as result, a reconstruction of the whole fossil plant of *C. microcharophorus* sp. nov. is proposed (Fig. 5).

Taphonomy and paleoecology. The comparison of sedimentology and microfacies analyses with paleontological results, including taxonomy and taphonomy, leads us to the characterization of the habitat and the paleoecology of the new species *C. microcharophorus* and associated fossil charophytes.

Sedimentology: The charophyte-rich limestones studied belong to small-order sedimentary cycles. The most abundant facies association is formed by basal organic marlstones followed by lignite and charophyte limestones at the top. This association is sometimes simplified to the reiteration of the lignite and limestones. These cycles are repeated dozens of times in the sections studied at Fumanya.

Marlstones contain locally low-diversity assemblages of mollusks dominated by brackish to freshwater taxa (Unionidae, *Corbicula laletana*, *Cerithium* sp., *Deianira* sp., *Melanopsis* sp., and *Pyrgulifera* sp.). Babinot et al. (1983) also report brackish ostracodes from this unit. Lignite upon previous marlstones forms tabular beds, <1.5 m thick and with lateral continuity of >1 km. The base of the first lignite seam at Fumanya Pass is a structural surface of kilometric continuity that shows abundant dinosaur trackways (Vila et al. 2005), abundant *S. longirhachis* leaf adpressions (Marmi et al. 2008), and massive accumulations of *Frenelopsis* sp. internodes (Riera et al. 2010). These lignite layers do not show root traces at their base, suggesting that they were formed by allochthonous accumulation of organic matter overlaying brackish marlstones. The water salinity under which these lignites were accumulated is unknown and may have been variable in the basin.

Charophyte limestones represent the end term of the low-order sedimentary cycles described. They are well-bedded wackestones-packstones, up to 1.5 m thick, and contain abundant charophyte thalli

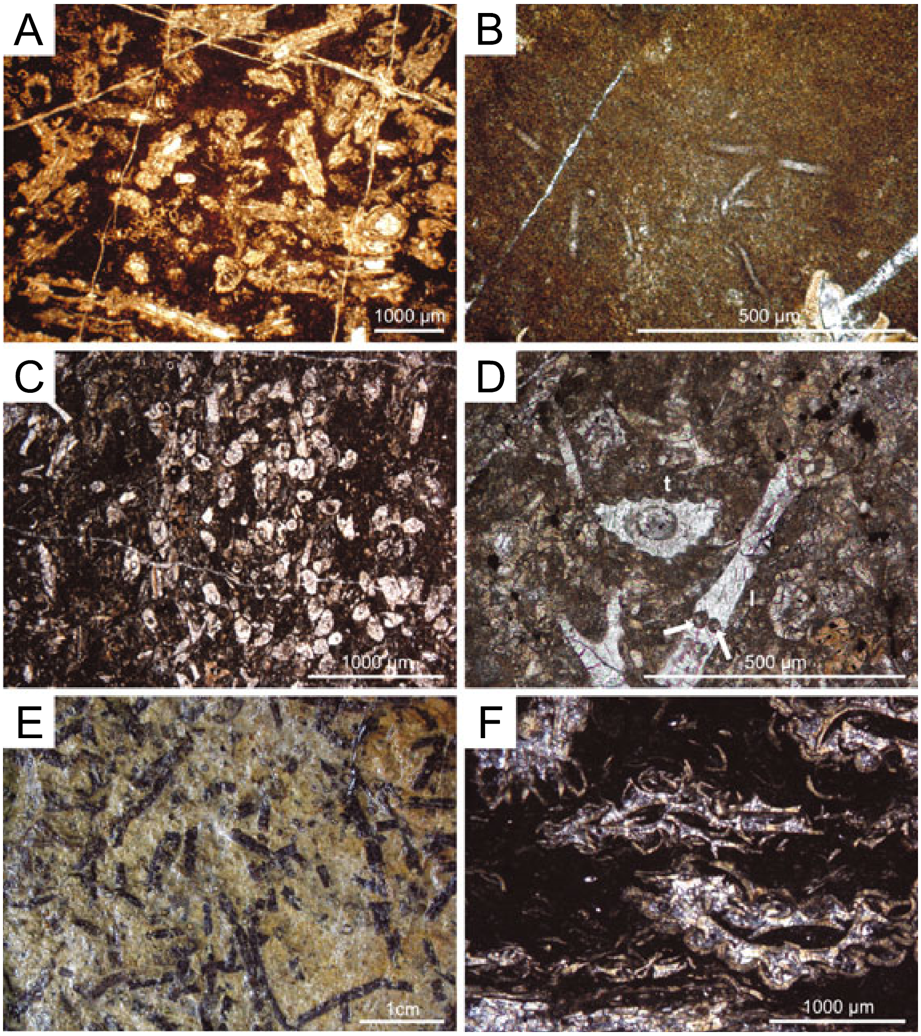

FIG. 6. Components distinguished in the microfacies analysis. (A) Wackestone-packstone of the new species *Clavatoraxis microcharophorus*; thin section 76961, sample FS-8. (B) Small calcified filaments attributed to the cyanobacteria *Girvanella* sp.; thin section 76958, sample FS-8. (C) Packstone of *Munieria grambasti*; thin section 76956, sample FS-3. (D) Transversal and longitudinal sections through an internode of *Munieria*. The transversal section (t) shows a triangular outline and crenulations corresponding to the internal side of cortical cells. The longitudinal section (l) shows the scars of two nodal cells (arrows); thin section 76956, sample FS-3. (E) Macroscopic view of large thalli of the *Charaxis* type associated to *Peckichara*; sample CS-6. (F) Transversal sections of collapsed *Charaxis* thalli showing poor calcification of cortical cells; thin section 76965, sample CS-6.

and gyrogonites, mainly belonging to *Peckichara* and *Microchara*. These genera suggest that in most cases charophyte limestones were deposited in freshwater lakes. In rare cases, the lake salinity may have been higher, as suggested by the occurrence of homogenous assemblages of porocharacean gyrogonites in some layers. Charophyte-rich limestones can be overtopped by lignite layers a few centimeters thick showing organic rootlet marks that penetrate the underlying layer. These rootlets provide evidence of small peat-swamps growing at the edges of charophyte lakes.

Microfacies: The study of carbonate microfacies from the charophyte-rich layers sheds light on the composition and paleoecology of charophyte assemblages.

Microfacies of C. microcharophorus *sp. nov. and cyanobacterial filaments:* The new species *C. microcharophorus* is found in wackestones-mudstones with small calcified filaments, 15 µm across, attributed to *Girvanella* sp. (Fig. 6, A and B). Charophyte thalli are well preserved; they include large portions of internodes and nodes with articulated branchlets. Also, as described above, small characean gyrogonites of *Microchara* sp. were found in anatomical connection. Calcified filaments are abundant in the muddy sediment and may represent poorly developed cyanobacterial mats. The high content in mud and the good articulation of plant remains suggest that this facies was formed in relatively deeper parts of the lake, below the wave motion line. In this belt, only the cyanobacterial mats were growing in situ. The scarcity of charophyte remains in this facies in comparison with other facies would indicate that they were gently transported from a neighboring growth area. A similar setting has been recently reported in deeper lacustrine facies from the Lower Cretaceous of the Iberian Chain (Climent-Domènech et al. 2009).

Microfacies of packstones of charophytes: A variety of packstones are formed of abundant charophyte thalli, generally collapsed, and disperse gyrogonites. The remains appear to belong in each case to a single, dominant taxon.

(a) *Packstones of* M. grambasti *(Fig. 6C).* These are relatively rare in the samples studied. This type of thallus is characterized in thin section by a particular pattern of calcification limited to the intercellular space between cortical and internodal cells. As a result, the transversal section of internodes is shaped like a toothed wheel with crenulations corresponding to the internal side of cortical cells and the internodal cell visible inside. Genus *Munieria* was related to dasycladales by some authors, such as Feist et al. (2003, 2005), while others, such as Schudack (1993) and Martín-Closas (2000), attributed them to charophytes. Most of the components of this microfacies are internode fragments of *M. grambasti* Bystrický 1976 associated to rare portions of *Charaxis* thalli and a few characean gyrogonites. The whole remains of *M. grambasti* are recrystallized in sparry calcite, suggesting that the original mineralogy was aragonite rather than low-magnesium calcite. Some of the thalli show transversal sections with unusual irregular, sometimes triangular outlines of the intercellular space between cortical and internodal cells. In contrast, the internodal cells, still cylindrical, are located either in the center of the thallus, as usual, or to one side of the triangle (Fig. 6D). This peculiar preservation is probably diagenetic in origin.

The dominance of *M. grambasti* suggests that this microfacies corresponds to the remains of a meadow of this species. The high fragmentation of the remains indicates that it was deposited near the wave-affected shores of the lake.

(b) *Packstones of large* Charaxis *thalli and* Peckichara *sp. gyrogonites.* Laminated packstones of very large (several centimeters long and up to 3 mm wide) isostichous thalli of the *Charaxis* type are abundant and easy to recognize in the field, even without a lens, due the large size of the charophyte remains (Fig. 6E). The thalli are only calcified in the intercellular area between the internodal and the cortical cells, leading to the accumulation of collapsed intercellular fragments, typically triangular in shape (Fig. 6F). In the same horizons, there are abundant, disperse gyrogonites of the genus *Peckichara* (Fig. 7A). The constant association of these very large *Charaxis* thalli with *Peckichara* gyrogonites suggests that they belonged to the same plant. However, they were not found in anatomical connection. The thin sections of these gyrogonites are similar to several *Peckichara* species prepared and illustrated by Grambast (1971). However, only the gyrogonites of *P. cancellata* were found dispersed in marls by Feist and Colombo (1983) or at the top of some limestones layers. According to Massieux et al. (1987), the genus *Peckichara* appears to occur mainly in lacustrine facies.

Intercalated with the horizons rich in *Peckichara* sp. and large *Charaxis* thalli, there are other horizons formed by up to 125 µm wide tubes of sparry calcite without internal structures (Fig. 7B). From their size, they may be assigned to ecorticate thalli of charophytes, but it cannot be ruled out that they belong to other aquatic plants.

The lamination of this microfacies suggests that charophyte remains were deposited in a quiet, anoxic lake bottom devoid of bioturbation, after undergoing short lateral transport. In consequence, this facies is related to the deposition of parautochthonous remains of *Peckichara*-dominated meadows in relatively deeper areas of the lake.

(c) *Packstones-grainstones of* Clavatoraxis *thalli.* This microfacies is almost exclusively built up of *Clavatoraxis* sp. remains and could be termed a ‘‘characeite’’ in the sense of Soulié-Märsche et al. (2010) (Fig. 7C). Small characean gyrogonites, probably corresponding to the genus *Microchara*, are associated

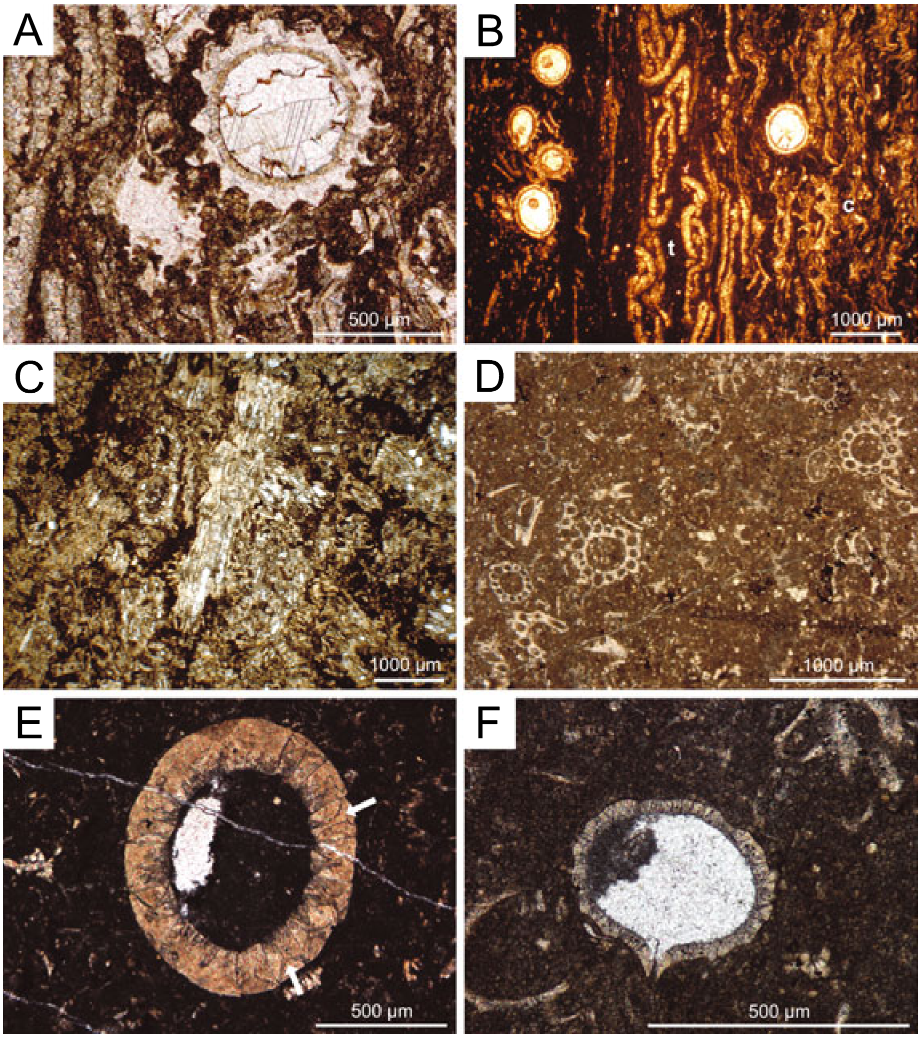

FIG. 7. Components distinguished in the microfacies analysis (continued). (A) Cross-section of a *Peckichara* sp. gyrogonite; thin section 76967, sample FS-10. (B) Laminated packstone of large collapsed *Charaxis* thalli (c), intercalated with *Peckichara* gyrogonites and tubes of sparry calcite (t); thin section 76966, sample FS-10. (C) Packstone-grainstone of *Clavatoraxis*-type thalli; thin section 76957, sample FB-3. (D) Wackestone-packstone of fragmented *Charaxis* thalli along with a few other small bioclasts of undetermined affinity; thin section 76964, sample CS-5. (E) Longitudinal section of a *Feistiella malladae* gyrogonite showing low number of convolutions, high thickness of spiral cells, and Y calcification (arrows); thin section 76963, sample CS-4. (F) Longitudinal section of a *Platychara* sp. gyrogonite; thin section 76963, sample CS-4.

but less frequent. Most of the thalli are well preserved, including large portions of partly articulated internodes, indicating that they were produced by plants growing nearby the deposition site. As a result, this facies is attributed to deposition within a *Clavatoraxis* charophyte meadow below lacustrine wave action.

Microfacies of fragmented charophyte remains: This facies consists of wackestones-packstones of abundant fragmented charophyte remains and a few other small bioclasts of undetermined affinity (Fig. 7D). Thalli, usually small portions of isostichous internodes, correspond to the form genus *Charaxis*. Characean gyrogonites are small in size and broken. They probably correspond to the genus *Microchara*. The poor preservation of charophyte remains, along with the abundance of bioclasts, indicates that this facies was deposited at the shore of freshwater lakes affected by significant wave action.

Microfacies of porocharacean gyrogonites: Wackestones with gyrogonites of porocharacean *Feistiella malladae* (Bataller 1945) Feist and Colombo 1983 nov. comb. are rare in the Vallcebre Basin. The gyrogonites are characterized in thin section by their rounded shape, limited number of convolutions, and the high thickness of spiral cells, usually showing the internal Y structure described by Feist and Grambast-Fessard (1984) (Fig. 7E). Other components of this facies are anisostichous (nonisostichous) thalli of the *Charaxis* type and characean gyrogonites of *Platychara* sp. similar to those reported in thin section by Grambast (1971, pl. 15, figs. 6–8) and Grambast and Gutiérrez (1977, pl. 14, figs. 9–11, and pl.

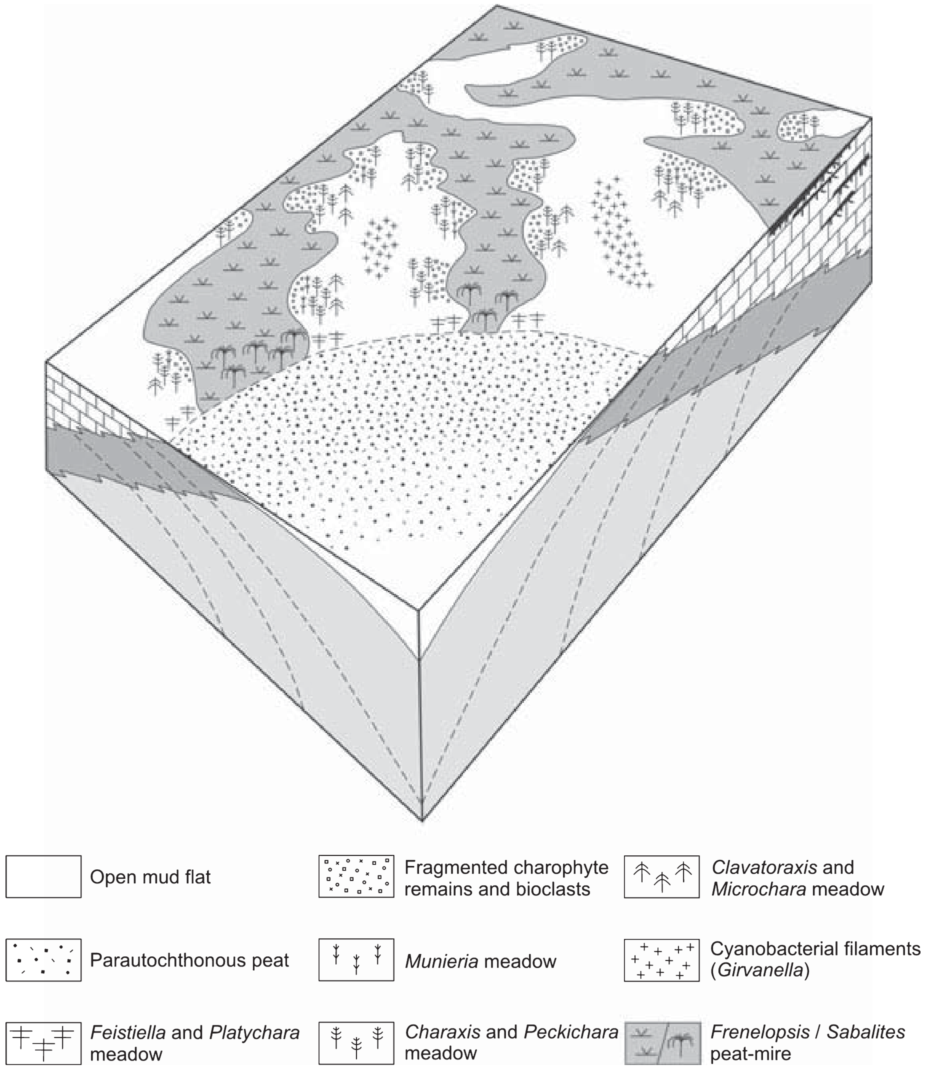

FIG. 8. Paleoenviromental reconstruction from the Lower Maastrichtian of Vallcebre Basin with the proposed zonation of charophytes.

15, figs. 1–3) (Fig. 7F). They are easy to recognize from their notable oblate (wider than higher) shape and basal column. This genus was previously unknown from the Vallcebre Basin. Charophyte thalli and some gyrogonites are broken, suggesting that transport occurred before deposition. The occurrence of homogeneous assemblages of porocharaceans is indicative of brackish water conditions (Mojon 1989, Schudack 1993). The fragmentation of many remains shows that deposition occurred in lakeshore facies.

Paleoecology: Charophyte-rich microfacies analysis has enabled us to distinguish three belts of freshwater lacustrine facies and one type of brackish facies (Fig. 8). Facies of filamentous cyanobacteria and reworked remains of a *Clavatoraxis* meadow occurred in the deepest zone, a belt of submerged vegetation made up of three different charophyte meadows grew in the shallow lake, and finally, the lakeshore belt was built up of facies of fragmented charophyte remains and bioclasts. The most diverse group of samples is represented by the facies attributed to charophyte meadows. These were dominated, respectively, by *M. grambasti*, *Charaxis* associated to *Peckichara* sp. gyrogonites, and *C. microcharophorus* sp. nov. and *Microchara* sp. The lateral relationships between the meadows are unknown, but from their relative abundance it appears that *Peckichara* sp. meadows were dominant, while the others only occurred locally, under particular conditions. Hence, the *M. grambasti* meadow appears to have grown in very shallow environments. In contrast, *C. microcharophorus* sp. nov. meadows had direct access to the open lake supplying their remains to the deeper lake bottoms after a gentle lateral transport. In these deeper areas, the depletion in oxygen, together with the embedding activity of the microbial mat in muddy sediment, would explain the excellent preservation of *C. microcharophorus* sp. nov. remains. Last but not least, charophyte meadows were dominated by *F. malladae* with subsidiary *Platychara* sp. in brackish environments.

CONCLUSIONS

The first whole-plant characean species *C. microcharophorus* sp. nov. is described from the Maastrichtian of Fumanya (Fígols-Vallcebre Basin, Eastern Pyrenees, Spain). This is the first time that a whole-plant fossil of a charophyte has been reconstructed from thin sections of lacustrine limestones. In contrast to other biocalcified fossil plants, this method has not been used with fossil charophytes previously, leading to the false impression that whole-plant charophyte fossils were rare and could not be reconstructed if they were not preserved under exceptional conditions of fossilization. On the contrary, since charophyte-rich limestones are extremely abundant in the fossil record of the Tethys Domain, it appears that significant potential exists to reconstruct whole-plant fossil charophytes from current thin sections.

The new species *C. microcharophorus* is characterized by relatively small isostichous thalli with spine-cell rosettes, which bore *Microchara* sp. gyrogonites attached to bract-cell rosettes of branchlets. Each gyrogonite was covered completely by an expanded bract cell, which corresponds to a structural tunica. The anatomical connection between these characean fructifications and a *Clavatoraxis* thallus clearly shows that this type of thallus is not exclusive of clavatoraceans, as previously thought, and provides significant new characters for a better distinction between *Microchara* and *Chara*. These genera are attached to different thalli, *Clavatoraxis* and *Charaxis*, respectively.

Sedimentological analysis combined with microfacies and taphonomic analyses allows description of the habitat of *C. microcharophorus* sp. nov. in freshwater charophyte lakes dominated by *Peckichara* sp. meadows and provides the key to recognizing those facies favorable to the preservation of well-articulated charophyte remains. These facies correspond to the deeper lake bottoms with poor oxygenation and inhabited by loose cyanobacterial mats. In contrast, the in situ charophyte meadows resulted in an accumulation of a large number of collapsed charophyte thalli with only a relatively small portion of sediment, forming lime packstone-grainstones where the detailed anatomical structures and especially the attachment of gyrogonites and thalli are difficult to recognize or absent altogether.

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Article 3

VILLALBA-BREVA, S., MARTÍN-CLOSAS, C. 2011. The onset of the non-marine sedimentation in the Upper Cretaceous of the Central Southern Pyrenean Basins (Catalonia, Spain) from charophyte biostratigraphy and palaeoecology. *Facies* (en revisió).

RESUM: Els dipòsits del Cretaci terminal del Pirineu corresponen a fàcies no marines tradicionalment anomenades "Garumnià", que representen la primera continentalització de les conques pirinenques. L'edat i la paleogeografia de les fàcies basals del Garumnià a les diferents parts de la conca pirinenca ha sigut molt debatudes des dels anys 1980'. La biostratigrafia de caròfits i l'anàlisi de microfàcies suggereixen que la continentalització va ser diacrònica i va progressar de sud a nord a les conques centrals sud pirinenques, és a dir entre les conques d'Àger i Tremp.

Així, a la conca d'Àger, situada més al sud, els primers materials no marins del Cretaci superior (Formació La Maçana), estan representats per calcàries lacustres amb un bandejat de color gris clar - gris fosc característic, organitzades en centenars de seqüències de somització decimètriques a mètriques, que van des de fàcies lacustres profundes, passant per ambients marginals, ben il·luminats dominats per herbeis de caràcies, fins a fàcies de vora de llac dominades per herbeis de clavatoràcies. L'associació de caròfits de la Fm. La Maçana està formada principalment per les espècies *Peckichara cancellata*, *P. sertulata*, *Microchara cristata*, *M. parazensis*, *Platychara caudata* i *Clavator brachycerus*, les quals pertanyen a la biozona de caròfits Peckichara cancellata (Campanià superior).

En canvi, a la conca de Tremp, localitzada al nord, l'inici de la sedimentació no marina està organitzada en diversos cicles de somització decamètrics de la Formació La Posa. Aquests cicles comencen amb dipòsits salabrosos formats per margues amb mol·luscs eurihalins a la base, seguits per lignits i culminen amb calcàries d'ambients salabrosos dominades per porocaràcies o, localment, amb calcàries d'aigua dolça amb caràcies. L'associació de caròfits de la Fm. La Posa està formada per les espècies *Feistiella malladae*, *Peckichara sertulata*, *Microchara cristata* i *Clavator brachycerus*, que pertanyen a la biozona de caròfits Septorella ultima (Maastrichtià inferior).

Facies
(under revision)

The onset of the non-marine sedimentation in the Upper Cretaceous of the Central Southern Pyrenean Basins (Catalonia, Spain) from charophyte biostratigraphy and palaeoecology

Sheila Villalba-Breva, S. · Carles Martín-Closas

Abstract The Latest Cretaceous deposits of the Pyrenees are non-marine facies traditionally called "Garumnian", which represent the first continentalisation of the Pyrenean Basins. The age and palaeogeography of the basal Garumnian facies in the different parts of the Pyrenean Basin has been a matter of debate. Charophyte biostratigraphy and microfacies analysis suggest that the continentalisation was diachronic in the Central Southern Pyrenean Basins, i.e. between the Ager and Tremp Basins, and progressed from south to north.

Thus, in the Ager Basin, to the south, the first Upper Cretaceous non-marine rocks are represented by the La Maçana Formation, which is mainly formed by lacustrine limestones organised into hundreds of shallowing-upwards sequences ranging from deeper lacustrine facies, through marginal, well-illuminated environments dominated by characean meadows, and finishing with lakeshores dominated by clavatoracean meadows. The charophyte assemblage from La Maçana Fm is mainly formed by *Peckichara cancellata, P. sertulata, Microchara cristata, M. parazensis, Platychara caudata* and *Clavator brachycerus*, which belong to the Peckichara cancellata charophyte biozone (Late Campanian).

In contrast, in the Tremp Basin, located to the north, the beginning of the non-marine sedimentation is organised into a few cycles of the well-known La Posa Fm, which begin with brackish deposits formed by thick marls with euryhaline molluscs at the base, followed by lignite and brackish to freshwater limestones dominated by porocharaceans. The charophyte assemblage of the La Posa Formation is formed by *Feistiella malladae, Peckichara sertulata, Microchara cristata and Clavator brachycerus*, which belong to the Septorella ultima charophyte biozone (Early Maastrichtian).

Key-words Charophytes · Non-marine carbonates · Upper Cretaceous · Montsec · Pyrenees · Spain

Introduction

The non-marine Upper Cretaceous – Palaeocene deposits of the Southern Pyrenees, known regionally as "Garumnian", following the term created by Leymerie (1862), represent the first continentalisation of the Pyrenean Basin, which was a prominent event in the evolution of the basin, related to the anticlockwise rotation of Iberia and the early rising of the Pyrenean chain (Capote et al. 2002). The upper part of the Garumnian has been the object of detailed investigations, aimed in particular at identifying the K/T boundary (e.g. Feist and Colombo 1983; Ullastre and

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Masriera 1983; Médus et al. 1988; Masriera and Ullastre 1990; Galbrun et al. 1993; Mayr et al. 1999), with the result that the lower part of the Garumnian has been relatively poorly studied. Most authors describe this lower part, also called "Grey Garumnian" by Rosell et al. (2001), as being mainly formed by grey lutites, coal, charophyte limestones and sandstones, but there is no agreement either about the age or the palaeoenvironmental conditions under which the first continentalisation of the Southern Pyrenean Basins occurred.

The dating of the first non-marine deposits of the Pyrenean Upper Cretaceous has been controversial. Although the Ager Basin deposits have not been dated, a Late Campanian age can be inferred for the Grey Garumnian based on biostratigraphic and magnetostratigraphic studies of the overlying red beds (Galbrun et al. 1993 recalibrated after Gradstein et al. 2004). In contrast, the age of the basal deposits of the Garumnian in the Tremp Basin was originally accepted as Early Maastrichtian on the basis of benthic foraminifera, rudists, pollen and spores, and charophyte biostratigraphy (Liebau 1973; Pons 1977, 1982; Feist and Colombo 1983; Gallemí et al. 1983; de Porta et al. 1985; Caus and Gómez-Garrido 1989). However, more recent interpretations of the age of the first non-marine deposits in the Central Southern Pyrenean Basins based on sequence stratigraphy have suggested that the first non-marine deposits were synchronous over the entire area and belonged to the Late Campanian (Ardèvol et al. 2000; Vicens et al. 2004). As a result of these contrasting views some confusion exists about the age of the first continentalisation of the Central Southern Pyrenean Basins.

From a palaeoenvironmental point of view, some disagreement also exists as to the facies of the first Upper Cretaceous non-marine deposits. The Grey Garumnian of the Tremp Basin is widely accepted as representing lagoon and coastal swamp deposits of varying salinity, laterally related to marine nearshore sandstones (Nagtegaal 1972; Díaz Molina 1987). In contrast, Cuevas et al. (1989) and Colombo and Cuevas (1993) have shown that the Grey Garumnian deposits in the Ager Basin belonged to lacustrine freshwater environments. An alternative scenario was recently put forward by Lopez-Martínez et al. (2009), who interpreted the entire Grey Garumnian as being basin-wide, peritidal and estuarine.

The aim of this study was: (1) to clarify the relative age of the first non-marine Upper Cretaceous deposits (Grey Garumnian) of the Central Southern Pyrenean Basins on the basis of charophyte biostratigraphy; and (2) to improve palaeoenvironmental knowledge of the first continentalisation of these basins on the basis of microfacies analysis of the charophyte-rich carbonates cropping out in the Tremp and Ager Basins.

Material and methods

In order to characterise the beginning of non-marine Upper Cretaceous sedimentation in the South Pyrenean Basin, two representative stratigraphic sections were studied in the depocentres of the Ager Basin (Serres Marginals thrust-sheet) and Tremp Basin (Montsec thrust-sheet), respectively. The La Maçana section is located in the southern part of the Ager Basin, along the road from Balaguer to Tremp at km. 51, not far from the village of Fontllonga (base coordinates N41 55'24.92" E00 52'23.37"). The Barranc de la Posa section was measured in the eastern part of the Tremp Basin, following the ravine to the north of the Mare de Deu de la Posa church, near the village of Isona (base coordinates N42 07’57.18” E01 04’43.20”). Additional charophyte samples were taken at the base of the Garumnian in Millà (Ager Basin) and Riera Barcedana, Alzina and Montrebei (Tremp Basin), in order to compare the stratigraphy of the two main sections. The physical stratigraphy, sedimentology, carbonate microfacies and charophyte biostratigraphy of these sections were then studied. Systematic sampling of the stratigraphic sections mentioned resulted in the selection of 43 samples for both charophyte biostratigraphic and microfacies analysis. Charophyte gyrogonites and utricles were obtained from unconsolidated marls after disaggregation in a solution of water and hydrogen peroxide, sieving with sieve mesh apertures of 0.2, 0.5 and 1mm and hand-picking under a binocular microscope. Fructifications were studied and measured under a Wild M5A binocular microscope, and photographed with a Quanta 200 scanning electron microscope at the “Serveis Cientificotècnics” of the Universitat de Barcelona. Thin sections, about 30 μm thick, were prepared from oriented rock slabs cut parallel and perpendicular to the bedding surface. Up to six 2.5x5 cm slides were prepared for each rock sample and studied under a Motic B3-220ASC optical microscope. Samples are housed in the charophyte collection of the Dept. Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona.

Geological setting

The Pyrenees are the Alpine fold-trust belt that was formed by the collision between the Iberian and the European continental plates. The mountain belt consists of a Hercynian basement and a sedimentary cover that developed from the Late Permian to Early Cretaceous in rift basins and later from the Late Cretaceous to the Oligocene in foreland and piggy-back basins. In the Southern Pyrenean Basin, these deposits were detached from their original position, moved southwards several tens of kilometres and piled up to form a succession of north to south thrust sheets eventually thrusting over autochthonous Palaeogene materials of the Ebro Basin (Muñoz 1989). In the Central Southern Pyrenean zone these are, from N to S, the Boixols, the Montsec and the Serres Marginals thrust sheets. Late Cretaceous non-marine deposits were recognised in the Montsec and in the Serres Marginals thrust sheets, and are the subject of the present study (Fig. 1). On the one hand, the Serres Marginals thrust sheet includes a Triassic – Palaeogene succession about 2500 m thick and subdivided into three groups of minor thrust sheets decreasing in size southward and eastward. Of these thrust-sheets the northern Ager-Montroig tectonic unit contains the Ager Basin (Saula and Samsó 1996). On the other hand, the Montsec thrust sheet bears a Triassic – Palaeogene series of about 3000 m thick and shows a simple structure, mainly consisting of a broad syncline which supports the Tremp Basin (Muñoz 1992).

Ager Basin

The Late Cretaceous Ager Basin infilling was continuous from the Campanian to the Thanetian. There are three main sedimentary units in the basin (Caus and Gómez-Garrido 1989). The lower unit is Early – Middle Campanian in age and is represented by the Serres Limestone Formation (Souquet 1967), formed by nearshore bioclastic limestones. The second unit is Middle – Late Campanian in age and consists of detritic limestones alternating with sandstones (Bona Formation), corresponding to a barrier-shoal system (Mey et al. 1968; Lopez-Martínez et al. 1996). The upper unit (Garumnian) is Late Campanian to Thanetian in age and is mainly formed by lacustrine limestones and fluvial red beds, described by Colombo and Cuevas (1993) as the Fontllonga Group, which is divided into four formations: the La Maçana, Figuerola, Millà and Perauba Formations. The type section of the La Maçana Fm is the subject of our study (Figs. 1a, 2).

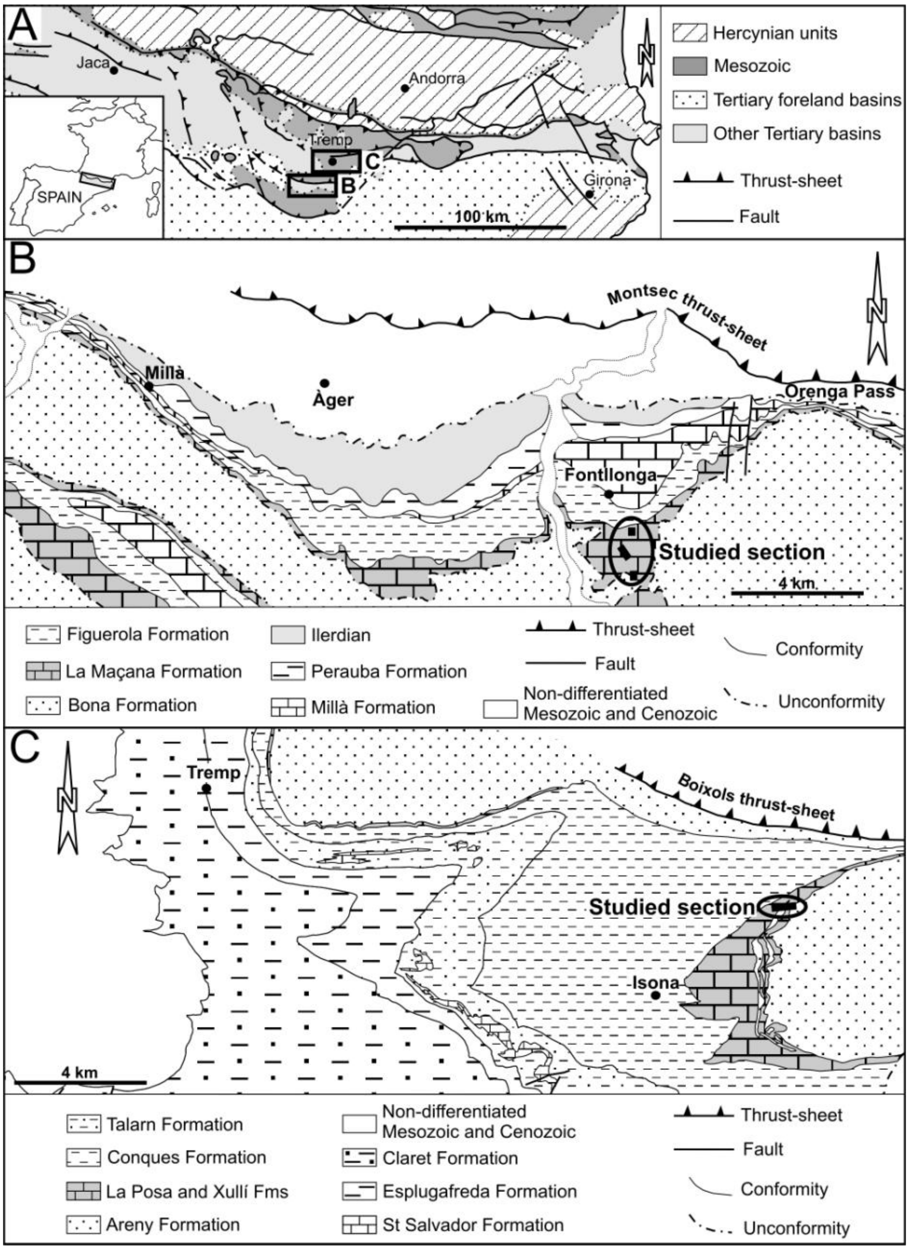

Fig. 1 Geological setting of the study areas. **a** Geological map of the Pyrenees with location of the study areas. **b** Geological map of the Ager Basin showing the location of the studied sections of the la Maçana Fm. **c** Geological map of the Tremp Basin showing the location of the Barranc de la Posa section. Geology adapted from Colombo and Cuevas (1993) and Cuevas (1992)

The La Maçana Fm is up to one hundred metres thick and crops out along the C-13 road between the Cal Magí farmhouse and the junction with the road to Fontllonga. The main thickness is built up by marls alternating with charophyte-rich limestones with a characteristic colour banding of white wackestones and dark grey packstones corresponding to small-order lacustrine cycles. Towards the top of this interval, marls are intercalated with dark grey wackestones topped with brecciation, ferric crusts and dinosaur footprints. This succession has been attributed to deposition in shallow lacustrine-palustrine environments with protected areas in which the preservation of organic matter occurred under anoxic conditions (Colombo and Cuevas 1993). The brecciation observed towards the top of the formation is an edaphic feature suggesting the occurrence of vegetation in periods of lacustrine restriction or water table fluctuations.

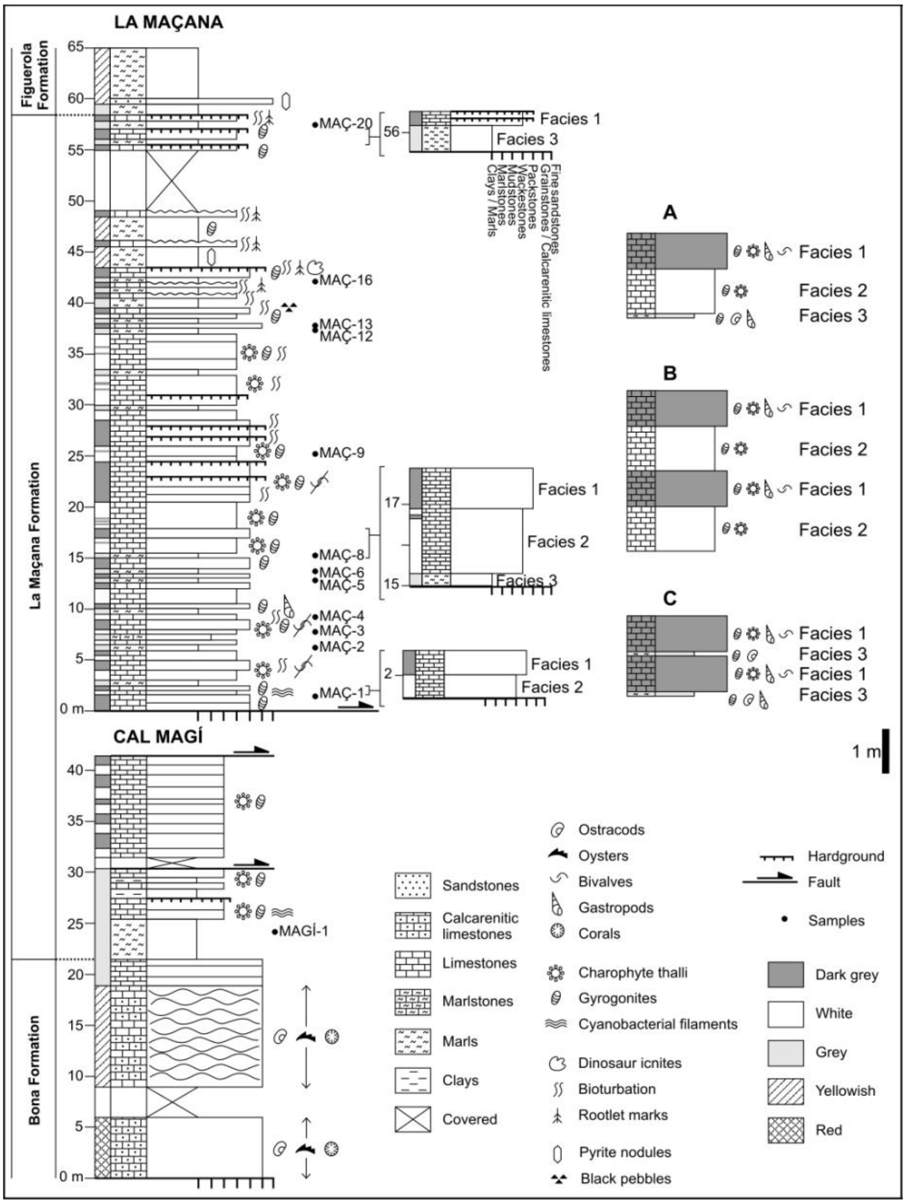

Fig. 2 Stratigraphic sections of the La Maçana Fm studied in the Ager Basin with samples studied and conceptual cycles resulting from the three facies associations (**a**-**c**) described. Facies components are described in the text

Along the southern flank of the Ager syncline, the La Maçana Fm shows a decreasing thickness. Thus, it is only 15 m thick in the area of Millà (in the western part of the Ager Basin), whilst at the Orenga Pass (the eastern part of the basin), it is only 20 m thick (Colombo and Cuevas 1993).

The age of the La Maçana Fm has not yet been studied in detail, but has been deduced from the age of the underlying and overlying formations (Bona Fm and Figuerola Fm, respectively). The age of the Bona Fm has been established as Middle-Late Campanian on the basis of benthic foraminifera (Caus and Gómez-Garrido 1989), whilst a magnetostratigraphic study of the Figuerola Fm by Galbrun et al. (1993) showed that the red beds overlying the La Maçana Formation ranged from chron C32r to chron C28n, i.e. Latest Campanian to Early Danian in age, according to recent recalibrations by Gradstein et al. (2004). On the other hand, charophyte biostratigraphy by Ullastre and Masriera (1983), Médus et al. (1988) and Galbrun et al. (1993) has indicated that the Figuerola Fm contains *Septorella brachycera* Grambast 1962, *S. ultima* Grambast 1971, *Peckichara sertulata* Grambast 1971 and *Maedleriella* sp. This assemblage is Maastrichtian in age. Hence a Late Campanian age could be inferred for the La Maçana Formation.

Tremp Basin

The Upper Cretaceous non-marine deposits of the Tremp Basin are known as the Tremp Group (Cuevas 1992). A complete succession of the Tremp Group base crops out along the ravine to the north of the Mare de Deu de la Posa church, near the village of Isona, where it was first described by Liebau (1973) and later by Cuevas (1992). The base of the section shows two intercalations of the marine nearshore sandstone of the Areny Fm, which contain abundant *Radiolitella pulchellus* rudists, other bivalves and corals. The Areny Formation has been related to deposition in coastal barriers (Mey et al. 1968; Nagtegaal 1972). In the Tremp Basin, the top of this formation has been attributed to the Latest Campanian on the basis of benthic foraminifer assemblages (Hottinger and Caus 2009).

The overlying succession is up to 130 m thick and shows alternating organic marls, lignite, and charophyte limestones with some intercalations of marlstones, siltstones and sandstones (Figs. 1b, 3). This succession was defined by Liebau (1973) and Cuevas (1992) as La Posa Fm and has been attributed to deposition in a coastal-swamp environment connected with shallow freshwater lakes (Nagtegaal 1972). A rudist-horizon formed by *Hippuritella castroi* marks the top of the La Posa Fm and indicates a Maastrichtian age (Riera et al. 2009). The two rudist horizons framing the La Posa Fm, together with the benthic foraminifer assemblage found at the base, indicate that the La Posa Fm was deposited at the earliest in the base of the Maastrichtian and probably later (Gallemí et al. 1983; Caus and Gómez-Garrido 1989). The gyrogonite assemblage reported by Feist and Colombo (1983) from the basal lutites and lignites of the La Posa Fm also belongs the Early Maastrichtian and is formed by *Feistiella malladae* (Bataller 1945) nov. comb. Villalba-Breva and Martín-Closas, *Peckichara sertulata* Grambast 1971, *P. caperata* Grambast and Gutiérrez 1977, *Platychara compressa* (Peck and Reker 1948) Grambast 1962, *P. caudata* Grambast 1971, *P. turbinata* Grambast and Gutiérrez 1977, *Amblyochara concava* ssp. *mucronata* Feist and Colombo 1983, *Microchara punctata* Feist and Colombo 1983 and *Peckisphaera clavata* Feist and Colombo 1983.

A succession of grey lutites and some intercalations of sandstones and variegated lutites cover the marl, coal and limestones of the La Posa Fm and were described within the Xullí Formation by Liebau (1973). It includes some intercalations of limestones with charophyte remains and ostracods. These materials have been attributed to deposition in a lower delta plain (Eichenseer 1988) or a tidal flat (Díaz Molina 1987).

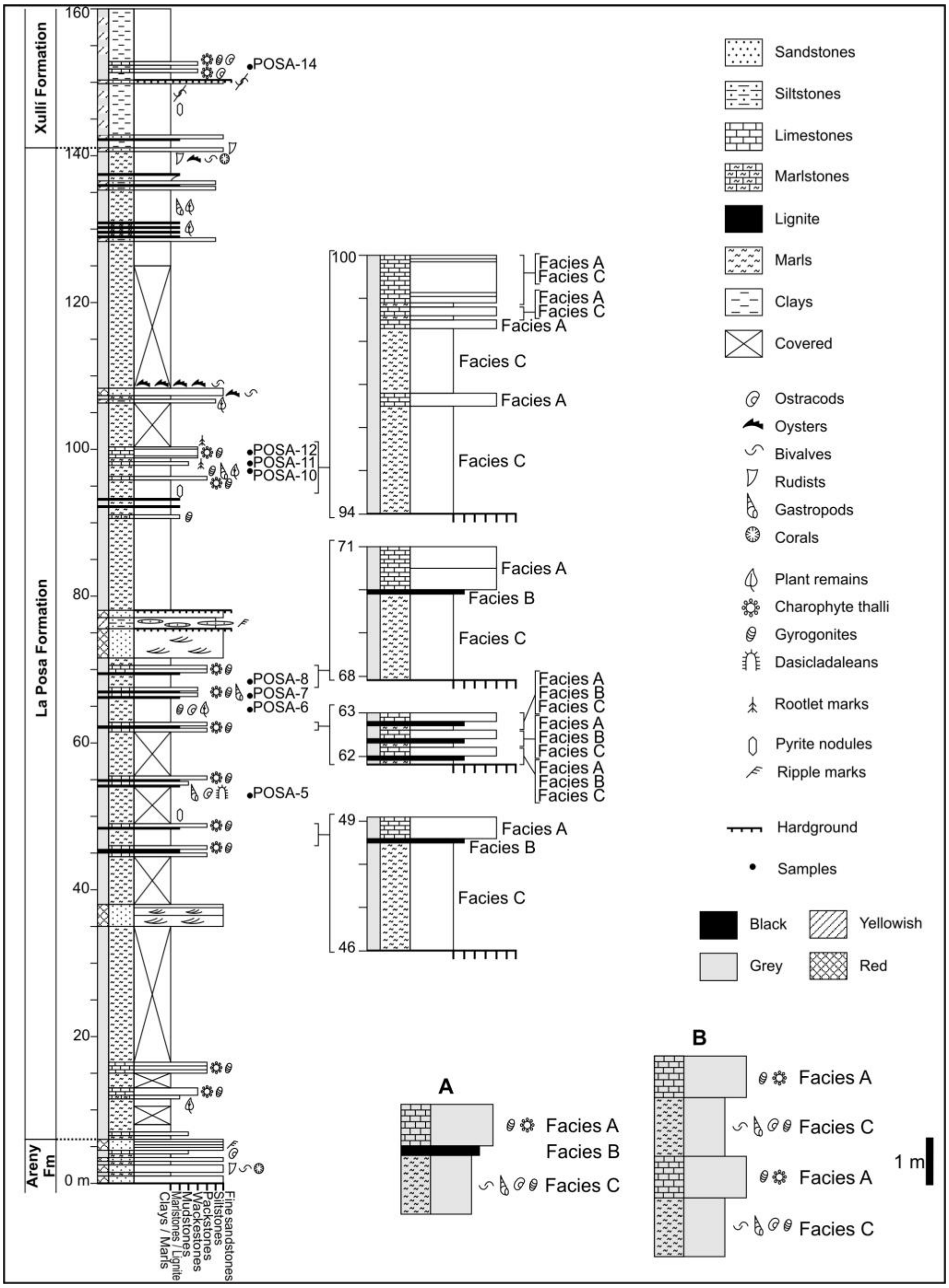

Fig. 3 Stratigraphic section of the La Posa Fm studied in the Tremp Basin with with samples studied and conceptual cycles resulting from the two facies associations (**a**-**b**) described. Facies components are described in the text

Along the southern flank of the Tremp syncline, the La Posa Fm shows a decreasing thickness. Thus, it is only 20 m thick in the area of Barcedana-Alzina-Beniure, in the southern central part of the Tremp Basin, where it is built up by grey marls and clays intercalated with charophyte-rich limestones. In the Noguera Ribagorçana valley (northern mouth of the Montrebei canyon), the La Posa Fm is even more reduced and is represented by only 5 m of grey marls with charophytes.

Systematic palaeontology

Division Charophyta MIGULA, 1897
Class Charophyceae SMITH, 1938
Order Charales LINDLEY, 1836
Family Porocharaceae GRAMBAST, 1962
Genus *Feistiella* SCHUDACK, 1986
Feistiella malladae (BATALLER, 1945) nov. comb. VILLALBA-BREVA AND MARTÍN-CLOSAS
Figs. 4a-d

1945 *Chara malladae* (Vidal sp.) – Bataller, p. 287, fig. p. 287.
1983 *Porochara malladae* (Bataller) n. comb. – Feist in Feist and Colombo, p. 310, pl. 2, figs. 10-11.

Material: Only 2 well preserved gyrogonites from samples MAÇ-20 and FONT-4, La Maçana (Ager Basin). 30 gyrogonites from samples ALZ-2and ALZ-5, Alzina-Beniure and about 300 gyrogonites from samples POSA-5, POSA-6, POSA-8, POSA-10 and POSA-14, Barranc de la Posa (Tremp Basin).

Description: Large gyrogonites, 882-1134 µm high (mean 1026 µm) and 738-900 µm wide (mean 810 µm), ellipsoidal (prolate or subprolate) to subglobular in shape with an isopolarity index (ISI) ranging from 117-150 (mean 127). Spiral cells 126-162 µm wide, planar or convex, and devoid of ornamentation, with 7-9 (mostly 7) convolutions visible in lateral view, separated by fine intercellular sutures. Apical pore rounded and 175 µm in diameter. Base slightly pointed with a pentagonal basal pore 150 µm in diameter. Basal plate unicellular.

Remarks: Porocharaceans similar to and perhaps synonymous of *F. malladae* (Bataller 1945) include *Porochara globosa* Grambast and Gutiérrez 1977, which displays a slightly lower number of convolutions, and *Porochara oblonga* Grambast 1975, which has a smaller apical pore. In both species the basal plate is unknown, which is the reason for provisionally keeping them outside the synonymy of *Feistiella malladae*.

Distribution: The porocharacean *F. malladae* is, up to now, an exclusively Pyrenean species. In the southern Pyrenees (Catalonia, Spain) it occurs in several localities from the Late Campanian and Maastrichtian of the Ager, Tremp, Coll de Nargó and Vallcebre synclines (Bataller 1945; Feist and Colombo 1983; Masriera and Ullastre 1988). In the Northern Pyrenean Basins (France) it occurs in the Maastrichtian of the Languedoc (Massieux et al. 1985, 1987).

Family Characeae AGARDH, 1824
Genus *Microchara* GRAMBAST, 1959
Microchara cristata GRAMBAST, 1971
Figs. 5e-f

1971 *Microchara cristata* n. sp. – Grambast, pp. 35-36, figs. 22 and 23; pl. XXVIII, figs. 1-8; pl. XXIX, figs. 1-10.

Material: 20 gyrogonites from samples MAÇ-16, FONT-3 and FONT-4, La Maçana (Ager Basin). Twelve gyrogonites from sample ALZ-2, Alzina-Beniure (Tremp Basin).

Description: Gyrogonites small to medium in size, 463-623 µm high (often 494-565 µm), 368-492 µm wide (often 391-454 µm), ovoid (subprolate, rarely prolate spheroidal) in shape. Isopolarity index ranges from 111-131 (often 124-129). Eight to ten, most frequently nine, convolutions visible in lateral view. Spiral cells 51-78 µm wide, ornamented with a mid-cellular crest. Apex rounded with weak nodules. Base rounded or pointed with a short column. Basal pore 48-60 µm in diameter.

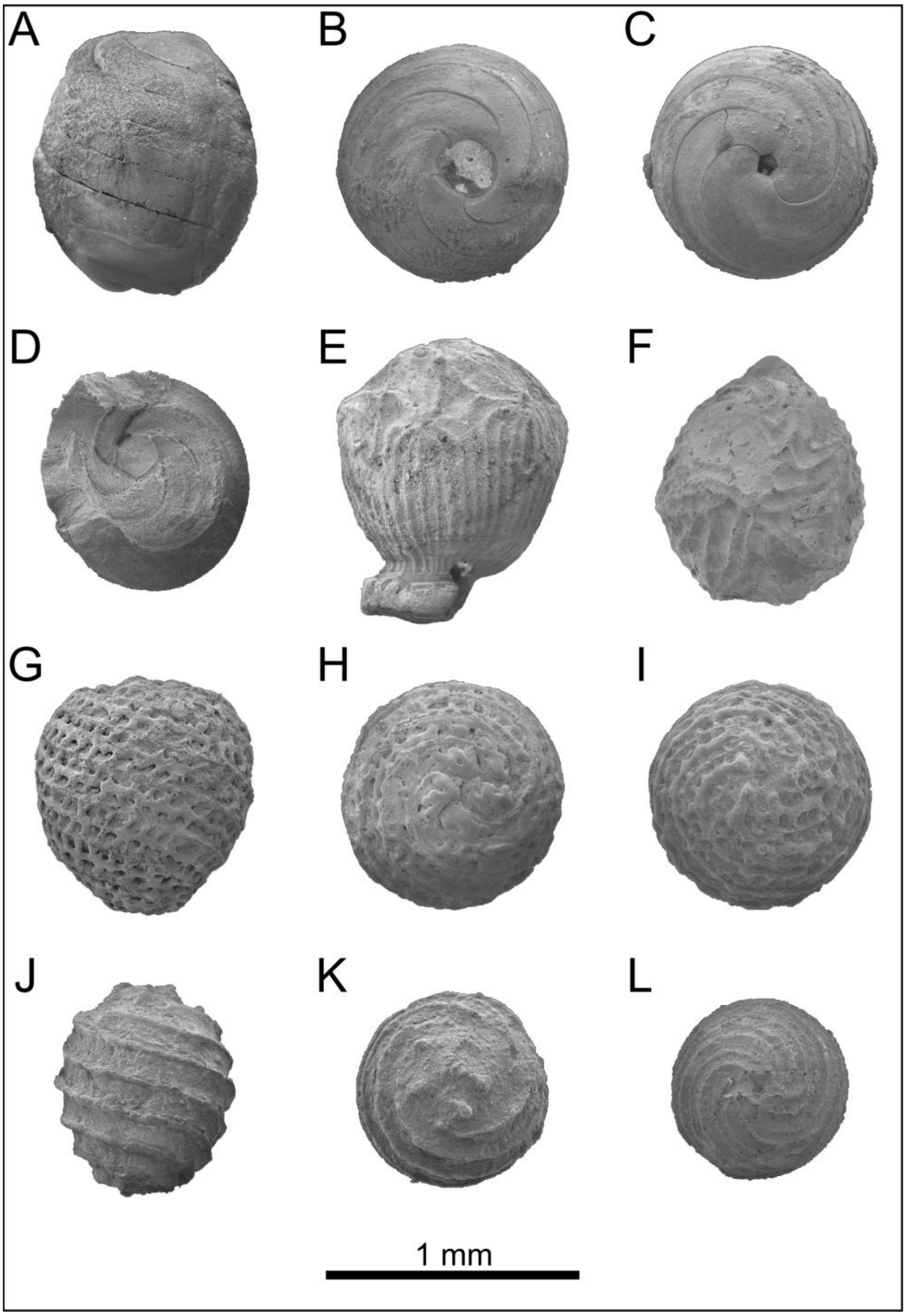

Fig. 4 Charophytes from the Late Cretaceous of La Maçana and La Posa Fms **a** to **d** *Feistiella malladae*, sample POSA-8, Barranc de la Posa section; **a** lateral view, **b** apex, **c** base, **d** base with basal plate as seen from inside. **e** and **f** *Clavator brachycerus*, sample ALZ-3, Alzina-Beniure section; **e** lateral view, **f** apex. **g** to **i** *Peckichara cancellata*, sample MAÇ-2, La Maçana section; **g** lateral view, **h** apex, **i** base. **j** to **l** *Peckichara sertulata*, sample ALZ-2, Alzina-Beniure section; **j** lateral view, **k** apex, **l** base

Remarks: This species is easily distinguished from other *Microchara* by the shape and features of its ornamentation, especially the mid-cellular crest.

Distribution: *M. cristata* appears to have a large distribution in the Upper Cretaceous of Eurasia. In France, it occurs in the Early Rognacian (Campanian) of Rognac (Provence) and in several localities of the Campanian and Maastrichtian of the Languedoc (Grambast 1971; Feist and Freytet 1983; Massieux et al. 1985; Lepicard et al. 1985). In the South Pyrenean Basins (Catalonia, Spain) it has been reported from the Ager, Tremp, Coll de Nargó and Vallcebre Basins (Feist and Colombo 1983; Masriera and Ullastre 1988; Villaba-Breva et al. 2012). In Europe, it is also known in the Maastrichtian of Rumania (unpublished own data), whilst outside Europe it has been reported from the Late Cretaceous of China, at Shalamulun (Inner Mongolia) and in the Junggar Basin, Xinjiang (Liu 1987; Liu and Wu 1987).

Microchara parazensis MASSIEUX, 1987

Figs. 5a-d

1987 *Microchara parazensis* n. sp. – Massieux in Massieux et al., pp. 154-156, fig. 2; pl. 1, figs. 6-13.

Material: About 40 gyrogonites from samples MAÇ-2, MAÇ-5 and MAÇ-8, La Maçana (Ager Basin).

Description: Gyrogonites small, 427-485 µm high (mean 453 µm) and 354-409 µm wide (mean 383 µm), ovoid (subprolate) in shape with an isopolarity index of 107-132 (mean 119). Spiral cells concave, 52-68 µm in width and devoid of ornamentation. Cell-sutures with undulations. Nine, rarely eight or ten, convolutions are visible laterally. Apex flat or rounded, without modification. Base generally pointed, with a short column. Basal pore 33-58 µm in diameter.

Remarks: *M. parazensis* is distinct from other non-ornamented *Microchara* species from the Upper Cretaceous: *M. leiocarpa* Grambast 1971, *M. tunicata* Grambast and Gutiérrez 1977 and *M. laevigata* Grambast and Gutiérrez 1977 are larger, more elongated than the population studied here and bear a large number of convolutions.

Distribution: This species has only been reported from the Maastrichtian of the Minervois (Languedoc, France) by Massieux et al. (1987). Here we report for the first time its occurrence in the Late Campanian of the Southern Pyrenees.

Genus *Dughiella* FEIST-CASTEL, 1975

Dughiella obtusa GRAMBAST AND GUTIÉRREZ, 1977

Figs. 5k-m

nomen nudum 1976 *Retusochara obtusa* n. sp. – Gutiérrez and Robles, pp. 5-8, 10, fig. 2.

1977 *Dughiella obtusa* n. sp. – Grambast and Gutiérrez, pp. 31-32, fig. 18; pl. XI, figs. 9-14; pl. XV, fig. 6.

Material: Eleven gyrogonites from sample MAÇ-2, La Maçana (Ager Basin), some of them poorly preserved.

Description: Gyrogonites are medium in size, 522-684 µm high and 558-630 µm wide, prolate spheroidal in shape with an isopolarity index (ISI) of 91-110. Spiral cells are convex or planar, 72-99 µm wide and devoid of ornamentation. In lateral view 7 or 8 convolutions are visible, separated by fine intercellular sutures. Apex flat or rounded, with slightly narrowed periapical zone. Periapical depression and nodules poorly marked. Base rounded with a basal pore 54-72 µm in diameter.

Remarks: The specimens from the population studied here are slightly smaller than the type material, but all other features are alike. The other species of *Dughiella* are Palaeogene in age and differ from the population of La Maçana in their size and ornamentation.

Distribution: *D. obtusa* appears to be an Iberian endemism. Previously it was only known from the Campanian-Maastrichtian boundary of Villalba de la Sierra (Iberian Chain, Spain) by Grambast and Gutiérrez (1977). In addition, we now report it from the Upper Campanian of the Ager Basin (Catalonia, Spain).

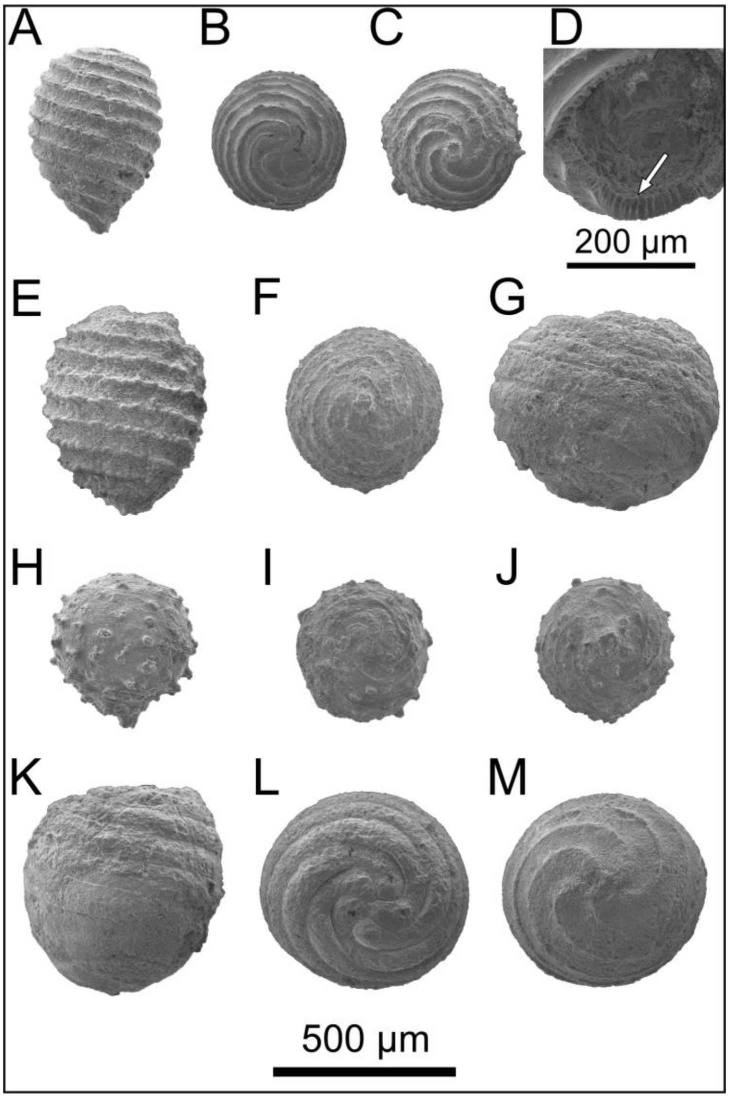

Fig. 5 Charophytes from the Late Cretaceous of La Maçana and La Posa Fms (continued). **a** to **d** *Microchara parazensis*, sample MAÇ-2, La Maçana section; **a** lateral view, **b** apex, **c** base, **d** detail of cell-sutures with undulations (*arrow*). **e** and **f** *Microchara cristata*, sample MAÇ-16, La Maçana section; **e** lateral view, **f** base. **g** lateral view of *Platychara turbinata*, sample MAÇ-2, La Maçana section. **h** to **j** *Platychara caudata*, sample MAÇ-2, La Maçana section; **h** lateral view, **i** apex, **j** base. **k** to **m** *Dughiella obtusa*, sample MAÇ-2, La Maçana section; **k** lateral view, **l** apex, **m** base

Genus *Peckichara* GRAMBAST, 1957
Peckichara cancellata GRAMBAST, 1971
Figs. 4g-i

1971 *Peckichara cancellata* n. sp. – Grambast, pp. 23-25, figs. 12 and 13; pl. XVIII, figs. 1-6; pl. XIX, figs. 1-9; pl. XX, fig. 1.

Material: About 800 gyrogonites from samples MAGI-1, MAÇ-2, MAÇ-5, MAÇ-6, MAÇ-8, MAÇ-12, MAÇ-16, and FONT-1 to FONT-4, La Maçana (Ager Basin).

Description: Gyrogonites medium to large, 558-972 µm high (often 792-846 µm), 468-972 µm wide (often 774-864 µm), ovoid (prolate spheroidal or frequently subprolate) in shape with an isopolarity index (ISI) ranging from 71-120 (often 95-107). Apex flat or rounded, with periapical depression and prominent nodules. Base flat. Basal pore pentagonal, 36-54 µm in diameter. Spiral cells flat, 108-144 µm wide and forming 6-8 convolutions in lateral view, separated by fine intercellular sutures. The ornamentation consists of small perpendicular rods placed on both sides of a mid-cellular crest and spaced at irregular intervals. The central crest disappears around the apex but forms a wider line near the basal pore.

Remarks: This species differs from *P. pectinata* Grambast 1971 since the latter is more spheroidal and has a more prominent mid-cellular crest, which results in the perpendicular rods resembling a comb (pectina/ae, in Latin). *P. sertulata* Grambast 1971, *P. caperata* Grambast and Gutiérrez 1977 and *P. cristatella* Grambast and Gutiérrez 1977 differ in their smaller size and in the ornamentation.

Distribution: *P. cancellata* occurs abundantly in the Late Cretaceous of southern Europe. In the Early Rognacian (Campanian) of France it has been reported from Rognac in Provence and in the Languedoc (Grambast 1971; Feist and Freytet 1983). In the Maastrichtian it occurs in the Languedoc, France (Massieux et al. (1987), whilst in Catalonia, Spain it has been reported from the Vallcebre and Ager Basins (Feist and Colombo 1983, Médus et al. 1988, Masriera and Ullastre 1988, 1990), and in the south-western Iberian Chain (Grambast 1975).

Peckichara sertulata GRAMBAST, 1971
Figs. 4j-l

1971 *Peckichara sertulata* n. sp. – Grambast, pp. 25-27, figs. 14-15; pl. XX, figs. 2-5; pl. XXI, figs. 1-7.

Material: About 80 gyrogonites from samples FONT-2 to FONT-4, La Maçana (Tremp Basin). 14 gyrogonites from samples ALZ-2 and ALZ-3, Alzina-Beniure and 5 gyrogonites from sample POSA-10, Barranc de la Posa (Tremp Basin).

Description: Gyrogonites medium in size, 540-720 µm high and 558-684 µm wide, ovoid in shape with an isopolarity index (ISI) 91-123. Six to eight convolutions are visible laterally, separated by fine intercellular sutures. Spiral cells concave, 90-126 µm wide and ornamented with an undulated mid-cellular crest. Apex flat, with poorly marked periapical depression and nodules. Base rounded. Basal pore 36-72 µm in diameter.

Remarks: The specimens from the populations studied here are slightly smaller than the type material. This species is easily distinguished from *P. cancellata* because of its smaller size and lack of ornamentation. According to Grambast (1971), together with *P. pectinata* these two species form a single evolutionary lineage, *P. pectinata* being the common ancestor for both *P. cancellata* and *P. sertulata*. In comparison to other species not related to this lineage, *P. sertulata* differs from *P. caperata*, which is smaller, more rounded, and displays a wider mid-cellular crest, and from *P. cristatella*, which is smaller than the population studied here.

Distribution: In France, *P. sertulata* occurs in the Early Rognacian (Campanian) and in the Late Rognacian (Maastrichtian) of Provence and the

Languedoc (Grambast 1971; Feist and Freytet 1983; Massieux et al. 1985; Lepicard et al. 1985). In Spain, it occurs in the Maastrichtian of the south-western Iberian Chain (Grambast 1975) and in the South Pyrenean Basins of Ager, Tremp, Coll de Nargó and Vallcebre (Feist and Colombo 1983; Médus et al. 1988; Masriera and Ullastre 1988, 1990).

Genus *Platychara* GRAMBAST, 1962

Platychara caudata GRAMBAST, 1971

Figs. 5h-j

1971 *Platychara caudata* n. sp. – Grambast, pp. 18-20, figs. 7-8; pl. XIV, figs. 1-5; pl. XV, figs. 1-8.

Material: About 100 gyrogonites from sample MAÇ-2, La Maçana (Tremp Basin).

Description: Gyrogonites small, 342-405 µm high (mean value 375 µm) and 342-396 µm wide (mean value 380 µm). Oblate spheroidal, rarely suboblate. Isopolarity index ranges from 86 to 110, with a mean value of 99. Six to eight, often seven, convolutions are visible laterally, separated by fine intercellular sutures. Spiral cells planar or convex, 36-72 µm wide and ornamented with small prismatic tubercles, spaced at irregular intervals. Apex rounded, with slightly narrowed periapical zone and poorly marked nodules. Base pointed, to form a small column 35-55 µm long. Basal pore 36-54 µm in diameter.

Remarks: *P. peltata* Grambast 1975 is smaller than *P. caudata*, and displays a more prominent basal column. Its ornamentation has larger and more widely-spaced tubercles. *P. spiculata* Grambast and Gutiérrez 1977 is smaller and shows more rounded tubercles, spaced at regular intervals. *P. stipitata* Grambast and Gutiérrez 1977 is smaller and the ornamentation consists of acute tubercles, spaced at irregular intervals. Other *Platychara* species are not ornamented.

Distribution: The genus *Platychara* was probably cosmopolitan as it has been recorded in the Late Cretaceous of North and South America, Europe, India and China (Feist et al, 2005). The species *P. caudata* occurs in the Begudian (Campanian) of Provence and the Languedoc, France, and in the Late Rognacian (Maastrichtian) of the Languedoc (Grambast 1971; Feist and Freytet 1983; Massieux et al. 1985). In the Spanish Maastrichtian it occurs in several localities from the south-western Iberian Chain, and in the Tremp and Ager Basins, Pyrenees (Grambast 1975; Feist and Colombo1983). Similar forms have been reported from the Late Cretaceous of Argentina (Musacchio1973; Peck and Forester 1979).

Platychara turbinata GRAMBAST AND GUTIÉRREZ, 1977

Fig. 5g

1977 *Platychara turbinata* n. sp. – Grambast and Gutiérrez, pp. 17-18, figs. 9; pl. V, figs. 4-12; pl. XIV, figs. 9-10.

Material: Only 4, poorly preserved, gyrogonites available from sample MAÇ-2, La Maçana (Tremp Basin).

Description: Gyrogonites small to medium in size, 360-648 µm high and 630-756 µm wide, sub-oblate in shape, with an isopolarity index (ISI) of 57-89. Six or seven convolutions are visible in lateral view, separated by fine intercellular sutures. Spiral cells are planar or convex, 72-108 µm in width and without ornamentation. Apex flat, with periapical depression and well-marked apical nodules. Base flat with a basal pore 52-74 µm in diameter.

Remaks: In comparison to the type material from the Iberian Chain described by Grambast and Gutiérrez (1977), the Pyrenean *Platychara turbinata* is more oblate. This taxon is distinguished from other species of *Platychara* by the apical features and the lack of ornamentation.

Distribution: The species *P. turbinata* is so far an exclusively Iberian species, which has been recorded from the Campanian-Maastrichtian boundary in the Iberian Chain by Grambast and Gutiérrez (1977) and in the Maastrichtian of Tremp and Coll de Nargó (Eastern Pyrenees, Catalonia) by Feist and Colombo (1983).

Family Clavatoraceae PIA, 1927
Genus *Clavator* PECK, 1941
Clavator brachycerus (GRAMBAST, 1962) MARTÍN-CLOSAS, 1996
Figs. 4e-f

1962 *Septorella brachycera* n. sp. – Grambast, pp. 69-71, fig. 1.

1996 *Clavator brachycerus* (Grambast, 1962) – Martín-Closas, comb. nov., p. 280, figs. 10-11.

2005 *Heptorella brachycera* Grambast, 1962– Feist and Grambast-Fessard in Feist et al., p. 110, fig. 56,1a-c.

Material: 350 utricles from samples MAÇ-5, MAÇ-6, MAÇ-8, MAÇ-12, MAÇ-16, MAÇ-20, FONT-1, FONT-2and FONT-4, La Maçana (Ager Basin). About 1000 utricles from samples ALZ-2, ALZ-3 and ALZ-5, Alzina-Beniure (Tremp Basin).

Description: Utricles medium to large, 648-1314 µm high (often 846-954 µm) and 612-1116 µm wide (often 720-828 µm), completely coating the bottle-shaped gyrogonite. Internal utricular layer nodular. External utricular layer composed of 6 bract-cells, rarely 5 or 7, directly attached to a branchlet basal node. The six bract-cells bear a fan of spine-cells on their tips. These fans are made up of 10-12 elements, including 3 apical, filiform cells, 2 lateral largely triangular cells and 5-7 long basal cells. Apical pore unknown or absent altogether. Basal plate unknown but probably single celled as in other Clavatoroidae.

Remarks: The distinction between *Clavator brachycerus* and *C. ultimus* (Grambast 1971) Martín-Closas 1996 is limited to the size and a different number of bract cells, after Massieux et al. (1979) showed that a distinction based on the presence/absence of an apical pore, as claimed by Grambast (1962), was unfounded. Thus, *C. ultimus* is several hundreds of micrometres larger and bears 8-9 instead of 5-7 lateral bract cells.

Distribution: The species *C. brachycerus* is one of the latest clavatoraceans and appears to be restricted to the Late Cretaceous of south-western Europe. In France, it has been reported from the Begudian – Rognacian (Campanian) of Provence and in the Campanian and Maastrichtian of the Languedoc (Grambast 1962; Massieux et al. 1979, 1985, 1987; Feist and Freytet 1983). In Spain, this species occurs in the Campanian and Maastrichtian of several Pyrenean localities from the Tremp, Ager, Coll de Nargó and Vallcebre Basins (Feist and Colombo 1983; Ullastre and Masriera 1983; Masriera and Ullastre 1988, 1990).

Charophyte biostratigraphy

The La Maçana Formation (Ager Basin)

This is the first biostratigraphic study of the La Maçana Fm. The charophyte assemblage is composed of *Peckichara cancellata*, *P. sertulata, Platychara caudata, P. turbinata*, *Dughiella obtusa*, *Microchara cristata*, *M. parazensis*, *Clavator brachycerus* and *Feistiella malladae* (Table 1). The species *Peckichara cancellata* is biostratigraphically significant and represents the index species of the homonymous charophyte biozone. According to Riveline et al. (1996), this biozone has been correlated with magnetozones C32r to C32n (middle and upper part of the Late Campanian). However, new magnetostratigraphic data in the Vallcebre Basin by Oms et al. (2007) allowed the extension of the top of the biozone to at least chron C31r, or Earliest Maastrichtian in age (Villalba-Breva et al. 2012). These results are compatible with the age inferred for the La Maçana Fm based on the age of overlying and underlying formations (Caus and Gómez-Garrido 1989; Galbrun et al. 1993, recalibrated with data from Gradstein et al. 2004).

La Posa Formation (Tremp Basin)

The charophyte assemblage from La Posa Fm, studied in Barranc de la Posa and Alzina-Beniure sections, is formed by *Feistiella malladae*, *Peckichara sertulata*, *Microchara cristata* and *Clavator brachycerus* (Table 1). The two species *Microchara cristata* and *Clavator brachycerus* have a wide range from the Middle Campanian to the Late Maastrichtian. They have been reported in the Peckichara pectinata, Peckichara cancellata, Septorella ultima and Microchara cristata biozones of Riveline et al. (1996). However, this range can be limited to the Early Maastrichtian by the occurrence of homogeneous assemblages of *Peckichara sertulata*, considered to develop in the Septorella ultima biozone, Early Maastrichtian in age (Riveline et al. 1996).

These results are compatible with former biostratigraphic data obtained for the same section and other equivalent sections by Feist et al. (1983), Gallemí et al. (1983) and Caus and Gómez-Garrido (1989). However our results do not agree with the age obtained from sequence stratigraphic interpretations by Ardèvol et al. (2000) and Vicens et al. (2004).

Table 1 Charophyte assemblages of the Grey Garumnian from the Ager and Tremp Basins

Lithostratigraphy	**La Maçana Fm**												**La Posa Fm**							
Locality	Cal Magí	La Maçana							Fontllonga				Barranc de la Posa					Alzina-Beniure		
Species \ Samples	**MAGÍ-1**	**MAÇ-2**	**MAÇ-5**	**MAÇ-6**	**MAÇ-8**	**MAÇ-12**	**MAÇ-16**	**MAÇ-20**	**FONT-1**	**FONT-2**	**FONT-3**	**FONT-4**	**POSA-5**	**POSA-6**	**POSA-8**	**POSA-10**	**POSA-14**	**ALZ-2**	**ALZ-3**	**ALZ-5**
Feistiella malladae								•				•	●	•	●	⬤	•	●		•
Microchara cristata							•				•	•						•		
M. parazensis		•	●		●															
Dughiella obtusa		•																		
Peckichara cancellata	•	●	●	●	⬤	•	•		•	•	•	•								
Peckichara sertulata										●	●	●				•		•	•	
Platychara caudata		⬤																		
Platychara turbinata		•																		
Clavator brachycerus			⬤	•	•	•	●	•	●	•		●						⬤	⬤	⬤

• 1-20 gyrogonites ● 21-100 gyrogonites ⬤ > 100 gyrogonites

Charophyte-rich microfacies and charophyte palaeoecology

The study of carbonate microfacies sheds light on the composition and palaeoecology of charophyte assemblages. Fourteen different categories of components were taken into account in carbonate microfacies: (1) Thalli of the genus *Charaxis*, which display *Chara*-like cortication of internodes (Fig. 6a). (2) Thalli of the genus *Clavatoraxis*, which bear characteristic spine-cell rosettes and correspond to *Clavatoraxis microcharophorus* Villalba-Breva and Martín-Closas 2011 (Fig. 6b). (3) Thalli of *Munieria grambastii* Bystrický 1976. Transversal sections show irregular, mainly triangular, outlines in contrast to the typically rounded shape of this species (Fig. 6c). This peculiar shape probably results from diagenetic deformation. (4) Porocharacean gyrogonites, characterised by their large spiral cells, rounded section and strong calcification of spiral cells, usually showing the internal Y-structure described by Feist and Grambast-Fessard (1984). These sections were attributed to *Feistiella* even if the unicellular basal plate characteristic of the genus was only observed in sieved gyrogonites (Fig. 6d). (5) Clavatoracean utricles attributed to *Clavator brachycerus* are distinguished by their bottle-shaped longitudinal section and by transversal sections with a crenulated outline and showing six pores within the wall, which correspond to the six bracts of its external utricular layer (Fig. 6e).

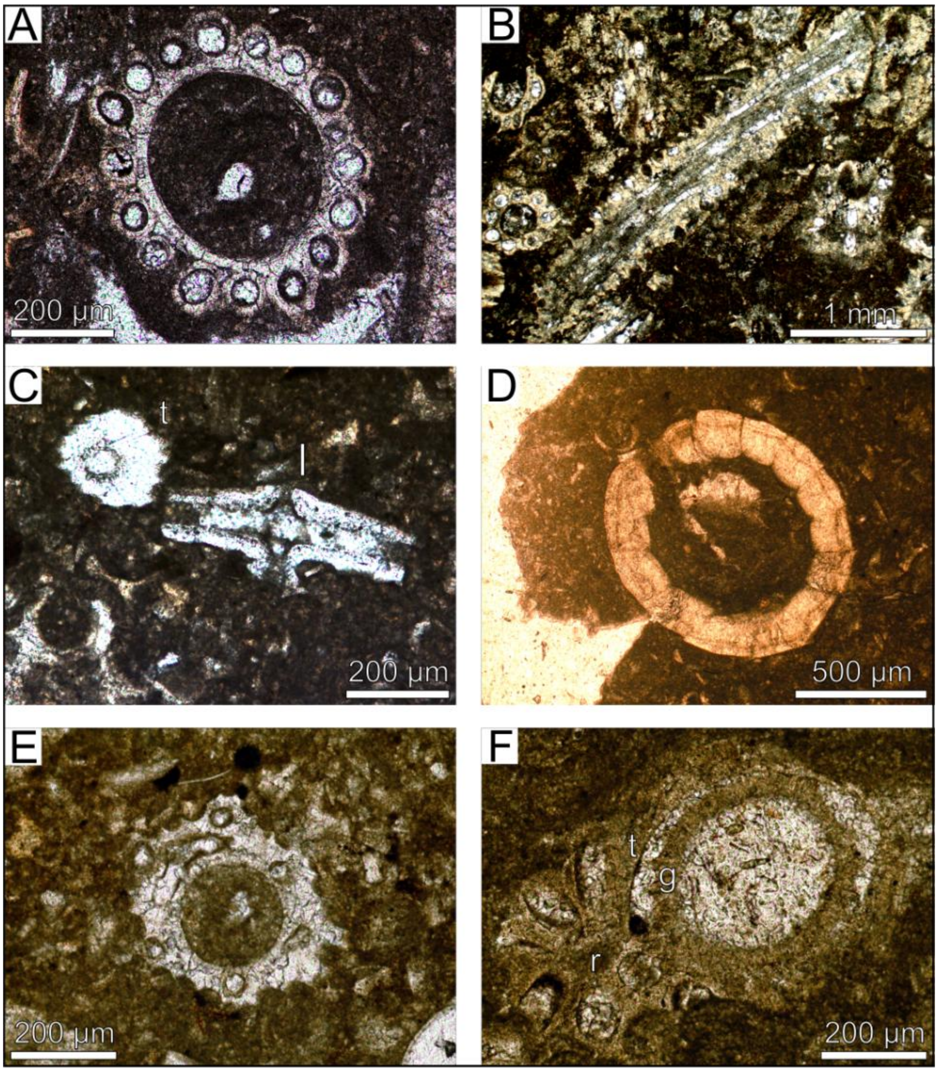

Fig. 6 Components distinguished in the microfacies analysis. **a** Transversal section through a *Charaxis* internode; thin section MAÇANA-3C. **b** Tangential section through a *Clavatoraxis* internode; thin section POSA-12C. **c** Transversal (*t*) and longitudinal (*l*) sections of *Munieria grambastii*; thin section MAÇANA-13C. **d** Longitudinal section of a *Feistiella* sp. gyrogonite showing high thickness of spiral cells; thin section MAÇANA-3C. **e** Transversal section of a clavatoracean utricle showing six pores corresponding to six bracts of the external utricular layer; thin section MAÇANA-13D. **f** Longitudinal section through a *Microchara* sp. gyrogonite (*g*) attached to a bract-cell rosette (*r*) and covered by a tunica (*t*); thin section MAÇANA-9E

(6) Characean gyrogonites, some of which are determinable at the genus level. Small prolate (ellipsoidal) characean gyrogonites (280-400 µm

high) probably correspond to the genus *Microchara* (Fig. 6f); small characean gyrogonites with a marked oblate shape (wider than higher gyrogonites) and basal column attributed to the genus *Platychara* (Fig. 7a); finally, large characean gyrogonites (850-920 µm high) with an ornamentation that consists of a mid-cellular crest, are related to the genus *Peckichara* (Fig. 7b). (7) Small calcified filaments without internal compartmentalisation, about 30 µm across, are attributed to cyanobacteria. (8) Collapsed tubes of sparry calcite, 120 µm thick and up to 1.5 mm across, without internal structures, are attributed to lime crusts upon stems of submerged macrophytes (Fig. 7c). (9) Brown wood with tracheidal structures preserved (Fig. 7d). (10) Black wood attributed to fusinite. (11) Ostracod shells, mainly devoid of ornamentation. (12) Gastropod shells. (13) Vertebrate eggshells, which were attributed to reptiles or birds, on the basis of their thickness and internal structure (Fig. 7e). (14) Intraclasts, mainly black pebbles showing composition and texture similar to the surrounding sediment (Fig. 7f).

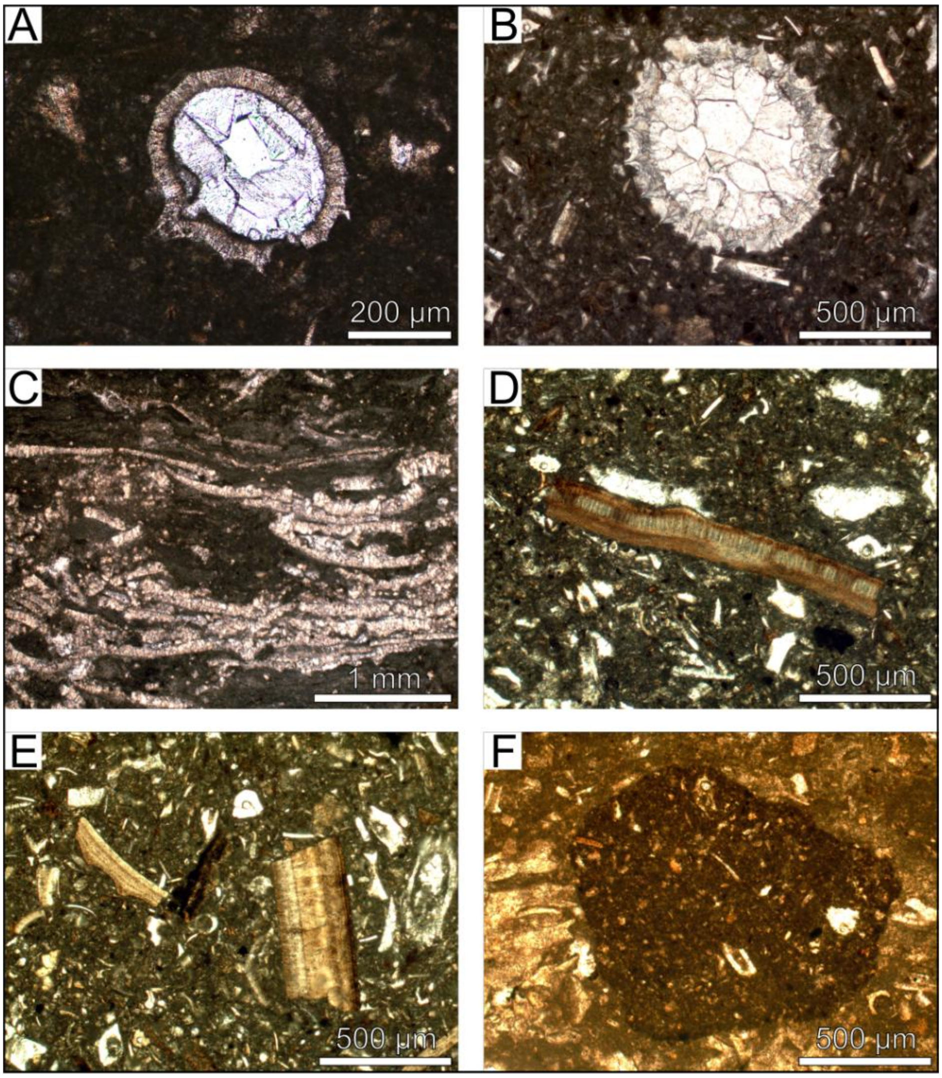

Fig. 7 Components distinguished in the microfacies analysis (continued). **a** Longitudinal section of a *Platychara* sp. gyrogonite; thin section MAÇANA-3A. **b** Longitudinal section of a *Peckichara* sp. gyrogonite; thin section MAÇANA-1B,. **c** Collapsed tubes of sparry calcite; thin section MAÇANA-4A. **d** Brown wood with tracheidal structures; thin section MAÇANA-1A. **e** Vertebrate eggshells; thin section MAÇANA-1A. **f** Black pebble; thin section MAÇANA-13A

Microfacies and charophyte palaeoecology of the La Maçana Fm (Ager Basin)

An analysis of the sedimentary facies present in the middle part of the La Maçana Fm allowed us to distinguish a number of microfacies related to each other to form three facies associations.

1. Lakeshore facies and microfacies

Facies 1 are represented by dark-grey packstones. They are well-bedded, frequently 80 cm thick, and contain abundant charophyte thalli, gyrogonites, comminuted carbonaceous plant debris, gastropods and bivalves. Two microfacies were distinguished:

Microfacies 1.1 are dark-grey packstones dominated by fragments of *Munieria grambastii* Bystrický 1976, sometimes forming horizons built up solely of these remains (Fig. 8a). These thalli are locally associated with clavatoracean utricles related to *Clavator brachycerus*, which allows us to attribute *Munieria grambastii* to this charophyte fructification, as already suggested by Fabre-Taxy and Chatelet (1971). Other skeletal components include abundant fragments of ostracods and undetermined bioclasts. Small portions of *Charaxis* thalli internodes, broken or deformed characean gyrogonites of *Peckichara* and *Microchara,* vertebrate eggshell fragments, brown wood and fusinite are less frequent. The high fragmentation of the remains indicates that this facies corresponds to the washed remains of a *Munieria grambastii* – clavatoracean meadow deposited on the shores of lakes subjected to significant wave action.

Microfacies 1.2. On top of the La Maçana section dark grey packstones with *Munieria grambastii* show some variation, since the limestone beds are overtopped by brecciation similar to pseudomicrokarst in the sense of Freytet and Plaziat (1982), ferric crusts, tubular bioturbation and rootlet-marks. The microfacies is similar to other dark-grey packstones but it includes a larger number of black-pebbles. This indicates that the lakeshores were affected by subaerial exposure and the development of hydromorphic soils.

2. Shallow lacustrine facies and microfacies

Facies 2 are white limestones. They are well-bedded wackestones, frequently 1 m thick, and rich in charophyte thalli and gyrogonites. Three different types of light-coloured carbonate microfacies were defined (Figs. 8b-d):

Microfacies 2.1 are wackestones-packstones of charophyte thalli belonging to *Clavatoraxis microcharophorus* Villalba-Breva and Martín-Closas 2011. They are usually well-preserved and include large portions of internodes. Small characean gyrogonites attributed to the genus *Microchara* were found in anatomical connection with the thalli. There are also collapsed tubes of sparry calcite, corresponding to crusts of submerged macrophytes. Calcified filaments attributed to *Girvanella* sp., are abundant in the muddy sediment and may represent poorly developed cyanobacterial mats. The good articulation of plant remains suggest that this facies should be attributed to deposition within a *Clavatoraxis* charophyte meadow, below the wave motion line.

Microfacies 2.2 are wackestones-packstones of *Charaxis* sp. type thalli, 425-740 µm across. Associated with these thalli are disperse gyrogonites attributed to the genera *Peckichara* and *Microchara*. Intercalated with the thalli and gyrogonites, there are horizons formed by collapsed tubes of sparry calcite attributed to lime crusts upon stems of submerged macrophytes. The preservation of the somewhat disarticulated charophyte remains suggests that this facies is related to the deposition of autochthonous to parautochthonous remains of *Charaxis*-dominated meadows and submerged macrophytes.

Microfacies 2.3 are mudstones-wackestones of abundant fragmented charophyte remains and other small bioclasts of undetermined affinity. Thalli, usually small portions of isostichous internodes, correspond to the genus *Charaxis*. Most characean gyrogonites are small in size, fragmented and probably correspond to the genus *Microchara*. Other types of gyrogonites found were generally broken and are attributed to the genera *Feistiella* and *Platychara*. The poor preservation of charophyte remains indicates that they were transported from a neighbouring growth area and deposited in relatively deeper parts of the lake.

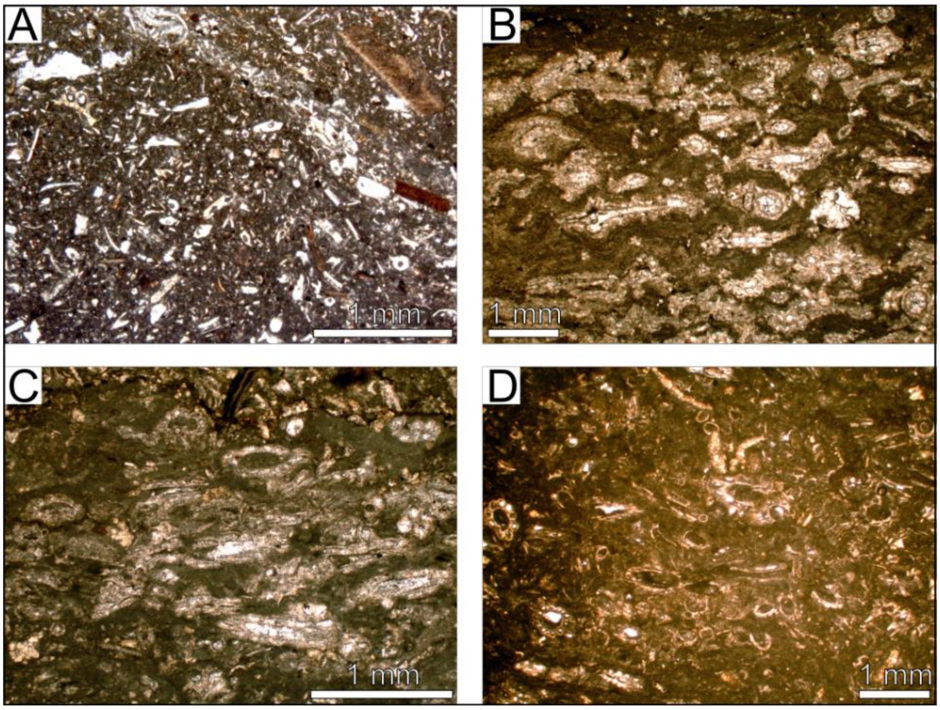

Fig. 8 Microfacies of La Maçana Fm. **a** Packstone of *Munieria grambastii*; thin section MAÇANA-1A. **b** Wackestone-packstone of *Clavatoraxis microcharophorus*; thin section MAÇANA-9C. **c** Wackestone-packstone of *Charaxis* sp. type thalli; thin section MAÇANA-4A. **d** Mudstone-wackestone of fragmented *Charaxis* thalli and other small bioclasts of undetermined affinity; thin section MAÇANA-3

3. Deeper lacustrine facies

Facies 3 consists of marls. They are up 10 cm thick and contain ostracods, gastropods, and charophyte remains. Charophyte remains include small portions of two types of thallus, *Charaxis* and *Clavatoraxis*, and a number of fructifications, i.e. gyrogonites of *Peckichara cancellata*, *P. sertulata, Platychara caudata, P. turbinata*, *Dughiella obtusa*, *Microchara cristata*, *M. parazensis* and *Feistiella malladae*, and utricles of *Clavator brachycerus*. This assemblage is dominated by *C. brachycerus* and *P. cancellata*. This facies is related to deposition of parautochthonous to allochthonous charophyte remains beyond the lake margins, in relatively deeper areas, where the deposition of suspended mud predominated over biogenic carbonate precipitation.

The most abundant facies association in the La Maçana Fm is formed by basal marls, followed by white wackestones and dark-grey packstones at the top (Fig. 2a). These cycles are several decimetres thick and repeated hundreds of times. Vertical distribution of facies suggests that they correspond to infilling sequences of highly alkaline lakes, which graded upwards from deeper lacustrine facies (facies 3), marginal, well-illuminated and vegetated lake environments (facies 2) to lakeshores (facies 1). Another type of association is built up from the reiteration of light-coloured wackestones and dark packstones, without marls at the base (Fig. 2b). Finally, a third type of facies association is built by the reiteration of marls (facies 3) overlain by dark packstones overtopped by brecciation (facies 1.2) (Fig. 2c).

Charophyte-rich microfacies have enabled us to distinguish a number of facies belts in the lacustrine environment of the La Maçana Fm (Fig. 9).

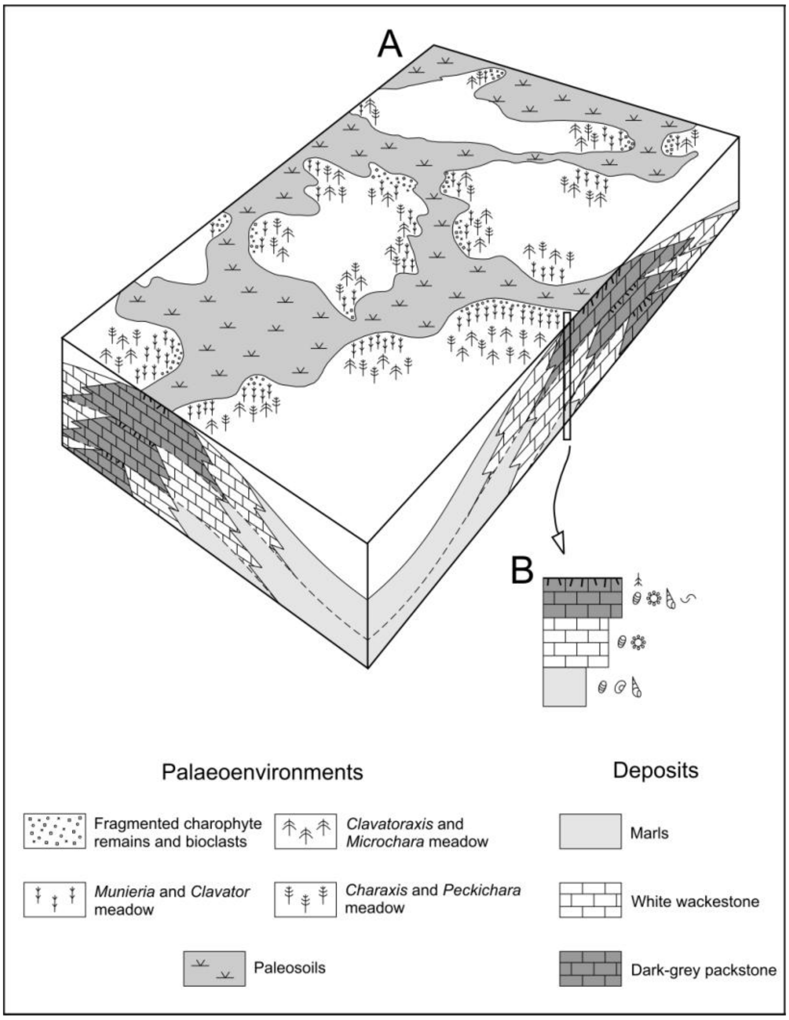

Fig. 9 Palaeoenvironmental reconstruction from the Late Campanian of the Ager Basin. **a** Palaeoenvironmental diagram with the proposed zonation of charophyte meadows. **b** Section showing the vertical development of a basic sedimentary cycle, as shown in Figure 2a

The lakeshore belt is represented by facies of fragmented charophyte remains and bioclasts (microfacies 1.2.).

The shallow lake is represented by three different types of charophyte meadows. These were respectively dominated by

(1) *Munieria grambastii* and *Clavator brachycerus*, (2) *Charaxis* sp. and *Peckichara* associated with submerged vascular plants, probably angiosperms and (3) *Clavatoraxis microcharophorus* and *Microchara*. The lateral relationships between these two latter meadows are unknown. However, the repeated change in the shallowing-upward cycles from white wackestones of *Charaxis* - *Peckichara* and *Clavatoraxis* - *Microchara* to dark-grey packstones with *Munieria grambastii* and *Clavator brachycerus* suggests that, in palaeoecological terms, this last meadow grew in very shallow environments. In contrast, the *Charaxis* – *Peckichara* and *Clavatoraxis microcharophorus* – *Microchara* meadows occurred in relatively deeper parts of the shallow lake. The fact that clavatoraceans occurred in the shallower and better illuminated vegetation belt is remarkable since *Clavator brachycerus* represents one of the last clavatoraceans, occurring shortly before the extinction of the family during the Maastrichtian.

Microfacies and charophyte palaeoecology of the La Posa Fm (Tremp Basin)

An analysis was conducted of the sedimentary facies and carbonate microfacies in the stratotype of the La Posa Fm as defined by Liebau (1973). Four facies were recognised on the basis of lithology, sedimentary structures, fossil content, shape and thickness of beds, and colour. The vertical and lateral relationships between these facies enabled us to establish three facies associations.

1. Lacustrine facies and microfacies

Facies A are grey wackestones. They are well-bedded, up to 1.5 m thick, and contain abundant charophyte thalli and gyrogonites. Two different types of microfacies (microfacies A1 and A2) were defined (Figs. 10a-c):

Microfacies A1 consist of laminated wackestones-packstones with abundant *Clavatoraxis microcharophorus* thalli. Rare characean gyrogonites, probably corresponding to *Microchara* sp., are associated with but not attached to the thalli. Most of the thalli are well-preserved and include large portions of internodes, indicating that they were produced by plants growing nearby the deposition site and later underwent short lateral transport. Some horizons formed by up to 1 mm-wide tubes of sparry calcite attributed to crusts upon submerged macrophytes are intercalated with charophyte-rich horizons. This facies is attributed to deposition within a meadow dominated by *Clavatoraxis*-bearing charophytes and other macrophytes below lacustrine wave action.

Microfacies A2 consist of laminated wackestones of ca. 2 mm-wide thalli of isostichous *Charaxis* sp. Normally, they are only calcified in the intercellular area between the internodal and the cortical cells, leading to the accumulation of collapsed intercellular fragments, typically triangular in shape. In the same horizons, there are dispersed characean gyrogonites corresponding to the genera *Microchara* and *Peckichara*. Intercalated with these horizons, there are other horizons dominated by *Munieria grambastii*. The lamination of this microfacies and the absence of bioturbation suggest that the charophyte remains were deposited on an anoxic lake bottom after undergoing a short lateral transport. In consequence, this facies is related to the deposition of parautochthonous remains of *Charaxis* and *Munieria grambastii*-bearing charophyte meadows in relatively deeper areas of the lake.

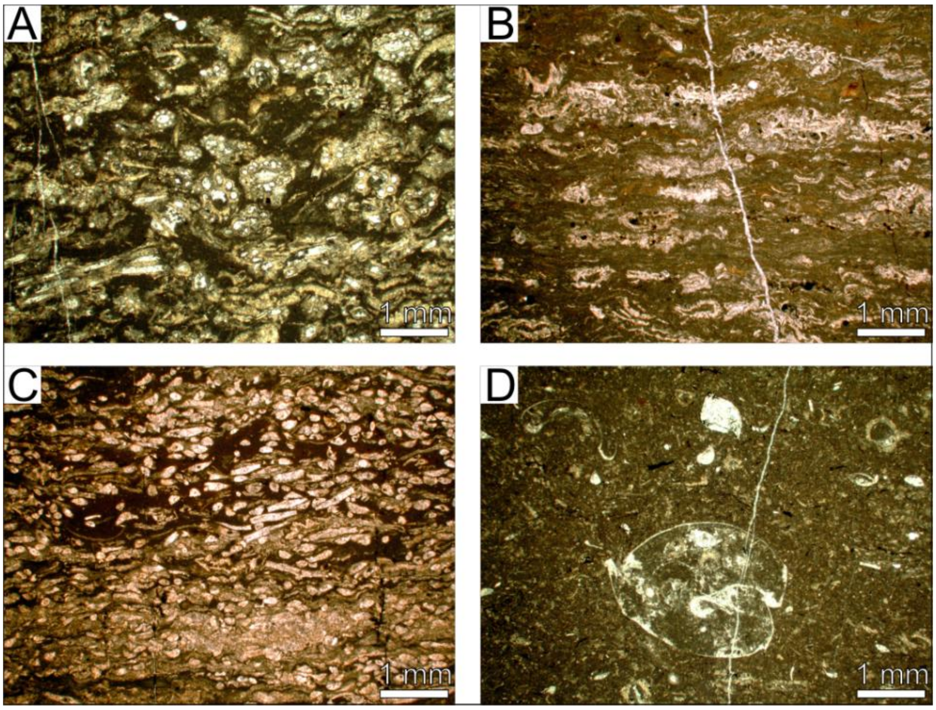

Fig. 10 Microfacies of La Posa Fm. **a** Wackestone-packstone of *Clavatoraxis microcharophorus* thalli; thin section POSA-12A. **b** Laminated wackestone of large isostichous *Charaxis* sp. thalli; thin section POSA-7B. **c** Packstone of *Munieria grambastii*; thin section POSA-7A. **d** Mudstone-wackestone of ostracods and fragments of bivalves and gastropods; thin section POSA-11B

2. Lignite from detrital peat

Facies B are lignite and black marls rich in organic matter. They form horizons less than 20 cm thick. 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 conifer wood as a precursor. These lignite beds do not show root traces at their bases which suggests that they resulted from a parautochthonous accumulation of organic matter rather than from deposition in peat mires or swamps. Recently, Villaba-Breva et al. (2012) found that the organic matter precursor of Southern Pyrenean Upper Cretaceous lignite was mainly formed by remains of the cheirolepidiacean conifer *Frenelopsis*. Liebau (1973) had already reported that brackish gastropods, ostreids and euryhaline bivalves (*Corbicula*) occur in this facies, indicating that the salinity under which the organic matter was deposited was variable.

3. Brackish lagoon facies and microfacies

Facies C are several metres thick marls and well-bedded grey marlstones up to 20 cm thick, containing euryhaline molluscs (*Corbicula, Ostrea*, potamids, ceritids), freshwater gastropods (planorbids), ostracods, charophyte gyrogonites and rare dasicladaleans. The charophyte flora found is generally dominated by monospecific assemblages of the porocharacean *Feistiella malladae*, which, in the Cretaceous, are indicative of brackish water conditions (Mojon 1989). From the point of view of microfacies, most of the components are ostracods (Fig. 10d). Other significant skeletal components in the microfacies include 1 mm-wide tubes of sparry calcite attributed to submerged macrophytes and fragments of *Charaxis* sp. thalli. Small characean gyrogonites, possibly belonging to *Microchara*, are less frequent. From the point of view of charophyte paleoecology, this facies is related to deposition of suspended mud and parautochthonous to allochthonous remains of a porocharacean meadow in relatively deeper areas of a lagoon, with both marine and freshwater influences.

The most abundant facies association recognised in the La Posa Fm is formed by basal marls, followed by lignite and grey wackestones at the top (Fig. 3a). These cycles are several metres thick and are repeated dozens of times. They are interpreted as showing a transition from brackish deposits (marls with euryhaline molluscs and *Feistiella malladae* of facies C), to freshwater deposits (limestones with *Clavatoraxis*, *Charaxis* and *Munieria grambastii* of facies A). The water salinity under which detrital peat was deposited (lignite of facies B) was probably variable. Another type of cycle is built up from the reiteration of marls and wackestones without lignite between them (Fig. 3b).

Charophyte-rich microfacies have enabled us to distinguish three charophyte meadows of freshwater lacustrine facies and one meadow of brackish facies in the transitional environment of the La Posa Fm (Fig. 11).

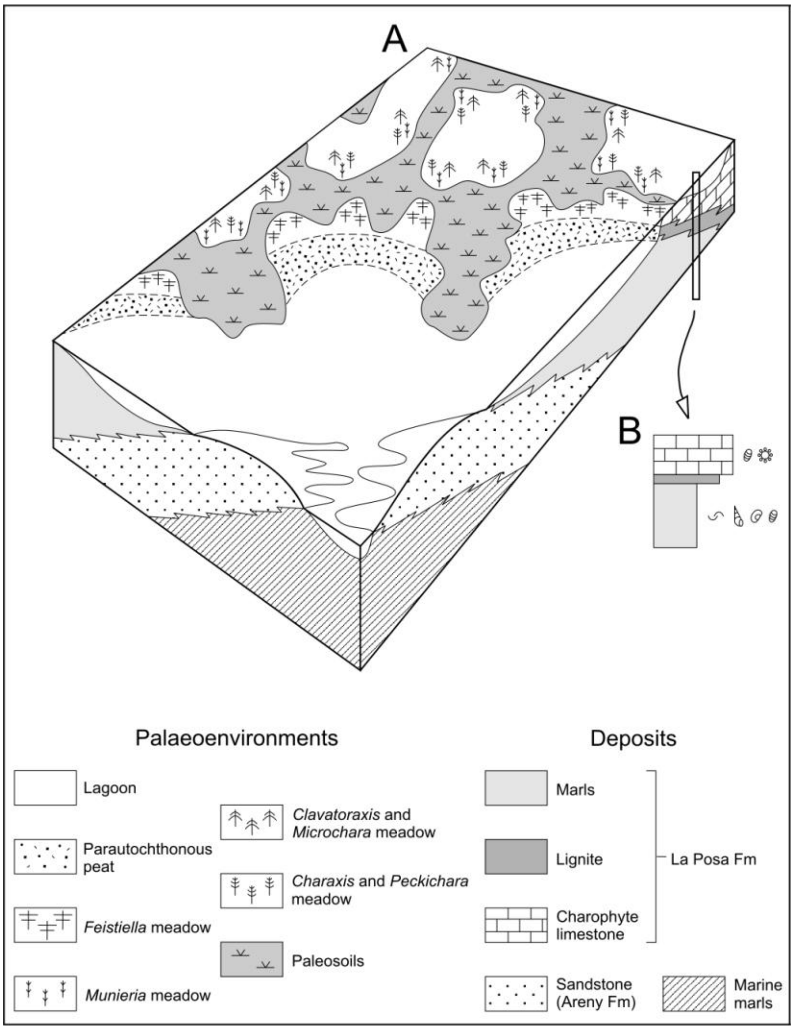

Fig. 11 Palaeoenvironmental reconstruction from the Early Maastrichtian of the Tremp Basin. **a** Palaeoenvironmental diagram with the proposed zonation of charophytes. **b** Section showing the vertical development of a basic sedimentary cycle, as shown in Figure 3a

The most abundant meadow was dominated by *Feistiella malladae* and grew in brackish environments of lagoon facies. In the freshwater lakes meanwhile, the different types of charophyte meadows only occur locally and were represented by: (1) *Munieria grambastii* meadows, (2) *Charaxis* sp. and *Peckichara* meadows, and (3) *Clavatoraxis microcharophorus* and *Microchara* meadows associated with submerged vascular plants, probably angiosperms. The lateral relationships between these three meadows are poorly known in La Posa.

Comparison

From a sedimentological point of view, the Ager and Tremp Basins show significant differences. In the La Maçana Fm (Ager Basin), the sedimentary succession is exclusively formed by freshwater lacustrine facies. It is organised into hundreds of small order sedimentary cycles corresponding to lacustrine infilling sequences. In contrast, the first continental deposition in the La Posa Fm (Tremp Basin) took place in more diverse sedimentary settings, ranging from brackish lagoons, swamp marshes and poorly developed freshwater lakes. These deposits are organised into a small number of cycles which correspond to the progradation of a deltaic-estuarine system eastwards (Rosell et al. 2001).

From the point of view of the microfacies and palaeoecology, a comparison of the La Maçana and La Posa Fms reveals that the lakes of both basins had three similar types of charophyte-rich facies, dominated respectively by *Clavatoraxis microcharophorus*, *Charaxis* sp. and *Munieria grambastii* thalli, sometimes with abundant remains of submerged macrophytes. However, there were significant differences both in the specific composition and richness of charophytes as determined from their fructifications. Thus, species richness in the La Maçana Fm (Ager Basin) is much higher than in the La Posa Fm (Tremp Basin), as is to be expected when charophyte assemblages from freshwater lakes are compared with assemblages from brackish water (García 1999). Not only was the species richness between both environments different, but also the species composition, since in the lacustrine La Maçana Fm the assemblages were dominated by characeans, especially *Peckichara cancellata* in the marginal lake and clavatoraceans (*Clavator brachycerus*) in the lakeshores, whilst in the La Posa Fm the most abundant species was the porocharacean *Feistiella malladae*.

Discussion

The beginning of the Late Cretaceous continentalisation in the Southern Pyrenean Basin differs between the Ager and the Tremp Basins both in terms of age and facies (Fig. 12). The La Maçana Fm (Ager Basin) was deposited during the Late Campanian (Peckichara cancellata biozone, within or below chron C32). The non-marine sedimentation was organised into hundreds of shallowing-upwards lacustrine cycles representing lake infilling sequences. Facies and microfacies change from turbid, deeper lacustrine facies (marls), to marginal, well-illuminated and vegetated lake margins dominated by characean meadows (white limestones with *Clavatoraxis microcharophorus* and *Microchara* or *Charaxis* and *Peckichara*), to lakeshore facies dominated by clavatoraceans (dark-grey packstones with *Munieria grambastii* and *Clavator brachycerus*). Coeval, i.e. Late Campanian, deposits to the north, in the Tremp Basin, are fully marine, represented by nearshore sandstone and calcarenite of the Areny Formation. The first Upper Cretaceous continental deposits of the Tremp Basin correspond to the La Posa Fm, and are already Early Maastrichtian in age (Septorella ultima biozone). The sedimentation there was organised into tens of cycles that show a transition from brackish deposits (marls and marlstones with porocharaceans and euryhaline molluscs) to lacustrine limestones with *Clavatoraxis microcharophorus*, *Charaxis* and *Munieria grambastii*), sometimes with the intermediary of coal representing detrital peat from swamps of varying salinity. Coeval, i.e. Early Maastrichtian, deposits from the Ager Basin to the north correspond to fluvial facies from the Figuerola Fm, according to magnetostratigraphic data recalibrated from Galbrun et al. (1993).

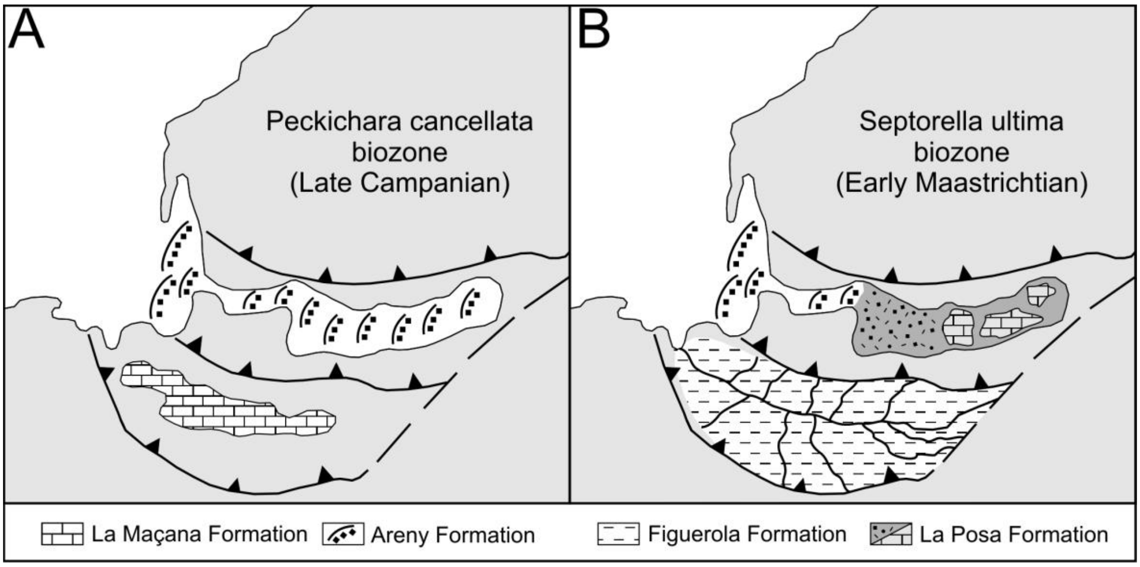

Fig. 12 Palaeogeographical evolution of the Central South-Pyrenean Basins during (**a**) the Late Campanian and (**b**) the Early Maastrichtian, showing a well-marked S-N facies distribution

Conclusions

The first non-marine facies (Garumnian) of the Central Southern Pyrenean Basins of Ager and Tremp show contrasting chronostratigraphical, sedimentological, and palaeoecological features. These differences are important from a palaeogeographic point of view since they suggest that the Southern Pyrenean Basin displayed a south to north shift of facies during the Campanian-Maastrichtian boundary. The more proximal, strictly lacustrine facies were deposited in the Late Campanian and were located to the south (La Maçana Fm, Ager Basin) whilst in the north (Tremp Basin) more distal, strictly marine facies of the nearshore Areny Fm occurred. In the Early Maastrichtian, the same facies polarity appears to occur, but this time the facies were fluviatile in the south (Figuerola Fm, Ager Basin) whereas in the north (Tremp Basin) the sedimentation displayed transitional facies ranging from brackish lagoons to the coal swamps and freshwater lakes of La Posa Fm.

This south to north facies distribution is somewhat reminiscent of the distribution of facies reported for Early Cretaceous Pyrenean Basins by Peybernès (1976). However, in the Late Cretaceous it was superimposed onto the well-known east to west polarity, related to Southern Pyrenean Basin infilling and to the anticlockwise rotation of Iberia (Capote et al. 2002).

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Annex 2: Altres publicacions rellevants de la tesi

Article 1

MARMI, J., GOMEZ, B., MARTÍN-CLOSAS, C., **VILLALBA-BREVA, S.** 2010. A reconstruction of the fossil palm *Sabalites longirhachis* (Unger) J. Kvaček et Herman from the Maastrichtian of Pyrenees. *Review of Palaeobotany and Palynology*, 163: 73-83.

RESUM: L'únic òrgan conegut fins ara de la palmera fòssil *Sabalites longirhachis* (UNGER) J. KVAČEK ET HERMAN eren làmines fragmentades de les seves fulles. A la localitat de Fumanya, Maastrichtià del sud del Pirineu, s'han trobat fulles senceres de *S. longhirachis*, associades a troncs i sistemes d'arrelament de palmera . Aquestes dades han permès proposar una hipòtesi sobre l'hàbitat i la paleoecologia d'aquestes palmeres extingides, fonamentada en la tafonomia. Les fulles fòssils estan representades per làmines completes amb pecíols. Les fulles i els troncs són parautòctons a la base del primer horitzó de carbó de la sèrie estratigràfica. Els sistemes d'arrelament proporcionen la prova de l'autoctonia de la palmera i es troben en capes de carbó poc potents que cobreixen les calcàries lacustres. L'arbre portador de fulles de *S. longirhachis* era relativament esvelt, de 20-30 cm de gruix i fins a 14 m d'alçada, amb un tronc llis, arrels adventícies a la base i una capçada que retenia les fulles marcescents. El sistema d'arrelament era radial i de fins a 1.5 m de diàmetre en total. Les anàlisis tafonòmiques i de fàcies dutes a terme a Fumanya suggereixen que els hàbitats colonitzats per aquesta espècie eren petites torberes a les vores de llacs alcalins d'aigua dolça colonitzats per caròfits.

Review of Palaeobotany and Palynology 163 (2010) 73–83

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Research papers

A reconstruction of the fossil palm *Sabalites longirhachis* (Unger) J. Kvaček et Herman from the Maastrichtian of Pyrenees

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A B S T R A C T

Fragmented leaf laminas were the only organ known of the fossil palms *Sabalites longirhachis* (Unger) J. Kvaček et Herman. Recently, isolated leaves of *S. longirhachis*, palm logs and rooting systems have been found associated in Fumanya, a new Maastrichtian locality from the Southern Pyrenees. This has allowed proposing a taphonomy-based hypothesis of the habit and paleoecology of these extinct palms.

Fossil leaves are represented by complete laminas bearing petioles attached. Leaves and logs are parautochthonous at the base of the first coal seam of the stratigraphic succession. Rooting systems provide evidence for autochthony in coal layers formed at the top of lacustrine limestones. The tree bearing *S. longirhachis* leaves is reconstructed as relatively slender, of up to 14 m high, showing a smooth trunk with adventitious roots at the base and a crown keeping the marcescent leaves attached. The rooting system consisted of straight radial rootlets of about 1.5 m in total diameter. Taphonomic and facies analyses carried out in Fumanya suggest that the habitats colonized by this species were small peat mires at the lakeshores of freshwater alkaline lakes.

1. Introduction

The fossil record of plants is mainly composed of fragmentary remains, with organs detached one from each other or even fragmented, making whole plant reconstructions a difficult task for paleobotanists. Since the very beginning of paleobotany, hypotheses were proposed to understand the complete body of fossil plants, mainly based on exceptionally well-preserved fossils showing anatomical connections or on repeated taphonomic associations of the different organs. Although misleading interpretations were proposed by the past, whole plant reconstructions continue to be one of the main goals of paleobotanical research. They contribute to a more complete understanding of plant evolution, help to correct mistakes in systematic paleobotany and are the basis for paleoecological and paleobiogeographical studies (Kvaček, 2008).

Some groups of fossil plants are more prone to be found with their organs attached, since they were living in the very same depositional setting in which they were later buried, such as in peat mires. However, land plants showing anatomically connected organs are extremely rare in most depositional settings and whole plant reconstructions can be only carried out hence based on taphonomic hypotheses. This is the case of most palms, which normally grow outside but sometimes not far from areas with a high sedimentation rate.

The evolutionary history of Arecaceae probably began in the Early Cretaceous, according to molecular data (Janssen and Bremer, 2004). The earliest unequivocal palm fossils are from the lower Upper Cretaceous (Harley, 2006). During the latest Cretaceous, palms were widely present in the Pantropical and part of the North Temperate Realms (Horrell, 1991). By this time, there is a range of variation within each organ category indicating that the family was already a well established lineage (Harley, 2006). Palm pollen grains, leaves and stems are particularly abundant in the fossil record. Records of fruits, rhizomes and roots are scarcer and rachillae, inflorescences or individual flowers are rare (Harley, 2006). Among the earliest megafossil palm remains there are leaves with long petiole bearing costapalmate lamina of *Sabalites longirhachis* (Unger) J. Kvaček et Herman. *Sabalites longirhachis* is known from the upper Santonian–Maastrichtian of southwestern, central and eastern Europe (Saporta and Marion, 1885; Tuzson, 1908, 1914; Kvaček and Herman, 2004; Marmi et al., 2008). The gross morphology and cuticular features of *S. longirhachis* were described by Kvaček and Herman (2004) and Marmi et al. (2008). However, other vegetative organs (e.g. stems and roots) as well as reproductive structures (e.g. flowers, seeds and fruits) of this fossil palm species were completely unknown so far.

In the Iberian Peninsula, Schulp and Brokx (1999) mentioned for the first time "well-preserved palm leaves" at the "titanosaur megatrack" localities from the Early Maastrichtian of Fumanya

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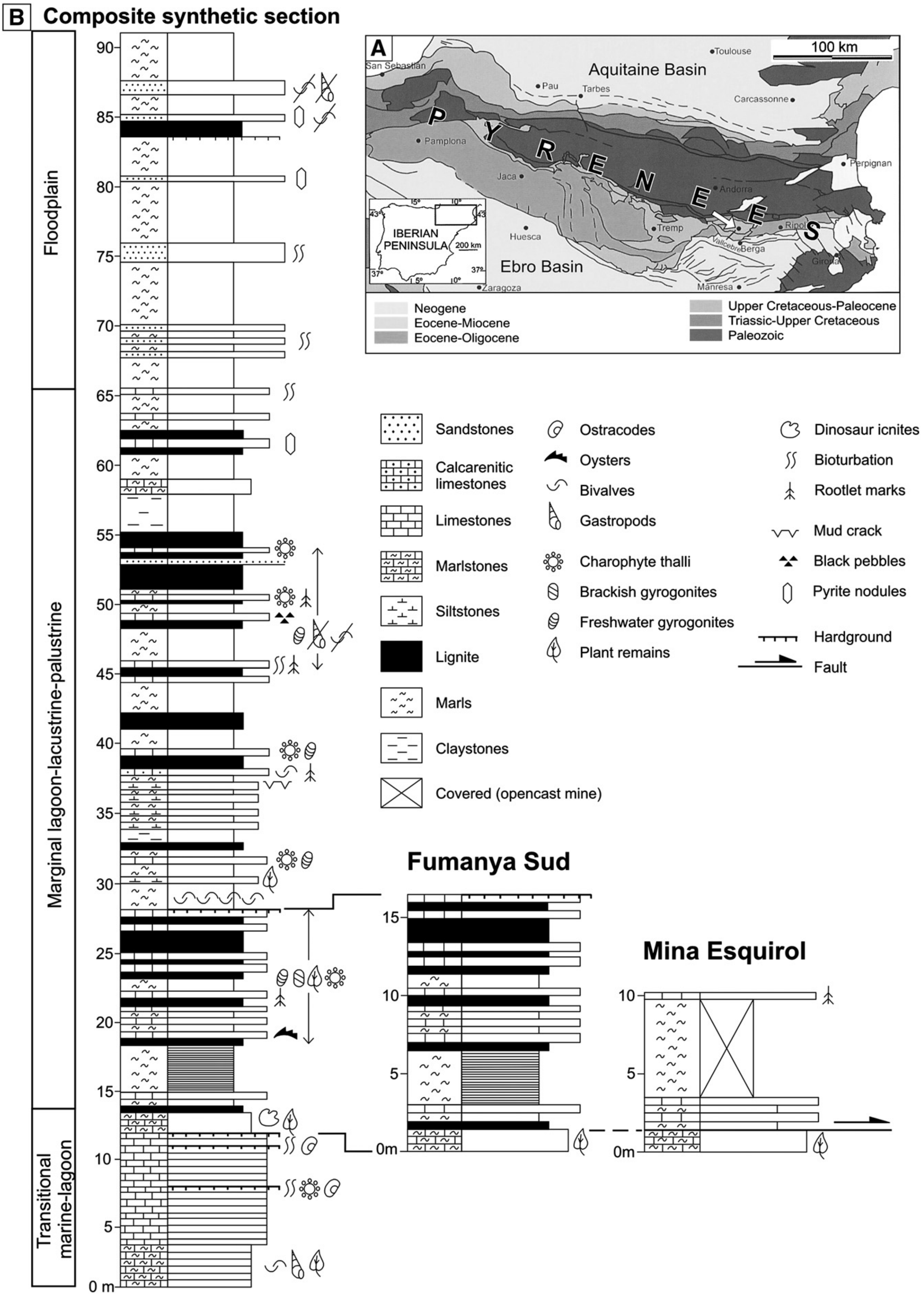
B
Composite synthetic section
Floodplain
Marginal lagoon-lacustrine-palustrine
Transitional marine-lagoon
0 m
5
10
15
20
25
30
35
40
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50
55
60
65
70
75
80
85
90
A
100 km
Toulouse
San Sebastian
Aquitaine Basin
Pau
Tarbes
Carcassonne
P
Y
R
E
N
E
E
S
Pamplona
Perpignan
Jaca
Andorra
Huesca
Tremp
Ripoll
Vallcebre
Berga
Girona
Ebro Basin
Manresa
Zaragoza
IBERIAN PENINSULA
200 km
15º
10º
43º
37º
5º
Neogene
Eocene-Miocene
Eocene-Oligocene
Upper Cretaceous-Paleocene
Triassic-Upper Cretaceous
Paleozoic
Sandstones
Calcarenitic limestones
Limestones
Marlstones
Siltstones
Lignite
Marls
Claystones
Covered (opencast mine)
Ostracodes
Oysters
Bivalves
Gastropods
Charophyte thalli
Brackish gyrogonites
Freshwater gyrogonites
Plant remains
Dinosaur icnites
Bioturbation
Rootlet marks
Mud crack
Black pebbles
Pyrite nodules
Hardground
Fault
Fumanya Sud
0m
5
10
15
Mina Esquirol
0m
5
10

(Eastern Pyrenees). In the last years, prospections on the Fumanya localities have allowed for documenting tens of *Sabalites longirhachis* leaf adpressions, more than one hundred log casts, many of them attributed to palms, and probable palm stumps with adventitious rooting systems. Although organs are unattached, they co-occur in the same bedding surface or in directly overlying and sedimentologically related horizons. This allows us to propose, for the first time, a hypothesis for the reconstruction of a Mesozoic palm habit based on a taphonomic approach and, on the same basis, to provide evidence for the habitat of *S. longirhachis*.

2. Geological setting

The studied plant fossils are contained in the Tremp Formation (Mey et al., 1968), regionally called "Garumnian" (Leymerie, 1862), which is formed by transitional to non-marine rocks deposited in the South Pyrenean Basin mainly during the Maastrichtian–Paleocene, when the sea gradually retreated westwards (Mey et al., 1968). The initial stage of the evolution of the South Pyrenean foreland basin in the Late Cretaceous, resulted in the development of successive thrusts-sheets. As a consequence, the basin was segmented into uplift-bounded depocenters or synclines, which are, from East to West, Vallcebre, Coll de Nargó, Tremp and Ager (Oms et al., 2007). Although Garumnian palm megafossil remains occur in almost all these areas, they have been found better preserved in the Vallcebre syncline.

The Tremp Formation or Garumnian in the Vallcebre depocenter is up to 850 m thick (Vergés et al., 1994) and was divided by Rosell et al. (2001) into four lithological units, of which the transitional basal unit (Grey Garumnian) was the subject of our study. It is formed by a heterolithic succession, up to 100 m thick containing grey lutites and marls with intercalations of lignite, charophyte limestones and sandstones (Fig. 1). Micritic marlstones comprise the dominating lithology at the base and contain frequent dinosaur trackways at the top. These trackways are close to the Campanian–Maastrichtian boundary and fall within the C32n.1n magnetochron (ca. 71 Mya) as indicated by paleomagnetic data (Oms et al., 2007). Marlstones are covered by a succession of alternating organic marl, lignite and charophyte limestones that correspond to the base of the C31r magnetochron. Thus, the age of this part of the transitional basal unit is early Maastrichtian, according to Oms et al. (2007). Coquinas may be associated with these materials. A succession of variegated siltstone with dinosaur eggshell fragments represents the top of the Grey Garumnian. These materials were deposited in peritidal to supratidal environments, including brackish lagoons at the base, followed by well-developed wetlands with brackish marshes and freshwater lakes and ending with floodplains to the top.

3. Materials and methods

In the Vallcebre syncline, the fossil localities studied occur near the Fumanya Pass, close to the villages of Fígols and Vallcebre and not far from the town of Berga, northern Catalonia (Fig. 1). A large structural surface, ca. 16,000 m^2 in size, containing most of the plant remains studied herein corresponds to the base of a relatively thick coal seam which was exploited in the opencast coal mines during the second third of the last century (Fig. 2).

Seventy-six partial to complete impressions and compressions of palm leaves have been observed at the base of the first coal seam from the Fumanya Sud (N42°10′50″ E01°47′42″) and Mina Esquirol (N42°11′8″ E01°47′51″) opencast mines (Figs. 1 and 2). They have been recorded by means of drawings and photographs. Thirty-three specimens consist of fragments of leaf laminas with a few fused segments and in some cases are very damaged by surface weathering. Among the best preserved specimens, there are nineteen leaves with complete or almost complete laminas, of which twelve maintain their petioles in anatomic connection. One hundred and thirty casts of logs have been documented by means of pictures on the same palm-leaf bearing surface (Fig. 2). Three casts preserve details of cortical structures. Some brush-like rooting systems appear at the top of a freshwater charophyte limestone bed, about 9 m above the marly limestone surface with palm leaves and logs of Mina Esquirol (Figs. 1 and 3). Resin replicas of leaves are stored in the collection of the Institut Català de Paleontologia under the codes IPS-41681 and IPS-41682.

4. Description of fossil organs related to the *Sabalites longirhachis*-bearing palm

4.1. Leaves

Leaves are costapalmate and ovalo-lanceolate symmetrical megaphylls (Plate I). They were highly variable in size and measured up to 125 cm long (Table 1). The most complete leaf laminas (Plate I, 1, 2) are 43-75 cm long and 10–41 cm wide. Laminas are longer than wider, having a length/width ratio from 1:1 to 4:1. The base angle of leaf lamina is acute (lower than 90°, see Table 1). The base and the apex shapes are convex. The leaf lamina is composed of approximately 25–30 pairs of opposite, induplicate and fused segments that are nearly linear and generally become wider in their apical part. Segment lengths range 16–41 cm, while basal widths are 0.15–1.6 cm. The segments merge into the costa at acute angles (11.3°–53.4°, see Table 1). The basal borders of segments are slightly decurrent on the costa. The costa is long and thick, and penetrates up to roughly the middle of lamina. In the best preserved specimens, narrow longitudinal grooves are observed on surfaces of costas and petioles (Plate I, 3). For each segment, the mid-vein and four parallel lower-order veins can be distinguished (Plate I, 4, 5). The smallest vein widths range 0.02–0.2 mm. The petioles are 44–53 cm long. The ratio between the lamina and petiole lengths is 0.8 for the most complete leaf (IPS-41682). Some petioles preserve circular to elliptic marks of 0.5–0.7 cm in their surface (Plate I, 3). These marks are interpreted as bases of spines.

Leaves studied herein show all macroscopic characters reported by Kvaček and Herman (2004) in the diagnosis of *Sabalites longirhachis* from the lower Campanian of the Grünbach Formation (Austria) (i.e. leaves costapalmate, induplicate, lanceolate; thick long costa; leave segments fused, nearly linear, slightly wider towards the apex, each of them V-shaped in transversal section and emerging at an acute angle from the costa). Kvaček and Herman (2004) introduced venation pattern and cuticle characters in the diagnosis of *S. longirhachis* leaves. However, cuticle characters were not preserved in the available Fumanya specimens, which led Marmi et al. (2008) to assign them to *Sabalites* cf. *longirhachis*. In the present study, the venation is reported for leaves from Fumanya showing a pattern similar to *S. longirhachis* from Austria (i.e. mid-vein and four parallel vein orders for each segment). According to Read and Hickey (1972), the genus *Sabalites* Saporta includes costapalmate palm leaves. *Sabalites* spp. from the Late Cretaceous and Paleogene of North America—*S. carolinensis* Berry, *S. tenuirachis* (Lesquereux) Read et Hickey, *S. ungeri* (Lesquereux) Dorf, *S. rugosa* (Knowlton) Read et Hickey, *S. powellii* (Newberry) Berry, *S. leei* (Knowlton) Read et Hickey, *S. inquerenda* (Knowlton) Read et Hickey, *S. grandifolia* (Newberry) Read et Hickey, and *S. grayanus* Lesquereux—showed clear differences in costa lengths and shapes and segment dissection compared to *S. longirhachis* (Read and Hickey, 1972; Kvaček and Herman, 2004 for a review). Thus, palm leaves from the lower

Fig. 1. Geographic and stratigraphic setting of Vallcebre syncline localities with *S. longirhachis* remains. (A) Geological map of the Pyrenees with location of the studied area. (B) Stratigraphic section of the Grey Garumnian in the Vallcebre syncline and detailed sections of Fumanya Sud and Mina Esquirol with plant remain locations.

Fig. 2. Fumanya Sud open cast mine showing the ca. 10,000 m^2 surface bearing *S. longirhachis* leaves and logs and titanosaur trackways, which corresponds to the base of the first coal seam. Palm logs are indicated as black lines and leaves as racket-like shapes showing their original orientations.

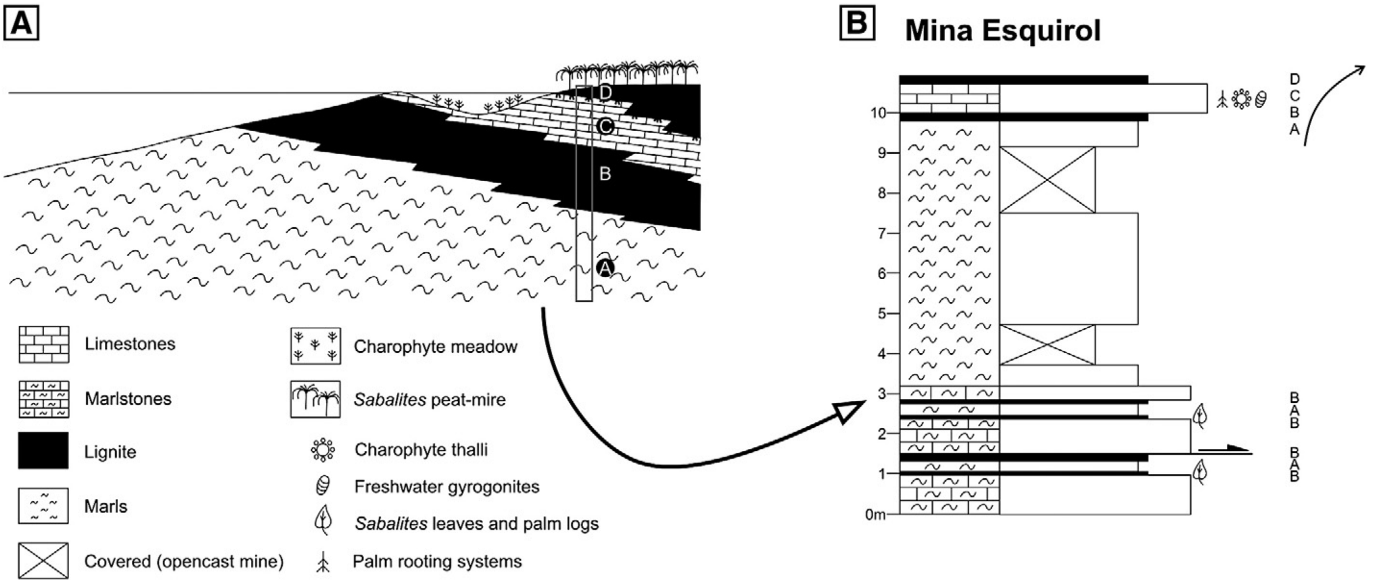

Fig. 3. Facies analysis and paleoenvironmental reconstruction of the Mina Esquirol locality showing that the different layers with palm remains belong to laterally equivalent facies. (A) Paleoenvironmental diagram showing vertical development of a sedimentary cycle. (B) Detailed stratigraphic section of Mina Esquirol, with indication of facies represented in (A).

Maastrichtian of Fumanya are identified as *S. longirhachis* based on gross morphology and venation features.

4.2. Stems

Logs are preserved as non-branched cylindrical impressions lacking internal anatomical details (Plate II). Dimensions of nine logs range 2.5–13.8 m long and 16–22 cm in maximum width. A few logs consist of casts showing structures on their surfaces (Plate II, 1, 3, 4). These external structures are ellipsoidal relieves of 1.0–1.8 cm long and 0.3–0.6 cm wide arranged in parallel, longitudinal rows compared to the log axis. Narrow, longitudinal grooves and circular to elliptic holes are also observable (Plate II, 3, 4). In some cases, these structures are covered by a 1–2 cm thick coaly lamina, sometimes also showing narrow longitudinal grooves.

Palm stems with internal anatomy preserved are included in the genus *Palmoxylon* Schenk and they are abundant in the fossil record (Harley, 2006). The diagnoses of this genus and its species are based on characteristics of fibrous and fibrovascular bundles, presence or absence of stegmata and presence of leaf traces (e.g. Trivedi and Verma, 1971; Nambudiri and Tidwell, 1998). Unfortunately, these structures are not preserved in logs from Fumanya Sud and Mina Esquirol. Nevertheless, even lacking the preservation palm synapomorphies, these logs show external features typical of living palms (i.e. they are straight, slender and of nearly uniform width, or tapered upwards). There is no evidence of spines or persistent bases of leaves suggesting that the original stems were smooth with only narrow grooves (Plate II, 3). The log surfaces showing ellipsoidal structures and holes are attributed to basal parts of the palm stems bearing adventitious roots (see Plate II, 4; Plate IV). This feature can be observed in some living palms (e.g. *Phoenix* spp.) in which adventitious roots may be visible at the base of the tree trunk above the soil surface (see Plate IV, 1 and Jones, 2007).

4.3. Stumps and roots

Rooting systems were only found in the Mina Esquirol outcrop (Plate III). The most complete specimen consists of an internal cast of a brush-like rooting system with a central circular mark of about 19 cm in diameter from which about sixteen rectilinear or slightly curved rays of 0.9–1.3 cm in diameter emerge, forming a conical structure (Plate III, 3, 4). The maximum diameter of the whole structure is almost 140 cm. A number of additional stumps are preserved in the same layer as adpressions. They measure between 20 and 21 cm in diameter and show remains of coaly adventitious roots radiating from a central depression (Plate III, 1, 2).

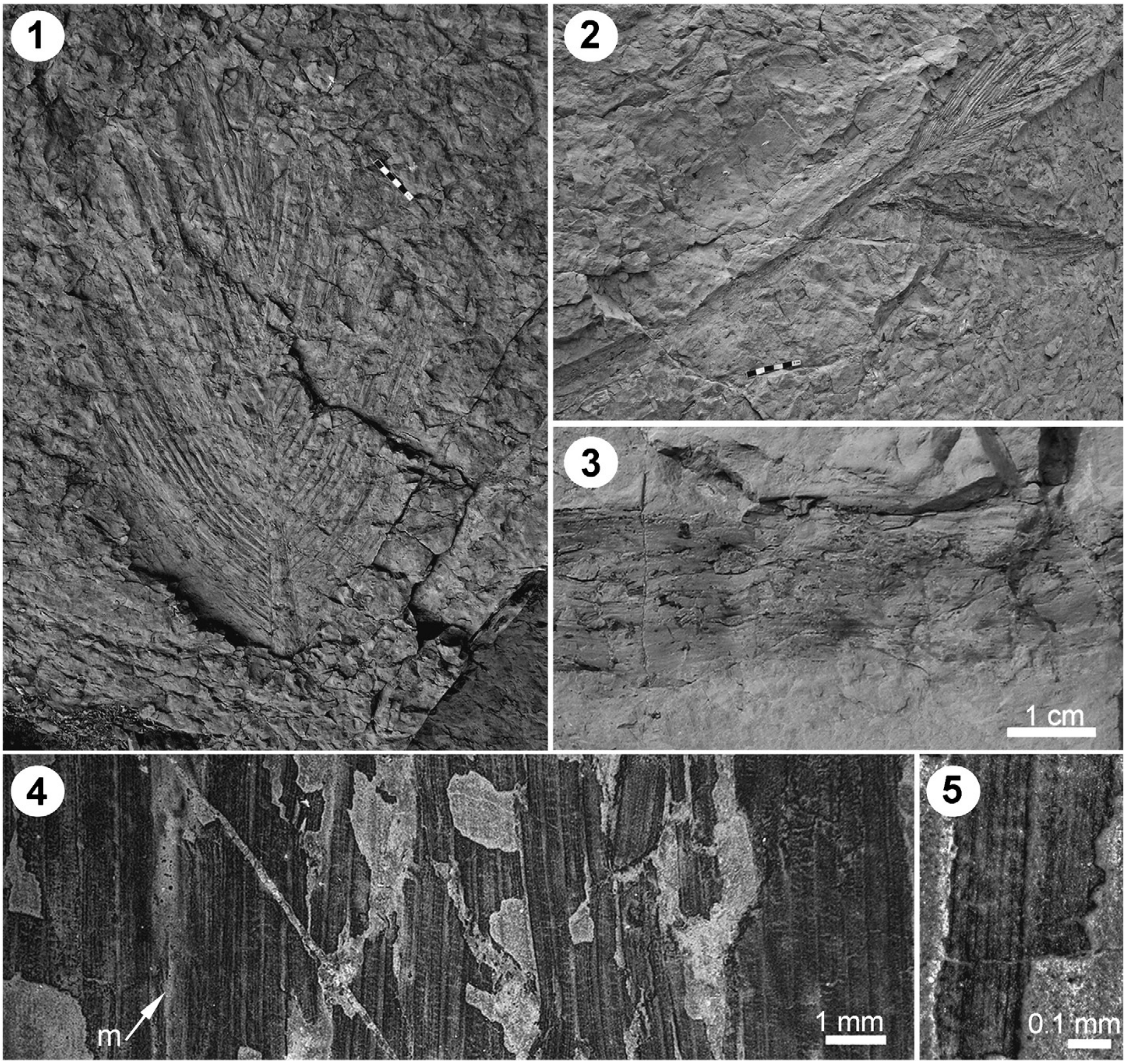

Plate I. *Sabalites longirhachis* leaves from the Fumanya opencast mines.

1. Complete lamina. Scale bar = 5 cm.
2. Complete leaf bearing a long petiole. Scale bar = 5 cm.
3. Detail of a petiole with circular marks that might be spine bases.
4. Detail of general pattern of venation (m = mid-vein).
5. Detail of thinnest veins.

These fossils are preserved as adpressions and internal casts without anatomical details. However, they can be interpreted as palm rooting systems based on their great similarity in shape and size to those of living palms (see Plate IV). The circular central mark may correspond to the palm stump and falls within the diameter range of logs reported from the Fumanya localities. Radiating structures are related to palm roots (see Plate III, 3, 4; Plate IV, 3). Adventitious roots at the bases of logs and preserved rooting systems range 0.3–1.3 cm wide, which fall within the ranges of root widths measured in living tree palms: *Phoenix canariensis* Chabaud (0.5–1 cm), *Phoenix dactylifera* Linnaeus (0.4–0.9 cm), and *Washingtonia* sp. (0.5–1.3 cm).

Other vascular plants identified in the Fumanya opencast mines are large amounts of conifer leafy axes attributed to *Frenelopsis* (Schenk) Watson, a fragment of pandan-like leaf (Pandanaceae) and a probable cycadalean leaf along with large number of angiosperm seeds (Villalba-Breva et al., submitted for publication). Rooting systems of these plants are different to palms in many features. Conifers and most angiosperms usually have axonomorph rooting systems. Cycadalean roots consist of a taproot with small, branched lateral roots arranged in two rows and reaching great depths (Singh, 2006). Pandanaceous trees like living *Pandanus* Parkinson produce many thick stilt roots near the trunk base to provide support (Dahlgren et al., 1985).

Table 1
Measures, in centimetres, of costapalmate leaves from the Maastrichtian of Fumanya.

	IPS-41681	IPS-41682	V-FUM27	VFUM40	VFUM86	VFUM137
Total length	125.5[a]	96.0	?	?	77.2[a]	99.8
Laminar size[b]	2126.5	281.2	?	?	400.1	486.5
Lamina length	75.0	43.0	?	?	26.7	51.5
Lamina width	41.0	10.0	?	?	20.3	11.6
Base angle[c]	84.4	50.9	?	?	?	?
Costa length	30.0	15.0	14.6	8.4	11.8	29.6
Costa width	3.6	2.0	2.2	2.3	?	1.8
Number segments	56	47	?	?	?	?
Segment length[d]	39.2	18.7	?	?	20.1	34.8
Segment width range	0.53–1.56	0.21–0.63	0.16–0.96	0.15–0.66	0.30–0.77	0.17–0.80
Cos-seg angle range	30.5–53.4	14.7–33.4	22.9-34.6	37.3-47.0	24.4-43.4	11.3-24.1
Petiole length	?	53.0	?	44.0	?	48.2

? Missing data.

[a] Inferred values.

[b] Measures in square centimeters (cm^2).

[c] Base angle is the angle from the vertex to the points where a line perpendicular to the costa (at 0.25 laminar length from the base) intersects the margin. The vertex of the angle lies in the centre of the base of costa at the point where the basal most laminar tissue touches the petiole.

[d] Mean value.

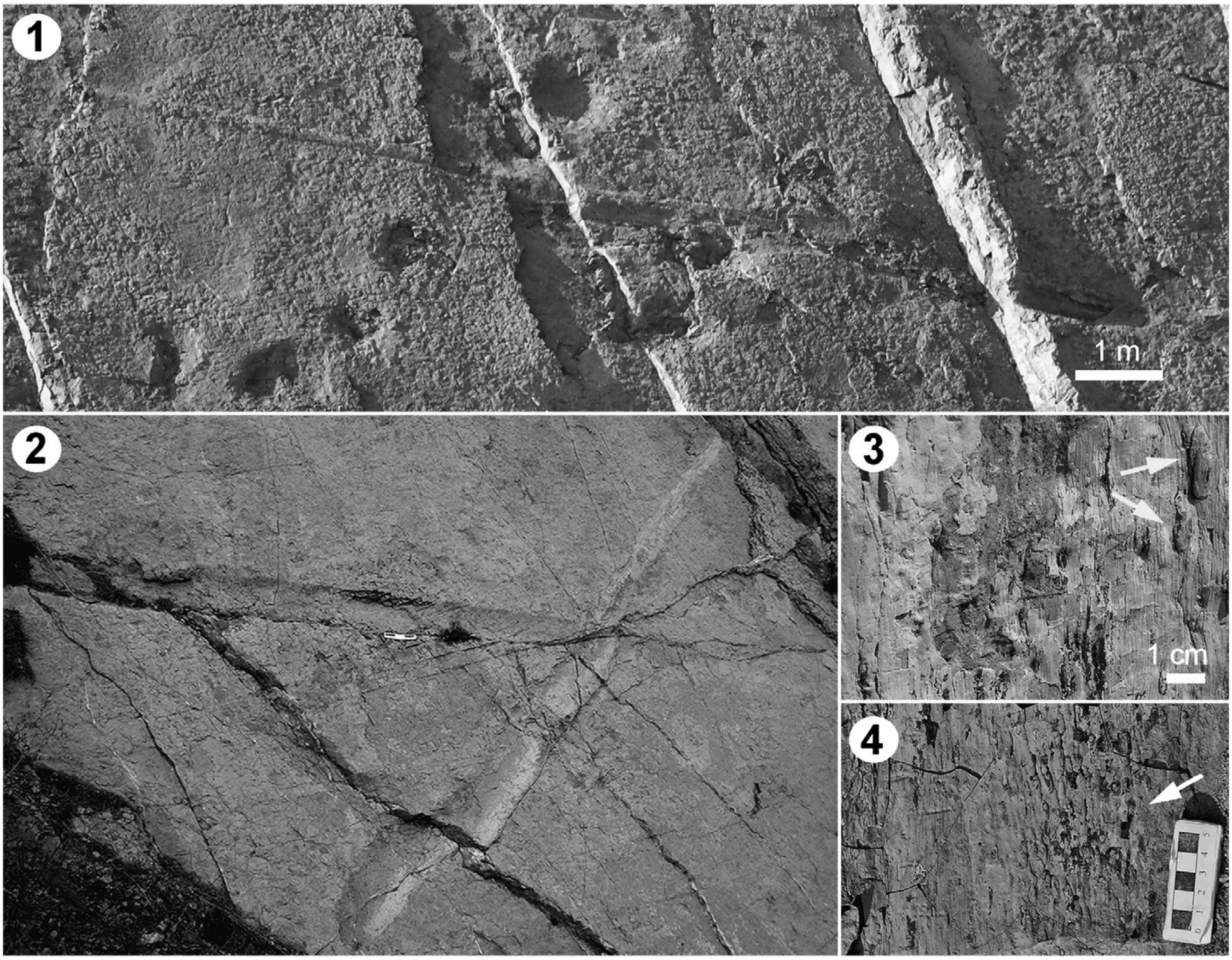

Plate II. Logs attributed to *Sabalites longirhachis* palms from the Fumanya opencast mines.

1. Large sized log of c. 14 m.
2. Two crossed impressions of logs. Scale bar = 15 cm.
3. Detail of the surface of the basal part of (1) showing narrow longitudinal grooves and some adventitious roots (arrows).
4. Detail of the surface of a log cast showing marks of adventitious roots (arrows). Scale bar = 5 cm.

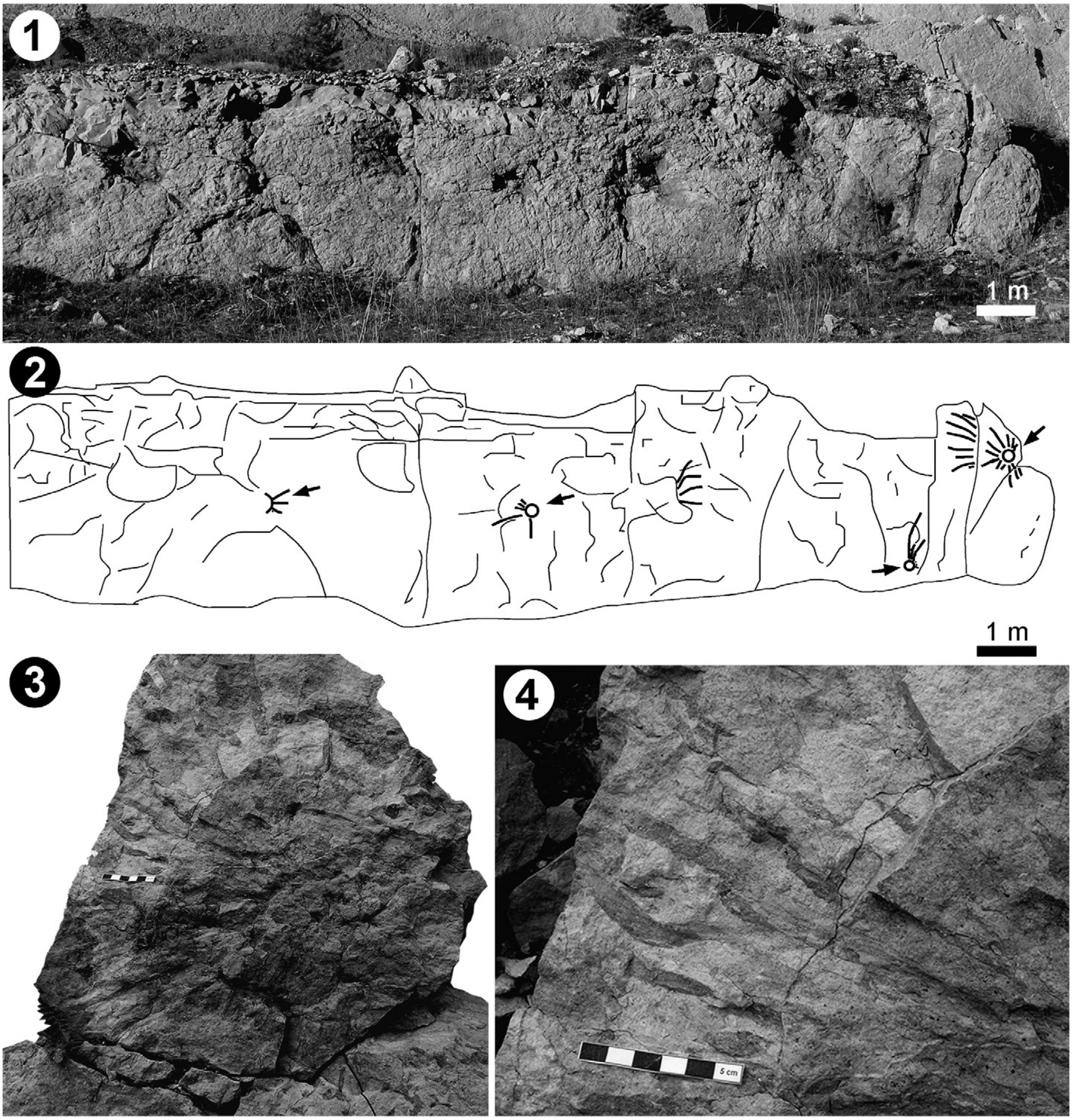

Plate III. Stumps attributed to *Sabalites longirhachis* palms from the Mina Esquirol locality.

1. Charophyte limestone surface with several palm stumps.
2. Scheme of the rock surface with stumps indicated by arrows.
3. Stem base with adventitious rooting system. Scale bar = 5 cm.
4. Detail of adventitious roots. Scale bar = 5 cm.

5. Sedimentology and taphonomy

From the sedimentological point of view the succession with palm remains at Fumanya is composed of alternating organic marlstones, coal and charophyte limestones. Facies analysis suggests that these lithologies are organized in small sedimentary cycles (Villalba-Breva et al., submitted for publication), representing a gradual shift from brackish to freshwater depositional environments. Thus, a basal brackish term formed by the marls is succeeded by coals resulting from the parautochthonous accumulation of plant remains, which is finally overtopped by a freshwater term with charophyte limestones and autochthonous coals with rootlet casts representing limnic peat mires around a lake.

Casts and adpressions of palm leaves and associated logs are randomly distributed and oriented on the bedding surface of the first coal seam (Figs. 2 and 3). Most leaves include entire laminas bearing

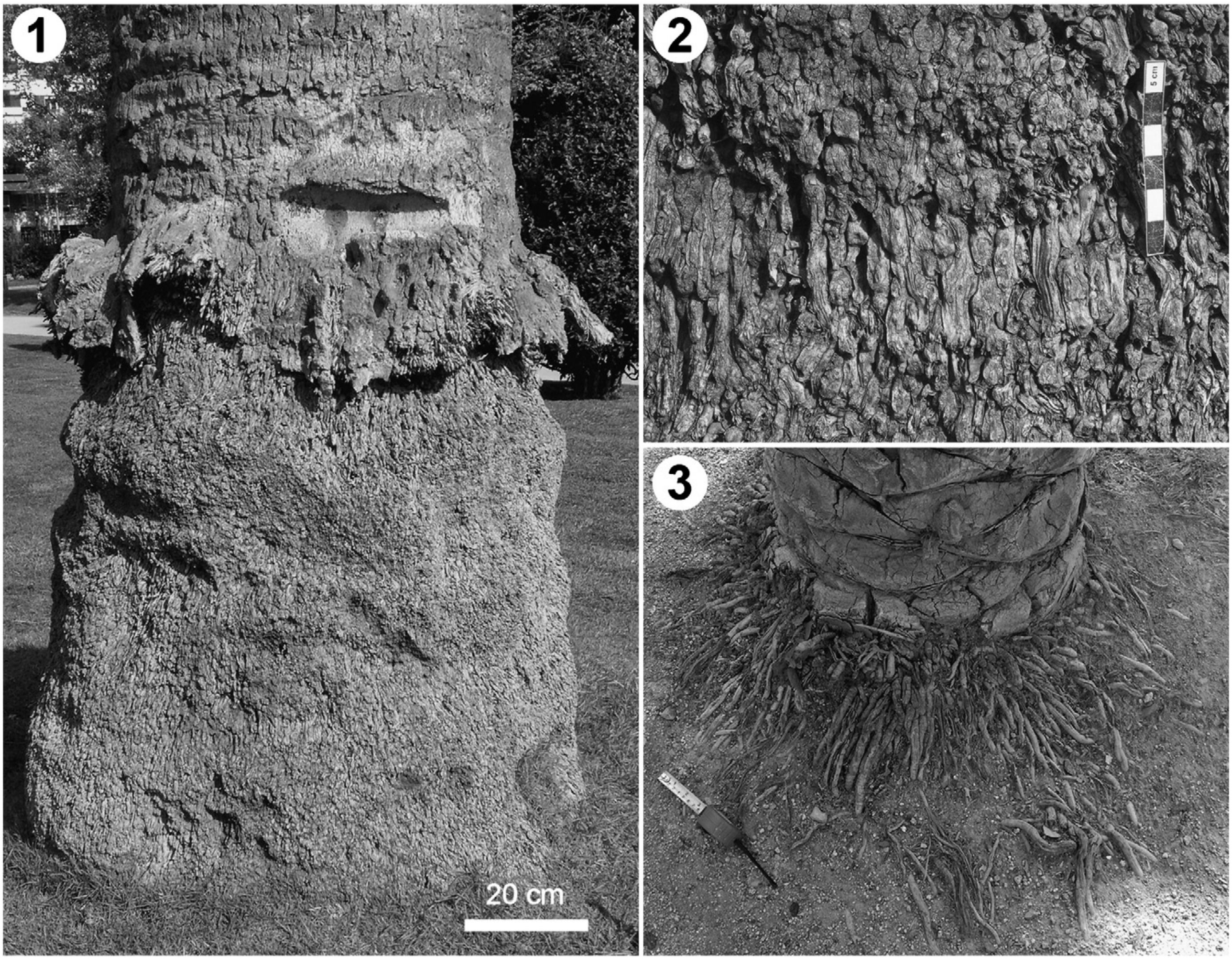

Plate IV. Tree bases of living palms.

1. Base of the stem of living *Phoenix canariensis* bearing adventitious roots.
2. Detail of adventitious roots of *Phoenix canariensis*. Scale bar = 5 cm.
3. Stump and roots of a living *Phoenix* sp. Scale bar = 10 cm.

almost complete petioles, which suggest a traumatic production and short transport before deposition at the bottom of the water table (Martín-Closas and Gomez, 2004). Also, laminas show fans opened out or folded down, suggesting that leaves were torn from the parental plants at different ontogenetic stages, i.e. when still green or being already marcescent respectively. All these data, along with the lack of rootlet marks at the base of the coal suggest that leaves accumulated as parautochthonous remains.

Logs are relatively long and do not show evidence of rounding at the ends. Some superficial characters, such as the marks of adventitious roots, have been preserved in the adpressions available, indicating short transport and absence of decay before deposition in the mudflat-edge bottom. However, the absence of rooting marks at the base of the first coal seam in Fumanya indicates that logs, like the leaves, were also parautochthonous.

Evidence of in situ palm growth comes from the top of an overlying charophyte limestone layer. The detailed stratigraphic succession shows the lignite layer with palm leaves and logs at its base, covered by up to 8 m of brackish marls and 1 m of the freshwater charophyte limestones with the palm rooting systems at the top (Fig. 3). These rooting systems depart from a thin coal layer covering the charophyte limestones. Facies analysis suggests that this coal represents small peat mire formed at the lakeshores of the charophyte lake. Also, according to sedimentological evidence, the palm rooting systems found at the top of the charophyte limestones and the coal layer bearing the palm leaves and logs in its base, may represent two laterally equivalent facies of the same sedimentary environment as shown diagrammatically in Fig. 3A.

The whole dataset obtained from Fumanya indicates that *S. longirhachis* palms were growing autochthonous in small peat mires at the lakeshores of freshwater alkaline lakes, where lime mud was accumulated by important meadows of charophytes. The aerial remains of these palms, including complete leaves and logs, were episodically torn out or uprooted by storms or strong winds and transported by flotation across the freshwater wetland, seawards. Finally they were deposited and preserved at the bottom of the mudflat edge, where a thick layer of parautochthonous peat was being accumulated in an anoxic bottom, thus preventing the decay. The detached palm organs may also have deposited into the freshwater lake but the oxic conditions and the active growth of charophyte meadows hindered their preservation there.

Although the three available organs attributed to palms (i.e. leaves, logs and rooting systems) found at Fumanya, were detached from each other, both morphological and taphonomic evidence suggest that they belong to the same plant species. From a morphological point of view, the three organs are in the same order of size and both logs and rooting systems are compatible in showing adventitious rootlets. Taphonomic evidence suggests that the three organs were deposited in laterally equivalent facies and came from a single site of growth. These conclusions lead us to propose a reconstruction of the habit of the plant on the basis of the remains described. We propose to use the term '*Sabalites longirhachis*-bearing plant' for the plant reconstructed here.

6. Discussion

6.1. Reconstruction of Sabalites longirhachis-bearing palm and systematic implications

According to the taphonomic hypothesis presented above, we suggest that *Sabalites longirhachis* were slender palm trees of up to ca. 14 m tall. Measurements of logs and leaves suggest that the *S. longirhachis*-bearing plant probably displayed heights similar to the living cabbage palm *Sabal palmetto* (Walter) Loddiges. Stems of the *S. longirhachis*-bearing plant were straight, a few decimetres thick, and tapered upwards (Plate V). Their surfaces were probably smooth, without marks of persistent bases of leaves. Adventitious roots covered the basal part of the tree trunk. The stumps were up to ca. 22 cm wide and straight roots emerged radially from their surfaces making a cone of up to ca. 150 cm in diameter. Leaves up to ca. 130 cm long, costapalmate and with long and probably armed petioles were borne at the top of the tree trunk in a crown, like in most living palms (Plate V). The presence of folded leaves, considered here as marcescent, suggests that the parental palm retained the leaves in the crown bottom, partially covering the upper part of the tree trunk. Tuzson (1914, pl. XVIII) reported a reconstruction of the fossil palm *Juranyia hemiflabellata* Tuzson from the Maastrichtian of Rusca Montana (Romania). Recently, Kvaček and Herman (2004) considered this species a synonym of *S. longirhachis*. However, in the Tuzson's paper only a fragment of a large costapalmate leave, a probable palm fruit and a partial inflorescence were represented (Tuzson, 1914, pl. XVII).

Field recognitions of living palm taxa are based on leaf morphology and inflorescence, flower and fruit features (Sitte et al., 2003; Dransfield et al., 2008). Fossil leaves are the most abundant organ of *Sabalites longirhachis* available. However, palm leaves show a high degree of homoplasy in gross morphology and anatomy, especially among major clades (Horn et al., 2009). This and the absence of reproductive characters in *S. longirhachis* fossil remains collected make difficult to infer any phylogenetic relationships with living palm subfamilies. Kvaček and Herman (2004) suggested that *S. longirhachis* represents the basal form from which both pinnate and palmate leaves evolved. The earliest costapalmate leaves are reported from the late Coniacian–Santonian of South Carolina and New Jersey (North America), while the earliest pinnate leaves are reported from the lower Campanian of northern Montana (North America) (see review by Harley, 2006 and references therein). In contrast, molecular phylogenies suggest the subfamilies Calamoideae and Nypoideae with pinnate or bipinnate leaves as basal groups within the Arecaceae, while palmate palms (many of them belonging to Coryphoideae) may be derived (Asmussen et al., 2006). Hence, Cretaceous palms bearing costapalmate leaves, such as *S. longirhachis*, may represent an extinct, intermediate lineage between palms with pinnate and palmate leaves.

6.2. Paleoecology of the Sabalites longirhachis-bearing plant

Combined taphonomic and sedimentological analyses suggest that *Sabalites longirhachis* palms from Fumanya were growing in the lakeshores of freshwater charophyte lakes, where small peat mires occurred. The outcropping structural surface of charophyte limestones with palm rooting systems is of 61.7 m^2. This area contains at least four well-preserved rooting systems, with a couple of other possible stump marks being present but difficult to document with precision. This gives a minimum density of one palm individual per

Plate V. Hypothetic reconstruction of *Sabalites longirhachis* palm trees based on taphonomic data from Fumanya.

15.4 m^2 and up to one plant each 10 m^2 as a maximum density. Accordingly, *S. longirhachis* palms might grow at very high densities, similar to densities of living palms in swampy areas, such as the *Nypa* Steck mangroves, where monotypic stands of palms completely cover the ground surface. However, the palm stands described were not similar to extant *Nypa* swamps since they were growing in a freshwater habitat; also they did not form monotypic stands. Villalba-Breva et al. (submitted for publication) and Riera et al. (2010) reported abundant parautochthonous remains of *Frenelopsis* sp. associated with the *S. longirhachis* organ remains described in detail herein. The inferred *Frenelopsis* peat mire vegetation was surely much more dense and significant in term of biomass than the palm stands. Isolated leaf fragments probably belonging to a cycadalean and a pandan-like plant and monotonous assemblages of unidentified angiosperm seeds were found in the same horizon bearing *Sabalites* and *Frenelopsis* remains. However, these plant remains probably were transported from large distances and their source plants grew far away from the habitat of *S. longirhachis* (Villalba-Breva et al., submitted for publication).

Fossil data indicate that palms first occurred in swamps, apparently starting a progressive replacement of conifers that inhabited these environments (Coiffard and Gomez, 2010). Lower energy cost for stem development might allow for a faster growth or better seed production in palms than conifers. Moreover, large palm leaves may shade out woody seedlings preventing their regeneration, as it has been observed in living palms (Denslow et al., 1991). The results documented here indicate that *S. longirhachis* might inhabit wetlands close to the cheirolepidiaceous conifer *Frenelopsis* during the Maastrichtian. Accordingly, the turnover of conifers by palms in swampy environments was still in course at the earliest Maastrichtian at least in the Iberian Peninsula. *Sabalites longirhachis* palms probably occupied during the Late Cretaceous a larger range of habitats. Hence, data from the Campanian Grünbach flora (Austria) suggest that *S. longirhachis* also dominated juglandaceous and palm wetland forests and probably lived in swamp/semiaquatic communities of *Pandanites trinervis* (Ettingshausen) J. Kvaček and Herman (Pandanaceae) in a large deltaic lowland (Herman and Kvaček, 2007, 2010). However, *S. longirhachis* is a morphotaxon and might be represented by more than one natural species. Thus, ecological inferences at a regional level should be taken with caution.

7. Conclusions

Although leaves, stems, inflorescences, flowers, fruits, seeds and pollen grains of palms are unequivocally present since the Late Cretaceous (Harley, 2006), a few examples of association of palm organs in the same assemblage were reported in the literature. Palm fruits and fronds from the upper lower Eocene of Tasmania were attributed to *Nypa* based on the presence of these organs and pollen grains intermixed in the same horizon (Pole and Macphail, 1996). *Nypa* fruits with remains of spathes were documented in the Eocene of the Ebro Basin (northeastern Iberian Peninsula) by Biosca and Via (1987) and the isolated fruits were recorded also from the Eocene London Clay (Collinson, 1983). Other noteworthy examples are five stems attached with petiole bases and roots and associated with isolated petioles and laminas from the middle Eocene Princeton chert (British Columbia, Canada) (Erwin and Stockey, 1991), and leaves connected to petioles and stems from the Miocene of the Lower Rhenish Plain (Germany) (Van der Burgh, 1984). The association of organs described herein is older than these examples. Moreover, it provides for the first time taphonomic evidence to reconstruct a palm tree habit in the earliest stage of the evolution of the family Arecaceae.

Data from Fumanya localities also provide evidence for physiological, anatomical and ecological adaptations of fossil palms in the earliest evolutionary history of this family. There is indirect evidence for keeping marcescent leaves at the top of stems, as suggests laminas with fans folded down. Whole leaf persisting attached on the stem after death is a typical pattern of some living species such as *Washingtonia filifera* (Lindley) Wendland. Also, fossil palms such as *Sabalites longirhachis* had already presented adventitious roots. These types of roots have high capacity to absorb water and minerals and allow adaptation to unstable substrates in habitats frequently subject to flooding such as wetlands (Kozlowski, 1984). More than two-thirds of living palms inhabit rainforests, many different species coexisting together in small areas. In open habitats, they form extensive colonies usually of a single species (Jones, 2007). Some species inhabiting open habitats prefer wetlands such as marshes, swamps, permanent stream margins, lakes and lagoons, growing in dense colonies or thickets (Jones, 2007). During the Maastrichtian palms were well represented in the tropical everwet and tropical seasonal biomes (Horrell, 1991; Willis and McElwain, 2002). This suggests that early palms already

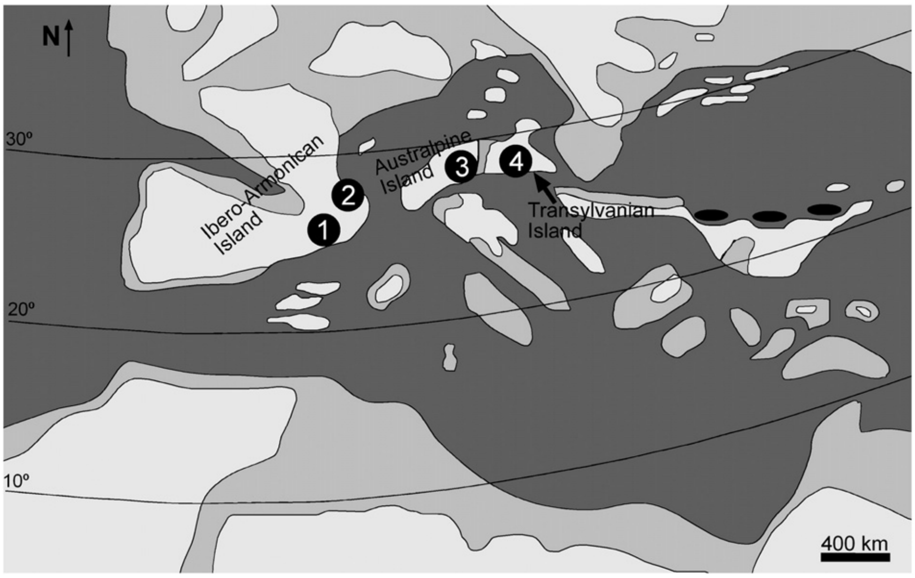

Fig. 4. Paleogeographic map of the Western Tethys during the latest Cretaceous based on Dercourt et al. (2000) and Benton et al. (2010). Numbers indicate the localities known with *S. longirhachis* leaf remains: 1, Southern Pyrenees (Maastrichtian); 2, Fuveau (upper Santonian-Campanian) and Barjols (Campanian–Maastrichtian) (both in the Ibero-Armonican island); 3, Grünbach (lower Campanian) (in the Australpine island); 4, Rusca Montana (Maastrichtian) (in the Transylvanian island). Light colour indicates emerged lands, light grey is shallow marine, dark grey is oceanic basins and black means volcanics.

inhabited rainforests as well as open habitats. *Sabalites* palms from Fumanya fit well with the open habitat ecological pattern of living palms.

Sabalites longirhachis was probably widespread through low to moderate diversity plant communities of wetlands from the Late Cretaceous of southwestern, central and eastern Europe (Fig. 4). Emerged lands corresponding to the present-day northeastern Spain and southern France margins were far and isolated by the Tethys Sea from those corresponding to Austria and Romania (Tyson and Funnell, 1987; Dercourt et al., 2000). The fruit type of *S. longirhachis* is unknown, as is its dispersal mechanism. Nowadays, palm fruits are usually fleshy and dispersed by flotation in sea water or, more frequently, by a wide variety of birds and mammals.

Sabalites species from the Late Cretaceous and Paleogene of North America clearly differ in gross morphology from *S. longirhachis*. Leaves of these species have partially dissected segments and/or shorter costas than *S. longirhachis* (reviewed in Kvaček and Herman, 2004). This suggests that the geographical range of *S. longirhachis* was restricted to the south European Cretaceous archipelago and that it became extinct at or just before the K/T boundary.

Acknowledgements

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Article 2

MARMI, J., GOMEZ, B., **VILLALBA-BREVA, S.**, MARTÍN-CLOSAS, C. 2012. *Bergacarpon viladricii* gen. et sp. nov., angiosperm seeds and associated fruits from the early Maastrichtian of the eastern Pyrenees (Catalonia, Spain). *Review of Palaeobotany and Palynology*, 171: 83-94.

RESUM: Es documenta una nova localitat amb llavors i fruits d'angiosperma al Maastrichtià del sud-est del Pirineu. Les llavors de *Bergacarpon viladricii* gen. nov. et sp. nov. poden haver estat produïdes per una monocotiledònia (probablement un commelínid) en base a la presència d'un micròpil amb opercle i un desenvolupament ortòtrop (àtrop). El fruit associat és tipus fol·licle i sembla contenir una sola llavor. Les llavors formen acumulacions massives dins una capa que correspon a un ambient deposicional de maresma fangosa. La mida, forma, i selecció d'òrgans així com l'absència d'altres macrorestes de plantes associades suggereixen que la capa amb llavors es va originar a partir d'una comunitat de plantes pauciespecífica i va ser transportada per flotació. Aquesta és una de les acumulacions monotípiques de llavors d'angiosperma més antigues del registre fòssil.

Review of Palaeobotany and Palynology 171 (2012) 83–94

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Research paper

Bergacarpon viladricii gen. et sp. nov., angiosperm seeds and associated fruits from the early Maastrichtian of the eastern Pyrenees (Catalonia, Spain)

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Pyrenees

ABSTRACT

A new locality yielding angiosperm seeds and fruits is reported from the Maastrichtian of south-eastern Pyrenees. The seeds *Bergacarpon viladricii* gen. et sp. nov may have been produced by a monocot (probably a commelinid) based on the presence of a micropylar lid and orthotropous (atropous) development. The associated fruit is follicle-like and likely contained a single seed. The seeds form a massive accumulation in one bed in a brackish mudflat depositional setting. Size, shape and organ selection as well as the absence of other associated megafossil plant remains suggest that the seed bed originated from a paucispecific source plant community and by transport through floatation. This is one of the oldest monotypical angiosperm (probably monocot) seed accumulations found so far in the fossil record.

1. Introduction

During the three last decades, various angiosperm reproductive structures collected from the Cretaceous worldwide have considerably improved the understanding of the reproductive biology and rise to dominance of early angiosperms. The earliest mesofloras containing angiosperm reproductive structures are known from the Barremian or Aptian of Portugal and North America (Friis et al., 1999; Friis et al., 2006a). They include small inflorescences and flowers, isolated or fragmented androecia and gynoecia, and fruits and seeds. In contrast, only a few studies are available based on the diversity of angiosperm seeds from the Upper Cretaceous of Europe (Friis et al., 2010 and references therein). Among these few examples, Knobloch and Mai (1991) described 270 species of fruits and seeds, most of which were assignable to 24 extant families, from the Cenomanian–Maastrichtian of central and western Europe. Batten and Zavattieri (1995) reviewed the genera *Costatheca* Hall and *Spermatites* Miner from the Cretaceous–Palaeocene boundary of several localities in Europe, North Africa and North America. More recently, angiosperm seeds were reported from the Late Cretaceous of Portugal (Friis et al., 2010) and Romania (Lindfors et al., 2010). According to Friis et al. (2010), mesofossil floras from the Late Cretaceous of the Iberian Peninsula clearly differ in taxonomic composition from those of North America and central and northern Europe. This view is consistent with the differences in palynological assemblages between the Iberian plate and other European regions, and probably reflects biogeographical, palaeoecological or palaeoclimatological constraints (Friis et al., 2010; Kedves and Diniz, 1983).

The present study provides further information on the seed floras from the latest Cretaceous of the northern Iberian plate, which was close to the Eurasian mainland during the earliest Maastrichtian, though they were still separated by only a narrow seaway. The seed assemblage studied is also significant since it sheds light on the origin of almost exclusively angiosperm – probably monocot – seed assemblages in an early evolutionary stage of this important group of plants.

2. Geological and palaeobotanical setting

Mesofossil plant remains have been collected from the sections representing the base of the Tremp Formation exposed at the Mina Esquirol site, Vallcebre syncline, eastern Pyrenees (Fig. 1). The Tremp Formation, informally called the "Garumnian facies", consists of transitional to fully continental sediments deposited in the south Pyrenean basin after a Maastrichtian marine regression (Mey et al., 1968). Based on the sedimentology, depositional settings of the basal Tremp Formation (the "Grey Garumnian" of Rosell et al., 2001) were interpreted as coastal wetlands with variable salinities ranging from brackish to freshwater (Oms et al., 2007; Villalba-Breva and Martín-Closas, 2011). At the base of the series, an up to 10-m-thick succession of marlstones with brackish molluscs is attributed to a transitional mudflat close to the sea and with tidal

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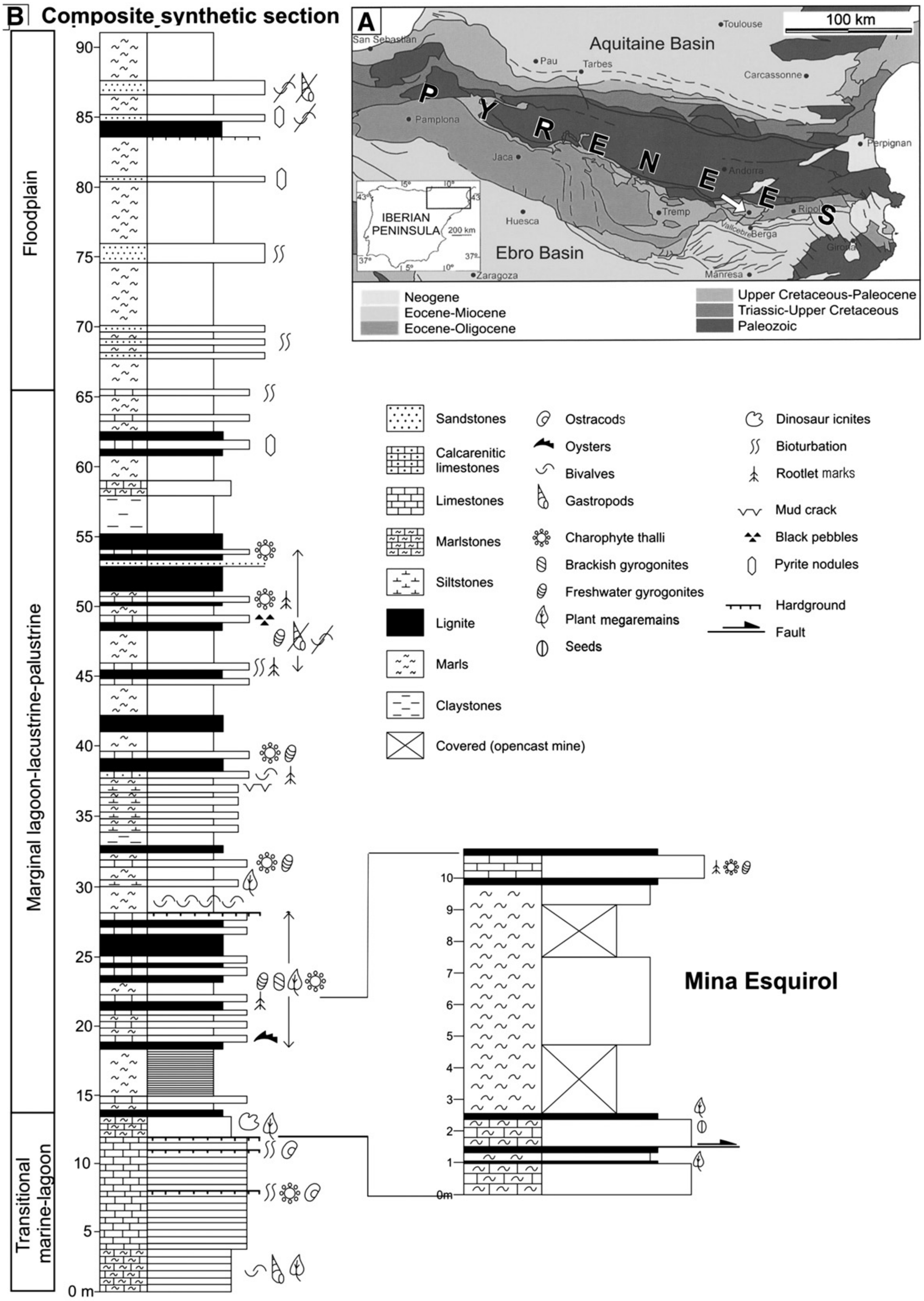


Fig. 1. Geographic and stratigraphic setting of the Vallcebre syncline in which Mina Esquirol site is located. (A) Geological map of Pyrenees with location of the Vallcebre syncline. (B) Stratigraphic section of the Grey Garumnian in the Vallcebre syncline and detailed section of Mina Esquirol with horizon bearing fossil seeds.

influence (Riera et al., 2010). Overlaying levels show a cyclic repetition of organic marl, coal and charophyte limestones corresponding respectively to marginal lagoon, parautochthonous peat accumulation and lacustrine facies (Villalba-Breva and Martín-Closas, 2011).

The mesofossil seeds and fruits studied here are concentrated in an up to 1.5-cm-thick marlstone bed located 15 cm below the first coal seam of the Fumanya mine district (Figs. 1 and 2). Based on magnetostratigraphic data, these rocks belong to the magnetochron C32n.1n and are earliest Maastrichtian in age (Oms et al., 2007).

Fig. 2. Detail of the rock surface showing the accumulation of fossil seeds.

This dating is consistent with previous biostratigraphic studies based on charophytes by Feist and Colombo (1983).

Palaeobotanically, the base of the Tremp Formation in the Vallcebre syncline shows abundant megafossil plant remains. These include well-preserved palm leaves of *Sabalites longirhachis* (Unger) J. Kvaček et Herman and associated logs and rooting structures attributed to the same plant (Marmi et al., 2008, 2010). Leafy axes of *Frenelopsis* sp. can form a dense leaf litter at the base of the first coal (Riera et al., 2010). The palynological assemblages at the base of the Tremp Formation 'Grey Garumnian' in Vallcebre have remained largely unstudied up to now. However, Médus et al. (1988) provided a study of the palynoflora of the upper part of the Tremp Formation, in layers close to the K–T boundary, which are of limited interest in our study. The limestones intercalated with lignite seams of the section studied are rich in charophytes, largely dominated by the gyrogonites *Peckichara cancellata*, *Microchara* cf. *cristata* and the thalli *Clavatoraxis microcharophorus* and *Charaxis* sp. (Villalba-Breva and Martín-Closas, 2011).

3. Material and methods

The rocks containing the mesofossil plant remains were macerated with HCl (30%) and H_2O_2 (130 volume) to dissolve the rock matrix. The seeds and fruits were dried and sorted out using a stereomicroscope. Selected specimens were photographed under Leica EZ4D and Leica DM2500P stereomicroscopes with integrated digital cameras. Selected seeds were examined with a Hitachi S1300 SEM microscope at the Serveis Científico-Tècnics of the Universitat de Barcelona. Other specimens were treated with Schulze's solution, which resulted in the dissolution of the coaly outer integument, and exposed the inner integument which has a cuticular nature. Specimens and preparations are housed in the collections of the Institut Català de Paleontologia Miquel Crusafont under the numbers IPS-56903 to IPS-56908. Measurements were made on the pictures using the freeware ImageJ v. 1.40 g (Rasband, 1997–2008). A Principal Component Analysis (PCA) was carried out with the freeware PAST v. 1.77 (Hammer et al., 2001) using log-transformed measurements of surfaces, lengths, widths and length/width ratios of 249 individual seeds.

4. Results

4.1. Systematic palaeontology

Division Magnoliophyta
Class Monocotyledoneae
Subclass Commelinids
Order unknown
Family unknown
Genus *Bergacarpon* gen. nov.

Generic diagnosis: Minute seeds, oval to round in outline and orthotropous (atropous). Seed coat consisting of two integuments. Thick outer integument with isodiametric cell marks on its surface. Thin inner integument with dome-like operculum in the micropylar end. Hilum circular.

Etymology: From Berga, the main town to which the Fumanya coal mines district belongs, and *carpon* (Greek) meaning seed.

Type species: *Bergacarpon viladricii* sp. nov.

Bergacarpon viladricii sp. nov.
Plates I–III

Specific diagnosis: Dome-shaped papillae covering the surface of inner integument. Hilum surrounded by a ring with 18 to 21 longitudinal and radiating crests.

Etymology: In honour of Lluís Viladrich i Pons, fossil collector and discoverer of the Fumanya fossil localities where seed and fruit fossils were collected.

Holotype: Slide IPS-56903.

Paratypes: Slides IPS-56903-56907.

Type locality: Mina Esquirol opencast mine from Vallcebre Village (N 42° 11′ 8″ E 01° 47′ 51″), Barcelona Province, Catalonia, Spain.

Stratigraphic position: Marlstone below the first coal seam of the Mina Esquirol coal mine.

Age: Earliest Maastrichtian (ca. 71 Ma) as determined by charophyte biostratigraphy and magnetostratigraphy.

Description: Most seeds are small, oval to round in outline, and many of them are laterally compressed. Some are flattened or folded in other planes (Plate I, 1–11). The apical (micropylar) end is obtusely rounded or truncate in outline. The basal (hilar) end is squared to round in outline. Flattened surface area of one side of seed ranges

Plate I. *Bergacarpon viladricii* gen. et sp. nov., holotype and paratypes from the early Maastrichtian of the Mina Esquirol photographed with the stereomicroscope (slides IPS-56903-56905).

1. Holotype of *Bergacarpon viladricii* gen. et sp. nov. photographed on both sides showing the coaly outer integument (h = hilum).
2–10. Paratypes of *Bergacarpon viladricii* gen. et sp. nov. showing variability in form and size (h = hilum).
11. Paratype of *Bergacarpon viladricii* gen. et sp. nov. with the outer integument removed (m = micropylar lid).
12. Paratype of *Bergacarpon viladricii* gen. et sp. nov. in longitudinal section showing the thick coaly outer integument and the brown to yellow thin inner integument.

from 0.9 to 3.3 mm^2, with a length from 1.1 to 3.0 mm and the width from 0.8 to 1.7 mm. The length/width ratio varies from 0.8 to 2.9. The PCA indicates that the variation in size is continuous with no clear boundaries between different forms (Fig. 3). The seed coat consists of two envelopes corresponding to the integuments (Plate I, 12; Plate III, 1). The outer envelope is dark and carbonaceous, and measures from 63.7 to 95.3 μm in thickness (Plate I, 12; Plate III, 1). Details of internal anatomy are not preserved in transverse section. The surface is smooth to rough, with faint isodiametric cell outlines from 28.4 to 36.1 μm long and wide (Plate III, 2). The inner integument

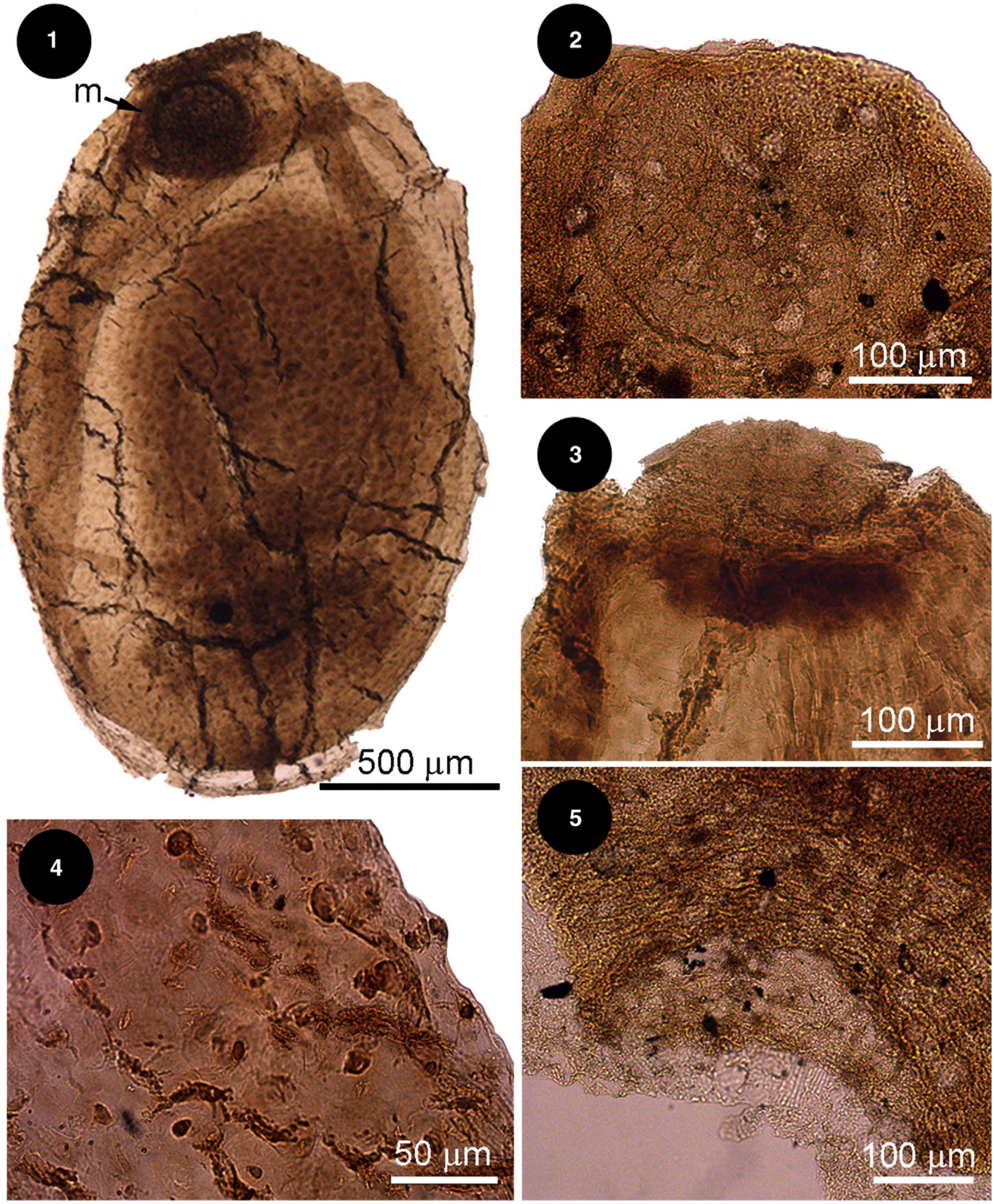
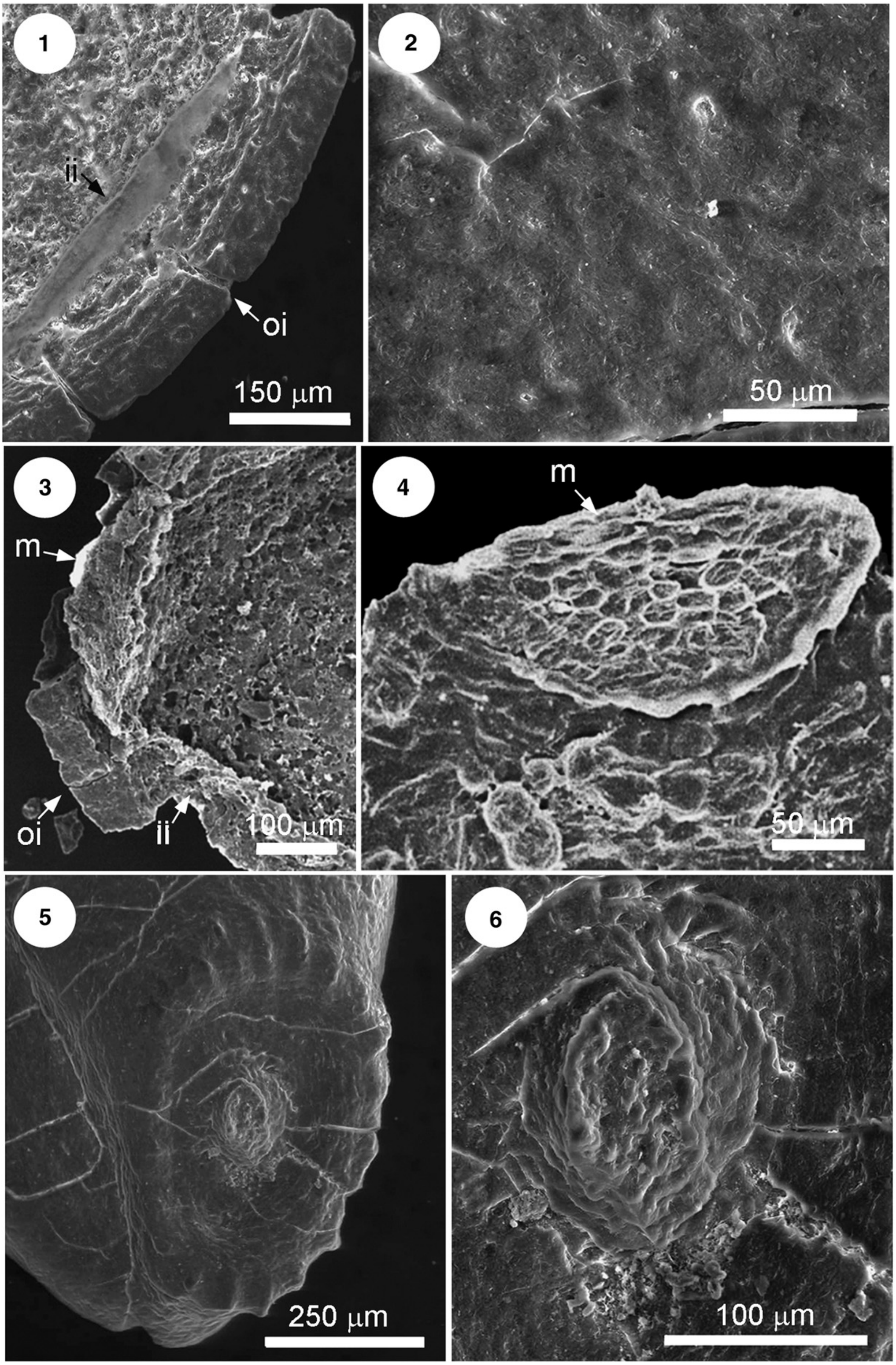


Plate II. Inner integument of *Bergacarpon viladricii* gen. et sp. nov. seeds examined under the light microscope (slides IPS-56906-56907).

1. Entire cuticle-like inner integument (m = micropylar lid).
2. Apical circular micropylar lid with isodiametric square cells.
3. Lateral view of the dome-shaped micropylar lid.
4. Detail of dome-shaped papillae on the surface of the inner integument.
5. Detail of the basal end of the inner integument.


1
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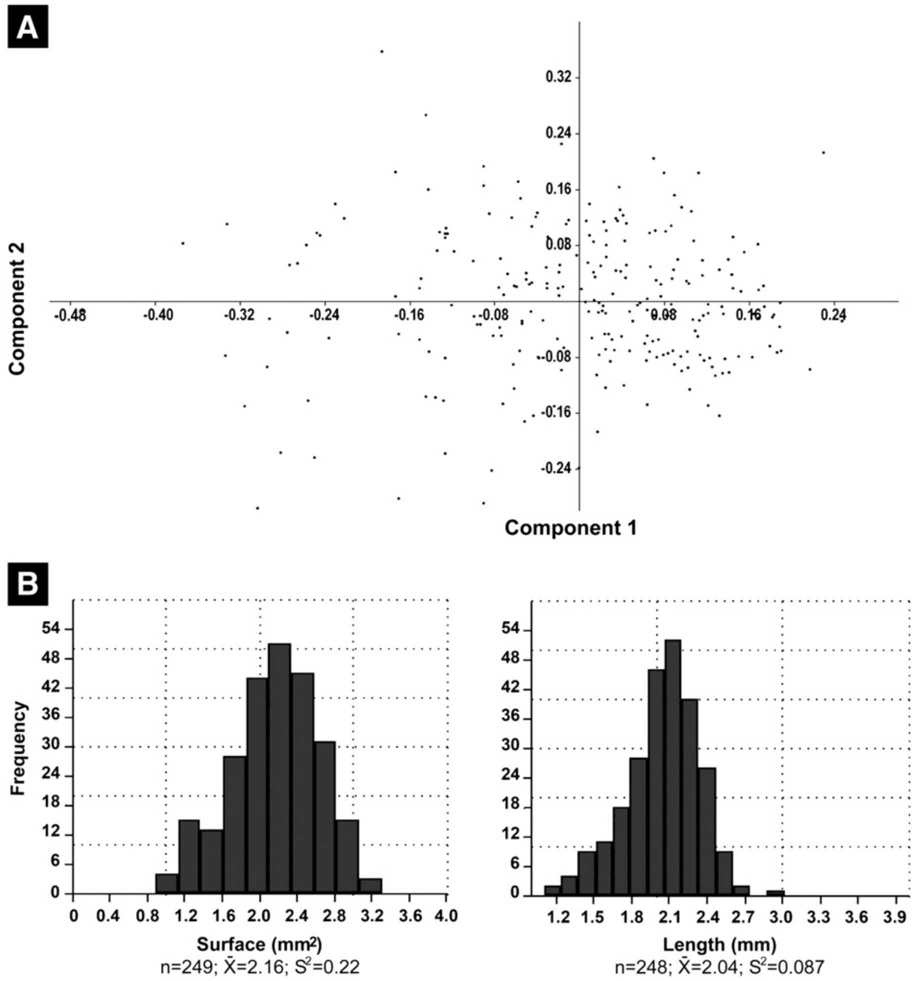

Fig. 3. Graphics of the measurements taken from seeds. (A) Principal Component Analysis of log-transformed seed measurements (surfaces, lengths, widths, length/width ratios). Component 1 explains 61% of variance and consists of surfaces (loading (l) = 0.8162), lengths (l = 0.4371), widths (l = 0.3721) and length/width ratios (l = 0.06563). Component 2 explains 38.6% of variance and the loads for the same variables are − 0.06502, 0.3738, − 0.44, 0.8139, respectively. (B) Histograms with the distribution of measurements of surface (in square millimetres) and of length (in millimetres). Both histograms show unimodal distributions and small variances.

consists of a clear brown to yellow cuticle, much thinner than the outer integument, from 6.3 to 10.3 μm in thickness (Plate I, 11–12; Plate II, 1; Plate III, 1). Its surface has dome-shaped papillae from 16.0 to 21.6 μm in diameter and 10.3 μm in height (Plate II, 4). A circular, lid-like operculum measuring from 242.4 to 305.0 μm in diameter is observed at the micropylar end in specimens when the outer integument is lacking due to taphonomic processes or was dissolved by oxidative treatment using Schulze reagent (Plate I, 11; Plate II, 1–3; Plate III, 3–4). Its cross-section is dome-like and extends from the inner envelope, being nearly completely covered by the outer integument (Plate II, 3; Plate III, 3). Isodiametric cells of 10.1–20.4 μm long and wide are present on the surface of the micropylar lid (Plate II, 2; Plate III, 4). The hilum is located at the opposite pole, suggesting that the ovule was orthotropous (atropous) (i.e. straight, symmetrical and erect on the funicle). The hilum is circular and measures 306–520 μm in diameter. It is outlined by a wall of 45.4–75.7 μm wide with longitudinal and parallel crests around the external side (Plate III, 5). The number of crests per seed varies from 18 to 21. Crests are 112.5–276.1 μm long and 14.7–32.9 μm wide. They are separated by a distance of 37.2–71.6 μm. Remains of the vascular bundles are observed in some hila (Plate III, 5–6). Diameters of vascular bundle measure 117.2–129.3 μm. The distance from the hilum to the point of seed maximum width is 0.4–1.5 mm.

Associated fruits: Two oblong fruits have been found in the assemblage. They are laterally flattened and measure up to 2.1–2.4 mm wide and 3.9 mm long (Plate IV, 1–2). The proximal end is narrow and probably tapered towards the carpel base. The fruit measures 0.46 mm in width at the base (Plate IV, 3). The distal end was probably rounded though it is mostly damaged in both specimens. The inner part of the cuticle is smooth (Plate IV, 2). The external surface shows very thin parallel grooves (Plate IV, 4).

We assume that the two fruits are related to the seeds described above based on the compatible morphology and size and their association in the same horizon. However, the fruits do not show enough characters to provide an independent taxonomic identification for this part of the plant.

Plate III. *Bergacarpon viladricii* gen. et sp. nov. seeds examined with SEM (slide IPS-56903).

1. Seed in section showing a thick outer integument and a very thin inner integument (oi = outer integument; ii = inner integument).
2. Outer integument showing cell walls.
3. Apical part of a seed in section (m = micropylar lid; oi = outer integument; ii = inner integument).
4. Micropylar lid showing isodiametric cells (m = micropylar lid).
5. Detail of the hilum showing a central vascular bundle.
6. Detail of the vascular bundle.


1
0.5 mm


2
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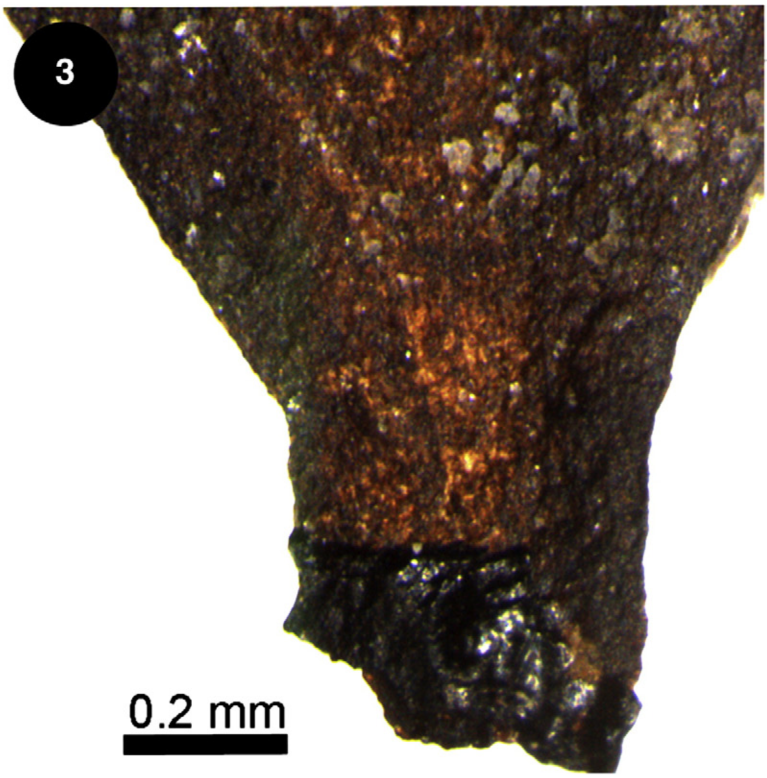
3
0.2 mm


4
0.2 mm

4.2. Sedimentology and plant taphonomy

The seeds under study accumulated in a large mass between 1.0 and 1.5 cm thick on the surface of a marlstone horizon. Seeds are randomly orientated, and their estimated density is 50,000 seeds per m^2. In stark contrast, the fruits associated and related to these seeds are extremely rare. The size distribution of the seeds is unimodal with an arithmetic mean of 2.16 mm^2 and a very small variance (Fig. 3). There are no other megafossil plant remains in the same bed. Especially significant is the absence of any elongated plant debris, such as small stems that are usually abundant in seed assemblages. Isolated seeds of the same species occur in the immediately overlaying marlstone.

The seed bed is located 15 cm below the base of the first coal seam of the series; this seam is also the thickest coal seam in the mining district and shows a lateral continuity of several kilometres. In contrast to the seed bed studied, the base of the first coal seam contains abundant megafossil plant remains of different sizes, shapes and types that consist of fragmentary leafy axes of the conifer *Frenelopsis* sp. and, less frequently, large palm leaves and logs of *Sabalites longirhachis* (Unger) J. Kvaček et Herman. Sedimentologically, the marlstone layers containing the seeds were formed as part of the brackish mudflat depositional system that is subject to low energy tidal currents (Riera et al., 2010), whilst palm and conifer vegetative organs were deposited in a parautochthonous peat at the margins of the brackish mudflat (Marmi et al., 2010). This suggests that the seed bed of Mina Esquirol and the overlying coal are sedimentologically related, that is, they correspond to two laterally equivalent environments of the same depositional system. With regard to the depositional environment, the seed bed occurs in a more distal position than the overlying coal (Fig. 4).

5. Discussion

5.1. Angiosperm affinities

Two seedless fruits have been found, versus much numerous isolated seeds, but a comparison of seed sizes and shapes suggests that each fruit bore a single seed. Based on the proximal and distal shapes of the fruit and seeds, the seed was most probably oriented hilum side down inside the fruit (Plate V). There is no evidence of the placenta scar. The pericarp is totally open, and the longitudinal dehiscence groove is well-marked. This large opening on one side of the pericarp suggests that it was a follicle-type fruit with a single dehiscence groove. The fact that numerous seeds were found and that all were found free (i.e., out of their pericarp) indicates that the follicle was dry and dehiscent. Also the dehiscence probably occurred when the follicle was still attached to the parent plant, leaving the empty fruit pericarps behind, which may explain the rareness of the fruit versus the abundance of the seeds. However, differential selection of both parts of the fructification during the transport cannot be excluded.

The seeds are covered by two integuments, a thick carbonaceous outer integument and a thin cuticular-like inner integument. Batten and Zavattieri (1996) considered the occurrence of two integuments as good evidence of angiosperm affinity. However, some angiosperm families, such as Siparunaceae and Circaeasteraceae, include taxa with seeds bearing a single integument (data matrix of Doyle and Endress, 2010). The homology between the inner integument and the single cupular integument of gymnosperms suggests that the outer integument is a novel character of angiosperms (Yamada et al., 2003 and references therein).

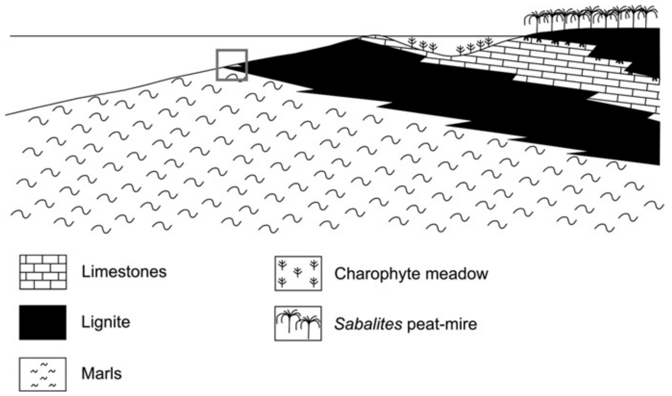

Fig. 4. Depositional and taphonomic setting of the seed-bearing layer (square) in the palaeoenvironmental model of the Lower Grey Garumnian of Vallcebre.
Modified from Marmi et al., 2010).

The location of the hilum and micropyle at opposite ends and the absence of a raphe indicate that the seeds developed from orthotropous (atropous) ovules. Anatropous ovules are the most widespread type within angiosperms, with more than 200 extant families being exclusively anatropous (Black et al., 2006). Moreover, anatropous ovules are the most common among basal clades, indicating that they might have appeared during an early stage of angiosperm evolution (Yamada et al., 2003 and references therein). In contrast, orthotropous (atropous) ovules have been considered derived from anatropous ancestors (Endress and Doyle, 2009). Indeed, orthotropous (atropous) ovules have evolved several times during the evolutionary history of angiosperms and are found in Nymphaeales, Chloranthales, Magnoliids (Piperaceae, Saururaceae, Gomortegaceae), Monocots (Acoraceae, Araceae, Zosteraceae, Arecaceae), basal Eudicots (Circaeasteraceae, Platanaceae, Proteaceae) and core Eudicots (Myricaceae, Juglandaceae) (Doyle and Endress, 2010; Friis et al., 2006b).

5.2. Hypotheses about the likely parent plant

All seeds belong to a single species, as they share similar morphology, size and sculpture. This is also supported by the continuous variation in several measurements (surface area, lengths, widths and length/width ratios) obtained from 249 specimens, which was demonstrated by the Principal Component Analysis (Fig. 3). Seeds from the Late Cretaceous mesofloras of Portugal, are typically anatropous or more rarely campylotropous (Friis et al., 2010). Thus, in contrast, seeds from the Mina Esquirol site probably all belonged to a taxon distinct from those known up to now from Portugal. Some seed morphotypes described by Knobloch and Mai (1986) from the Cenomanian–Maastrichtian of central and western Europe resemble those from Mina Esquirol in shape and size. However, most of them are anatropous except for the genera *Urticoidea* Knobloch et Mai (family Urticaceae) and *Brnikia* Knobloch et Mai (Magnoliophyta indet.), which are also orthotropous (atropous) but differ from the Mina Esquirol seeds in having ristate micropylar ends.

The anatomical structure and sculpture of the seed coat is highly variable in angiosperms and provide extremely valuable taxonomic information (Black et al., 2006). There are no anatomic details (e.g. cell morphology, number of cell layers in the outer integument) preserved in the cross sections of the seed coats from Mina Esquirol, except for the outer integument that is fairly thicker than the inner

Plate IV. Fruit associated with *Bergacarpon viladricii* gen. et sp. nov. seeds (slide IPS-56908).

1. External view of carpel.
2. Internal view of an opened carpel through the dehiscence groove.
3. Detail of the basal part of the carpel.
4. Detail of the external part of the carpel showing thin longitudinal grooves.

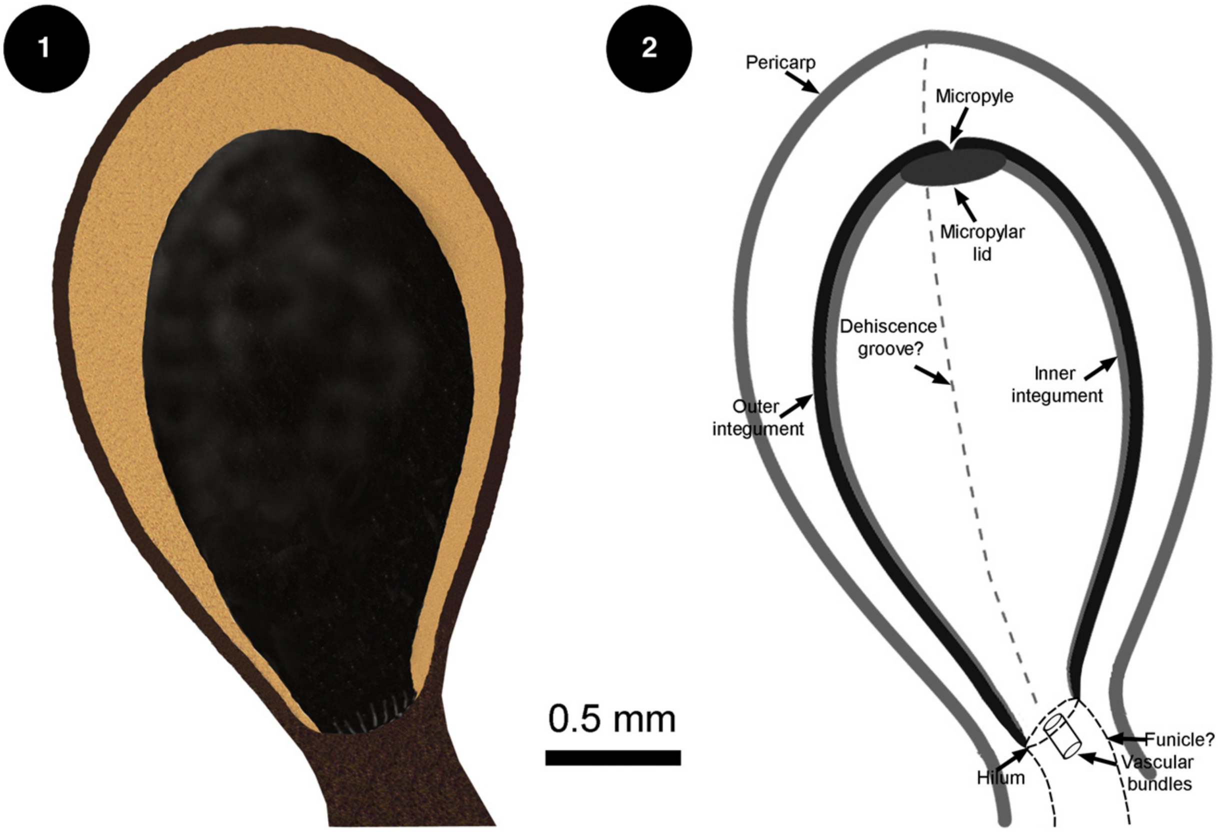

Plate V. Hypothetic reconstruction of the carpel containing the seeds *Bergacarpon viladricii* gen. et sp. nov.

1. Reconstruction of a carpel in longitudinal section containing a seed.
2.. Interpretative drawing and captions.

integument. According to the dataset compiled by Doyle and Endress (2010), integument thickness is an ambiguous taxonomic character in the absence of cellular details. The circular, lid-like operculum in the micropylar end may thus be more diagnostic than the previous characters. Operculate seeds are best known in monocots, especially in members of Commelinids (Arecales, Poales, Commelinales and Zingiberales), but also in Nymphaeales and in the core Eudicots Begoniaceae and Cactaceae (Black et al., 2006). The seeds studied herein do not belong to Nymphaeales because the latter are mostly anatropous and usually have more than two ovules per carpel and fleshy fruits (Doyle and Endress, 2010). Begoniaceae and Cactaceae have anatropous and campylotropous ovules, respectively, and probably originated during the Cenozoic (e.g. Goodall-Copestake et al., 2009; Ocampo and Columbus, 2010). Thus, the absence of ovule curvature (i.e., orthotropous) and the presence of a micropylar cap suggest that the Mina Esquirol seeds may have been produced by a monocot, probably a commelinid (sensu APG III, 2009).

It is noteworthy that leaves, logs and rooting systems of the fossil monocot palm *Sabalites longirhachis* are abundant in the same fossil assemblage or in closely related beds (Marmi et al., 2008, 2010). Data from Fumanya suggest that these palm trees grew in small peat mires on the shores of freshwater lakes and that leaves and logs were transported and deposited at the bottom of a brackish mudflat edge, in which seeds and fruits also accumulated (Marmi et al., 2010; Villalba-Breva et al., 2012).

5.3. Hypotheses on the origin of the seed bed at Mina Esquirol

Organ, shape and size selection in the depositional setting of a mudflat suggest that the seed bed of Mina Esquirol was formed under specific constraints. Selection may be produced either by ecological reasons, i.e. the supply of a single type of seed from the original source to the depositional site, or alternatively by selective transport mechanisms. These two possibilities are explored below.

The representation of a local flora by the corresponding seeds found in extant carpological assemblages is affected by the ecomorphological traits of plants (Sims and Cassara, 2009). Salinity and nutrient gradients are the two main factors explaining the vegetation richness and the seed bank composition in coastal wetlands (Steinhardt and Selig, 2009). In these environments, carpological assemblages are characterized by low number of species (about 6–7) but high seed densities (Riddin and Adams, 2009; Steinhardt and Selig, 2009). Both characters are recognized in the seed assemblage of Mina Esquirol. However, the fossil assemblage studied herein consists of a single species, which is much less diverse than present-day models. Also, the estimated density of seeds, which is about 50,000 seeds per m^2, falls into the maximum values reported in species from present-day coastal lagoons and intertidal salt marshes (Table 1).

Although there is a number of studies devoted to the transport and deposition of seeds in different sedimentary contexts, the present knowledge about these processes is still poor (Gee, 2005). Actuotaphonomic studies show that the proportion of local flora found in sedimented carpological assemblages is variable. It is well known that drift seeds from coastal settings may have undergone extremely long transport (Cadée, 1996). In mangroves exposed to significant tidal and coastal sea currents, there is no correspondence between the drifted seed assemblage and the local flora (Burnham, 1990). However the percentages of correspondence increase to 30–40% in tidal estuaries (Sims and Cassara, 2009) and 50–100% in swamps (Greatrex, 1983), which clearly reflects decreasing water velocities. The depositional setting of the Mina Esquirol seed bed falls into the

Table 1
Means of seed densities (seeds/m^2) reported in carpological assemblages from present-day coastal environments.

Species	Depositional environment	Density	Reference
Bolboschoenus maritimus (Linnaeus) Palla	Estuary	31	Riddin and Adams (2009)
Stukenia pectinata[a] Linnaeus	Estuary	77	Riddin and Adams (2009)
Sporobolus virginicus (Linnaeus) Kunth	Estuary	163	Riddin and Adams (2009)
Salicornia meyeriana Moss	Estuary	306	Riddin and Adams (2009)
Ruppia cirrhosa[a] (Petag.) Grande	Estuary	2852	Riddin and Adams (2009)
Sarcocornia perennis (Miller) Scott	Estuary	7929	Riddin and Adams (2009)
Zostera noltii[a] Hornem	Coastal lagoon	0–85	Steinhardt and Selig (2009)
Potamogeton sp.*	Coastal lagoon	0–245	Steinhardt and Selig (2009)
Zostera marina[a] Linnaeus	Coastal lagoon	0–821	Steinhardt and Selig (2009)
Najas marina[a] Linnaeus	Coastal lagoon	0–2309	Steinhardt and Selig (2009)
Ruppia maritima[a] Linnaeus	Coastal lagoon	0–3358	Steinhardt and Selig (2009)
Ruppia cirrhosa[a] (Petag.) Grande	Coastal lagoon	593	Gesti et al. (2005)
		73–5511	Steinhardt and Selig (2009)
Zannichellia palustris[a] Linnaeus	Coastal lagoon	590–26,648	Steinhardt and Selig (2009)
Salicornia europaea Linnaeus	Intertidal salt marsh	38,944–128,000	Philipupilla and Ungar (1984)
Ruppia cirrhosa[a] (Petag.) Grande	Marsh	2920–5030	Bonis et al. (1995)
Sarcocornia pillansii (Moss) Scott	Supratidal	3616	Shaw et al. (2008)

[a] Submerged species.

second category mentioned above, where selection by transport can be significant.

Transport as bedload, as is common with robust, woody fruits and seeds (Gee, 2005), or by suspension in the water column is not evidenced in the Mina Esquirol seed assemblage because of the excellent preservation of the delicate cellular structures in the seed cuticles and the absence of abrasion. Also sedimentological reasons, such as the absence of high-energy sedimentary structures and of grain sizes larger than mud, exclude wave action as a probable means of transport. In contrast, drifting by floatation may be a significant mechanism behind seed accumulations in coastal environments (Martín-Closas and Gomez, 2004; Spicer, 1989). Floatation is enhanced by the frequent presence of hollow spaces inside the seeds and appears to be independent of seed size and shape (Collinson, 1983).

In summary, the accumulation of seeds at Mina Esquirol was likely influenced by both ecological constraints and taphonomic processes. Ecological constraints of a local plant source at the margins of the brackish mudflat may explain why a single seed species makes up this assemblage, whilst taphonomic processes may explain why any other megafossil plant remains are not found associated with the seeds.

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